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SUMMARY

In 2014, commercial fisheries landed an estimated 161,823 metric tons (t) of fish and invertebrates from California ocean waters (fig. 1). This represents a decrease of almost 2% from the 165,072 t landed in 2013, a less than 1% decrease from the 162,290 t landed in 2012, and a 36% decline from the peak landings of 252,568 t observed in 2000. The preliminary ex-vessel economic value of commercial landings in 2014 was $233.6 million, decreasing from the $254.7 million generated in 2013 (8%), and the $236 million in 2012 (1%), but an increase from the $198 million in 2011 (18%).

Coastal pelagic species (CPS) once again made up four of the top five volume fisheries in 2014; red sea urchin (5,364 t) and Pacific pink shrimp (3,845 t) were ranked sixth and seventh respectively. California market squid continued to be the largest volume fishery, and it reemerged as the highest valued in the state with over 102,516 t landed and an ex-vessel value of approximately $71.8 million; a decrease of nearly 2% and 3%, respectively from 2013. For the fifth season in a row, market squid landings were projected to reach the seasonal catch limit of 107,048 t. However, by November 18, 2014, 97.2% of the catch limit had been landed, so the seine sector of the squid fleet made a voluntary decision to stop fishing so that the remaining portion of the catch limit could be set aside for the brail sector. The 2014/15 season also represents the first time in recent history that directed fishing for market squid has resulted in landings to the port of Eureka. Northern anchovy emerged as California's second largest volume fishery with 10,511 t landed worth greater than $1.6 million in ex-vessel revenue, which continues the dramatic increasing trend from 6,005 t in 2013 (>$1.0 million) and 3,485 t in 2012 ($872,820). For the first time since 1982, the northern anchovy fishery ranked as the largest by volume among the four federally managed CPS finfish (Pacific sardine, Pacific mackerel, jack mackerel, and northern anchovy), comprising nearly 42.9% of the total volume and 32.4% of the total value. Nearly all (98.7%; 10,378.8 t) of California's 2014 northern anchovy catch was landed in the Monterey port area. The Pacific sardine fishery has long been one of the largest in the state, and in 2014 it held its position as the fourth largest in volume, and was the twelfth largest in value, landing 7,768.0 t and generating an ex-vessel revenue of $2 million. Nearly all of California's 2014 sardine catch was landed in the Monterey port area (80.2%, 6,233.0 t). The recommended harvest guideline for 2014/15 season was 28,646 t based on a biomass estimate of 369,506 t (a 44% decrease from the 2013 biomass estimate of 659,539 t). A decrease in the biomass and harvest guideline in 2014 largely contributed to the general decrease in US commercial landings of Pacific sardine. Pacific mackerel was California's fifth largest volume fishery with 5,420 t landed generating over $1.2 million in ex-vessel revenue. Monterey area ports landed 243.4 t while landing nearly no Pacific mackerel in 2013. Landings of jack mackerel in California remained relatively low, with 784 t landed in 2014 (a decrease from 892 t in 2013); however, this still represents an increase over 2012 landings of 145 t. Landings of jack mackerel in Oregon and Washington increased with 800.4 t (549.7% increase from 2013) and 242.7 t (204.9% increase from 2013), respectively.

Dungeness crab ranked as California's third largest volume fishery in 2014 with 8,244 t landed, a decrease from the 14,066 t landed in 2013. The fishery dropped to the second highest valued fishery in the state with an ex-vessel value of over $65.8 million, decreasing from $88.7 million in 2013. Typically, the northern area contributes the majority of total crab landed statewide, however, for the 2013/14 season 61% of landings were reported from central area ports, between Bodega Bay and Morro Bay. The recent 2013/14 season is the first to implement the Dungeness crab trap limit program, the primary goal of which is to cap the overall amount of traps that are fished in California. Vessels in the fleet are now subject to fish up to a maximum trap number dependent on their placement in one of seven trap allotment tiers.

More than 90 species of bottom-dwelling marine finfish are included in the federally managed groundfish fishery. These groundfish species are grouped into 39 federal management units, consisting of species or

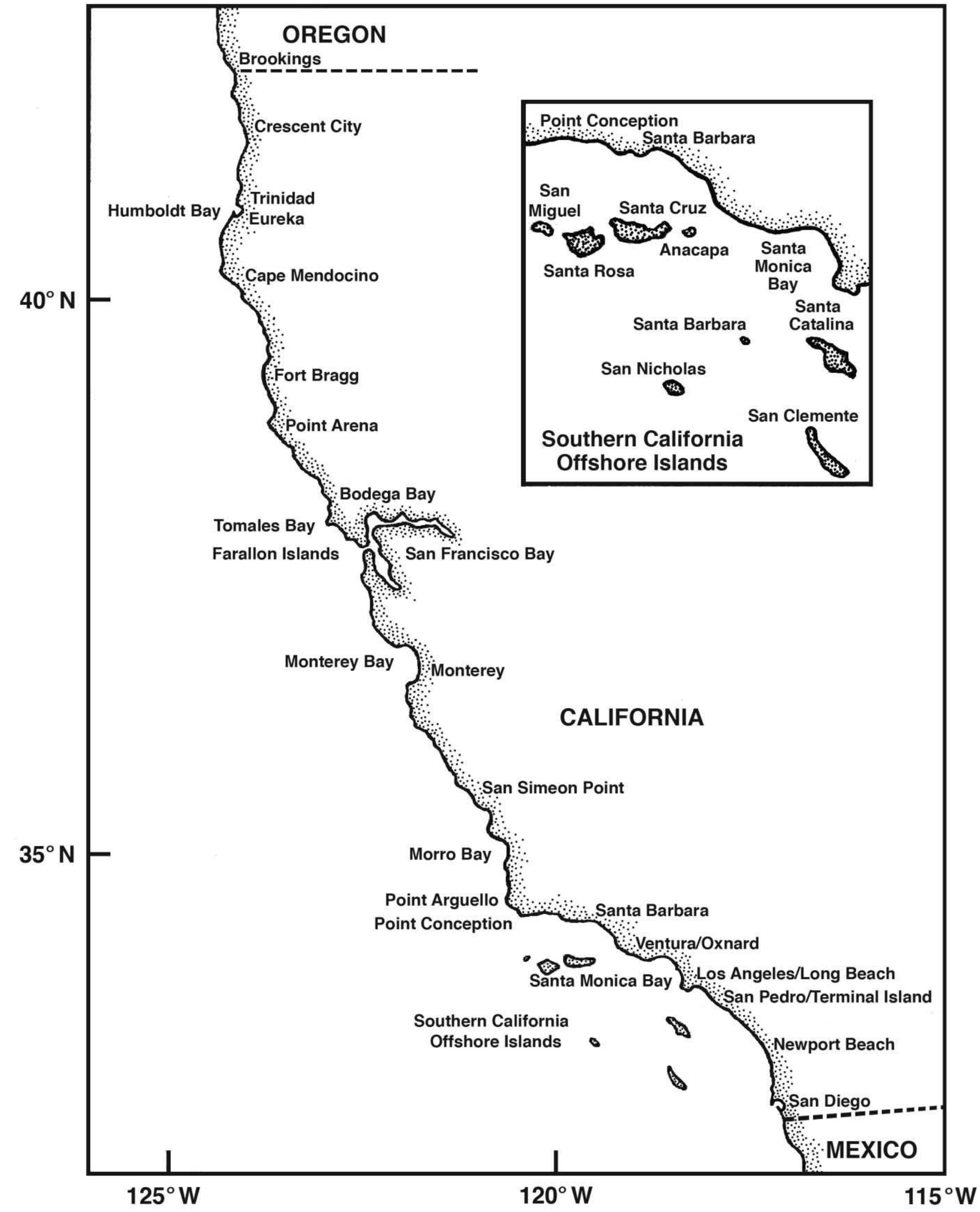


Figure 1. California ports and fishing areas.

species groups, to help facilitate management measures that balance biological and economical goals. In 2014, California's commercial groundfish landings totaled 6,603 t, worth an estimated ex-vessel value of $19.5 million. This represents a 2.4% increase in landings from 6,443 t in 2013 and an increase in ex-vessel value of 12% from $17.3 million. The majority (71%) of groundfish was landed between the California/Oregon border and the Monterey Bay area and generated 52% of the total ex-vessel value of the fishery. An estimated 2,220 t of groundfish were taken by the recreational fishery in 2014, which represents a 10% increase compared to 2013 (2,014 t). California anglers targeting groundfish participated in an estimated 950,801 trips in 2014, a small increase (<3%) from 2013 (925,682 trips). To date, full stock assessments have been completed for half of the nearshore species, including blue, black, brown, China, copper, and gopher rockfish, as well as California scorpionfish and cabezon. The remaining species have been assessed with less intensive data methods. Many stocks are considered to be healthy while others are in the precautionary zone; none are considered overfished.

Fishing effort for Pacific herring in 2014 continued at reduced levels when compared to historic landings for California. During the 2014 sac roe season (January 2014–March 2014), the San Francisco Bay fleet landed 2,901.2 t, an increase over the 2013 landings (2,115.6 t) and 93% of the 3,122.5 t quota. The San Francisco Bay herring-eggs-on-kelp (HEOK) fishery landed 0 t during the 2014 season, however the fishery was active during the 2013 season, landing 35.7 t of HEOK product. During the 2014 season, the Department conducted spawn deposition surveys in San Francisco Bay to estimate the spawning biomass of the herring stock. The spawning biomass estimate for San Francisco Bay was 54,999 t, a 23.8% decrease from the previous season's estimate of 72,130 t. However, 2014 was the fifth consecutive year of increased biomass since the historic low in the 2009/10 season of 4,394 t and was above the long-term average biomass for San Francisco Bay (1979–2014) of 47,445.8 t.

The 2014 commercial ocean salmon fishing season was more constrained compared to 2013, primarily due to lower ocean abundance projections and restrictions to protect ESA-listed California Coastal Chinook. The commercial ocean salmon fishery was open for 342 days in all four ocean management areas combined during 2014. Nearly 166,500 Chinook (1,011 t) were landed in approximately 14,200 days fished. The average nominal ex-vessel price was $12.19/kg ($5.54/lb), with an ex-vessel value of $12.3 million, the fourth largest in the state. Recreational ocean salmon fisheries were open for 743 days across four management areas in 2014, a slight increase in opportunity compared to the previous season primarily due to an increase in the allowable ocean impact rate on ESA-listed Sacramento River winter Chinook (SRWC). Nearly 74,700 recreationally caught Chinook were landed in approximately 120,300 angler days. Protections in addition to NMFS guidance for ESA-listed endangered SRWC were deemed prudent when developing the 2015 ocean salmon fishing seasons. As a result of the drought's continuing detrimental effects on SRWC and based on the best available data, the Pacific Fishery Management Council, adopted more stringent recreational and commercial management measures to provide additional protection to SRWC.

The family Osmeridae is comprised of approximately 11 genera and 30 species. These "true smelts" are small, soft-rayed, schooling fishes with an adipose fin and are found in marine, estuarine, and freshwater habitats in the Northern Hemisphere. They range from Pt. Arguello, California, to the Gulf of Alaska. Historically, most of California's Osmerids contributed to sport, commercial, and tribal fisheries; however, only surf and night smelt support these fisheries today. Most commercial and recreational Osmerid fishermen use cast nets (Hawaiian throw nets) and/or A-frame dip nets. In 2014, night smelt landings totaled 138.5 t with an ex-vessel value of $169,000; surf smelt landings totaled 102.2 t with an ex-vessel value of $157,000. Over 97% of the 2014 statewide commercial Osmerid harvest was landed in Eureka with the remainder landed in the ports of Crescent City, San Francisco, and Half Moon Bay.

Prior to 1988 hagfish landings in California were nonexistent. However, hagfish imports were in great demand by South Korea due to a localized depletion of two related species, brown hagfish (*Paramyxine atami*) and inshore hagfish (*Eptatretus burgeri*). In 1988, a Korean hagfish importer recruited San Francisco and Monterey fishermen to target hagfish for export to South Korea. Statewide landings and fishing effort expanded in 1989 leading to 1,199 t of landed hagfish. Landed in fresh-dead condition, hagfish were then frozen, and shipped for use in the Korean leather goods market. In 2005, hagfish were exported in live condition for human food at a greater ex-vessel price. Fishing effort and catch began to increase with 54 t landed, and again in 2006 with 77 t landed. In 2014, five port complexes and 33 vessels contributed to a landings total of 675 t at an ex-vessel value of $1.17 million. The top three port complexes were Eureka, Morro Bay, and Bodega Bay.

In December 2012, California implemented the largest scientifically designed network of Marine Protected Areas (MPAs) in the United States, following an MPA design and siting process led by the California Department of Fish and Wildlife (Department). Even before the Marine Life Protection Act and the implementation of California's redesigned MPA network, the Department has been at the forefront of efforts to use ROVs for subtidal ecosystem monitoring. In 1999, Department scientists began developing techniques for using ROVs for MPA monitoring and in 2001 completed the first extensive baseline survey of an MPA in California using an ROV at Punta Gorda Ecological Reserve on the remote rugged coast near Cape Mendocino. Since then, the Department has successfully completed substantial surveys in all four of California's MPA regions. Data gathered from these surveys, on the abundance and distribution of fish and invertebrates, have provided much needed characterization of the baseline ecological condition of California's vast deep water habitats.

Coastal Pelagic Finfish

Pacific sardine (*Sardinops sagax*), Pacific mackerel (*Scomber japonicus*), jack mackerel (*Trachurus symmetricus*), and northern anchovy (*Engraulis mordax*) form a finfish complex known as coastal pelagic species (CPS). These species are jointly managed by the Pacific Fishery Management Council (Council) and the National Marine Fisheries Service (NMFS) under the Coastal Pelagic Species Fisheries Management Plan (CPS FMP). In 2014, total commercial landings for these spe-

TABLE 1
Landings of Coastal Pelagic Species in California (metric tons).

Year	Pacific sardine	Northern anchovy	Pacific mackerel	Jack mackerel	Unspecified mackerel	Pacific herring	Herring roe	Market squid	Total
1977	2	101,132	3,316	47,615		5,286		12,811	170,163
1978	1	11,439	8,241	34,349	48	4,473		17,145	75,696
1979	51	48,880	22,404	21,548	301	4,257		19,982	117,424
1980	21	42,946	25,739	24,181	56	8,061		15,385	116,389
1981	34	52,308	35,257	17,778	132	5,961		23,510	134,980
1982	2	42,150	17,667	19,618	18,398	10,604		16,308	124,747
1983	1	4,427	17,812	9,829	23,659	8,024		1,824	65,576
1984	1	2,889	26,043	9,149	18,038	3,847		564	60,532
1985	6	1,626	18,149	6,876	19,624	7,984		10,275	64,540
1986	388	1,535	22,095	4,777	25,995	7,658		21,278	83,727
1987	439	1,390	26,941	8,020	19,783	8,420		19,984	84,978
1988	1,188	1,478	30,127	5,068	20,736	8,641		37,233	104,471
1989	837	2,449	21,067	10,746	26,661	9,296		40,893	111,950
1990	1,664	3,208	31,077	3,223	9,039	7,436		28,447	84,094
1991	7,587	4,014	31,680	1,693	339	7,347		37,389	90,048
1992	17,950	1,124	18,574	1,209	3	6,319		13,110	58,289
1993	15,346	1,958	11,798	1,673		3,846	0	42,722	77,345
1994	11,644	1,789	10,008	2,704	0	77	2,874	55,508	84,603
1995	40,328	1,886	8,625	1,728		3	4,664	72,433	129,667
1996	32,559	4,421	9,597	2,178	4	249	5,162	80,784	134,954
1997	43,246	5,718	18,398	1,160	1	0	9,147	70,387	148,057
1998	42,956	1,457	20,515	824		0	2,009	2,895	70,656
1999	59,493	5,179	8,688	953	0		2,279	91,950	168,542
2000	53,612	11,754	21,916	1,269	0	26	3,450	118,816	210,843
2001	51,894	19,277	6,925	3,624	1	0	2,768	86,385	170,873
2002	58,354	4,643	3,367	1,006	2	0	3,324	72,920	143,615
2003	34,732	1,676	3,999	156	0	34	1,808	45,061	87,467
2004	44,305	6,793	3,570	1,027	0	60	1,581	41,026	98,362
2005	34,633	11,182	3,244	199		219	136	58,391	108,005
2006	46,577	12,791	5,891	1,167	0	37	694	49,159	116,316
2007	80,981	10,390	5,018	630	1	336	261	49,474	147,091
2008	57,806	14,285	3,530	274	0	131	626	38,101	114,754
2009	37,578	2,668	5,079	119	1	74	460	92,338	138,317
2010	33,658	1,026	2,056	310	0			129,904	166,954
2011	27,714	2,601	1,357	80	0		1,566	121,556	154,874
2012	23,037	2,488	3,485	145	0		1,482	97,078	127,715
2013	7,074	6,005	8,066	892	1	0	2,086	104,404	128,528
2014	7,768	10,511	5,420	784	6		2,942	102,516	129,946

Data Source: Commercial Fishery Information System (CFIS)

cies equaled 24,483 t (table 1, fig. 2), with a combined ex-vessel revenue of over $4.9 million. When compared to landings in 2013, this represents an 11.1% and 15.3% increase in volume and value, respectively. For the first time since 1982, the northern anchovy fishery ranked as the largest by volume among these four species in 2014, comprising 42.9% of the total volume and 32.4% of the total value.

Pacific Sardine. The Pacific sardine fishery is composed of three subpopulations; northern, southern, and Gulf of California. While the fishery ranges from Baja California, Mexico, north to British Columbia, Canada, the majority of landings have occurred in southern California and northern Baja California since the 1980s. Landings of sardine have steadily increased in the Pacific Northwest and Canada since the recent expansion of the sardine fishery in 1999; however, there were no landings in Canada in 2014. Combined landings of Pacific sardine for California, Oregon, and Washington totaled 23,271.8 t, a 63.6% decrease from the 63,891.3 t landed in 2013 (fig. 3).

The US Pacific sardine harvest guideline (HG) for each calendar year is determined from the previous year's stock biomass estimate of the northern subpopulation (of ≥1-year-old fish on 1 July) in US and Mexican waters. The recommended HG for 2014/15 season was 28,646 t based on a biomass estimate of 369,506 t (a 44% decrease from the 2013 biomass estimate of 659,539 t). The Pacific sardine HG was apportioned coast-wide through the year with a 40% allocation of the annual HG from 1 July through 14 September, 25% (plus any portion not harvested) allocated from 15 September through 31 December, and the last 35% (plus any portion not harvested from the first two allocations) released on 1 January. Landings above the HG would be constrained by an incidental catch rate of 45% by weight when landed with other CPS with an additional 500 tons per allocation set aside for incidental catch.

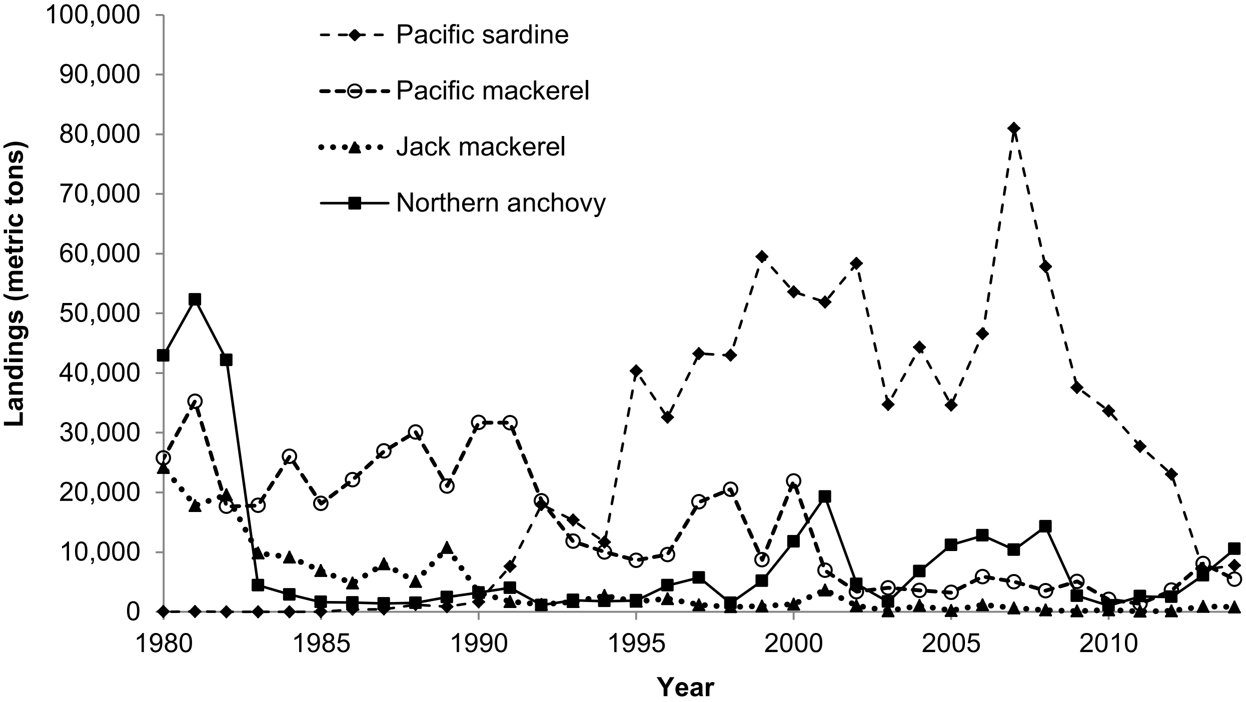


Figure 2. California commercial landings of Pacific sardine (*Sardinops sagax*), Pacific mackerel (*Scomber japonicus*), jack mackerel (*Trachurus symmetricus*), and northern anchovy (*Engraulis mordax*), 1980–2014.

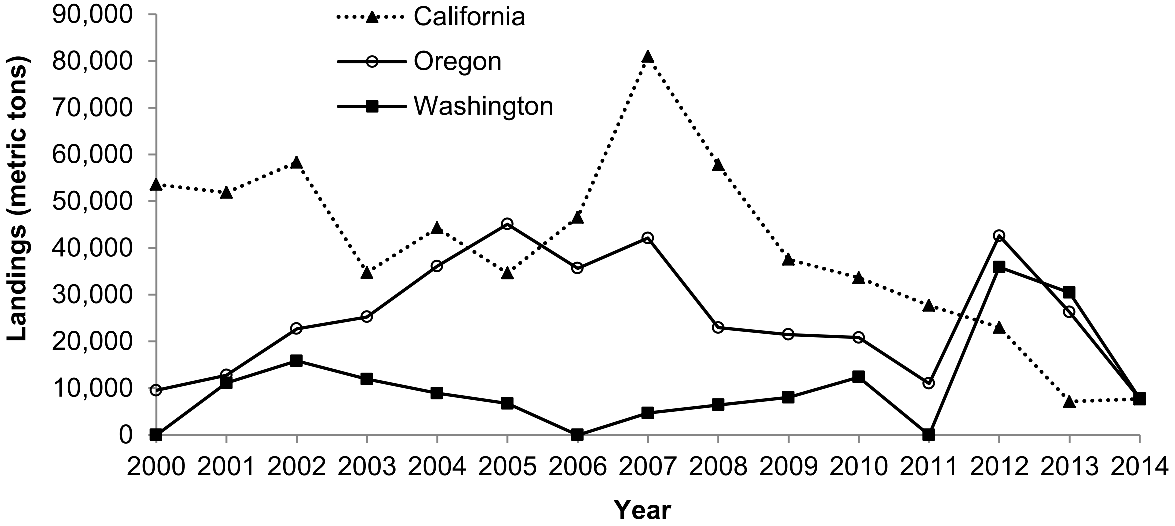


Figure 3. Commercial landings of Pacific sardine (*Sardinops sagax*) in California, Oregon, and Washington, 2000-2014.

In November 2013, the start date of the 12 month Pacific sardine fishery was changed from 1 January to 1 July; this changed the fishing season from one based on a calendar year (1 January–31 December) management cycle to a fishing season (1 July–30 June) cycle. This change better aligned the timing of the research and science required for annual stock assessments with the annual management schedule. A one-time interim harvest period from 1 January 2014 through 30 June 2014 was established with an allocation of 5,446 t to allow targeted fishing to continue during the transition to the new management cycle.

In 2014, the US West Coast fisheries harvested a large portion (81.2%) of the HG. The 2014 interim period (1 January–30 June) lasted almost the entire allocation period, 175 days. The first allocation period for the 2014/15 season (1 July–14 September) lasted 23 days. The second period (15 September–31 December) lasted only 5 days. A decrease in the biomass and harvest guideline in 2014 largely contributed to the

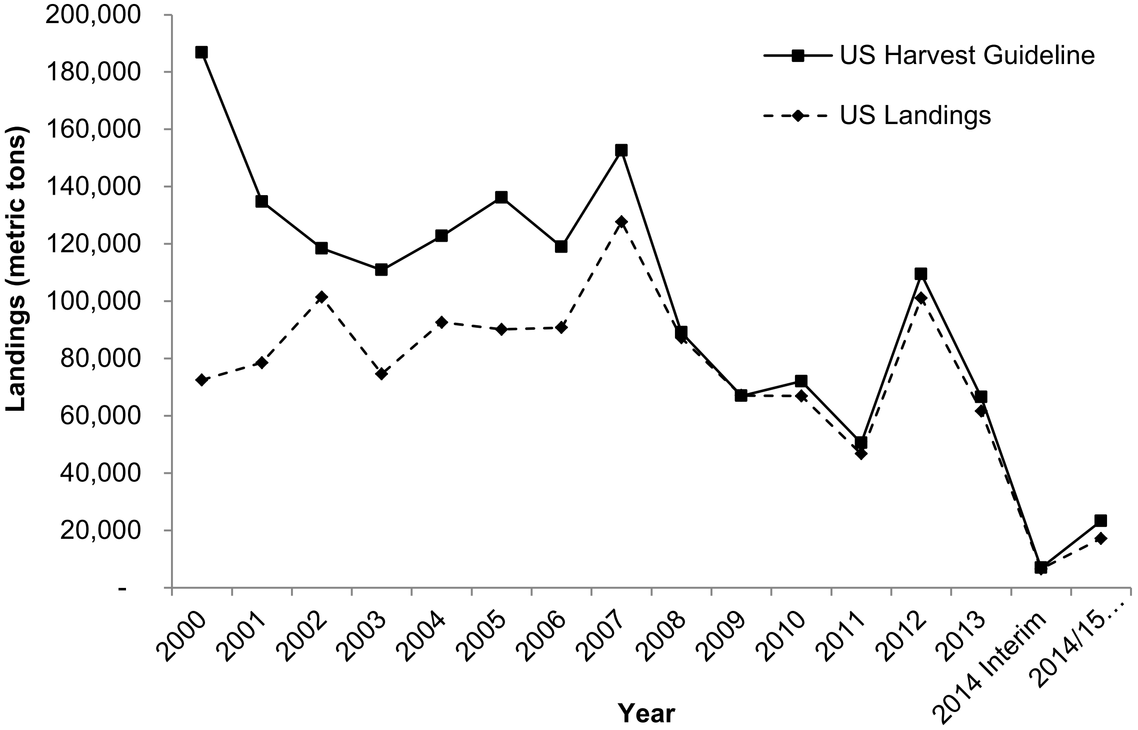


Figure 4. The US Pacific sardine harvest guideline (HG) for each calendar year; in November 2013, the start date of the 12 month Pacific sardine fishery was changed from 1 January to 1 July which changed the fishing season from one based on a calendar year (1 January–31 December) management cycle to a fishing season (1 July–30 June) cycle. A one-time interim harvest period from 1 January 2014 through 30 June 2014 was established to allow targeted fishing to continue during the transition to the new management cycle.

TABLE 2
Landings (metric tons) of Pacific sardine (*Sardinops sagax*) and Pacific mackerel (*Scomber japonicus*), jack mackerel (*Trachurus symmetricus*), and northern anchovy (*Engraulis mordax*) at California port areas in 2014.

	Pacific sardine		Pacific mackerel		Jack mackerel		Northern anchovy	
Area	Landings	% Total	Landings	% Total	Landings	% Total	Landings	% Total
Monterey	6,233.7	80.2	243.4	4.5	90.3	11.5	10378.8	98.7
Santa Barbara	96.1	1.2	182.2	3.4	3.5	0.4	66.3	0.6
Los Angeles	1,438.2	18.5	4,994.2	92.1	690.6	88.0	65.6	0.6
Total	7,768.0	100	5,419.8	100	784.4	100	10,510.7	100

*Monterey totals include San Francisco landings; Los Angeles totals include Oceanside/SoCal landings.

general decrease in US commercial landings of Pacific sardine (fig. 4).

California commercial landings of Pacific sardine come from the northern subpopulation. This fishery in California has long been one of the largest in the state. In 2014, it was the fourth largest in volume and twelfth largest in value, landing 7,768.0 t and generating an ex-vessel revenue of $2 million (fig. 2). This was a 9.8% increase from 2013 (7,074 t). Commercial landings of sardine averaged 39,979 t over the fourteen-year period from 2001–14. Nearly all (98.6%) of California's 2014 sardine catch was landed in Monterey (80.2%, 6,233.0 t) and Los Angeles (18.4%, 1,438.2.0 t) port areas (table 2). California exported 6,497.1 t of sardine product worth over $6.2 million. Twenty-six countries received sardine product from California; Japan and Australia received the majority at 25.6% and 9.9%, respectively.

Oregon landings appeared to be leveling off since 2008; they experienced a large jump in 2012 and decreased in 2013 and 2014. Landings of Pacific sardine totaled 7,788.5.4 t, a 70.4% decrease from 2013 (26,288.4 t). In 2013, Oregon exported 88 t of sardine product to 1 country (Malaysia) worth $113,021.

Washington landings of Pacific sardine totaled 7,783.8 t in 2014, a decrease of 74.4% from 2013 (30,457.1 t). They exported 16,614.6 t of sardine product to 20 countries, totaling $15.8 million in revenue.

The recreational Pacific sardine catch as sampled from the California Recreational Fisheries Survey (CRFS) was 12.6 t (127,321 fish). The majority (94.8%) of the

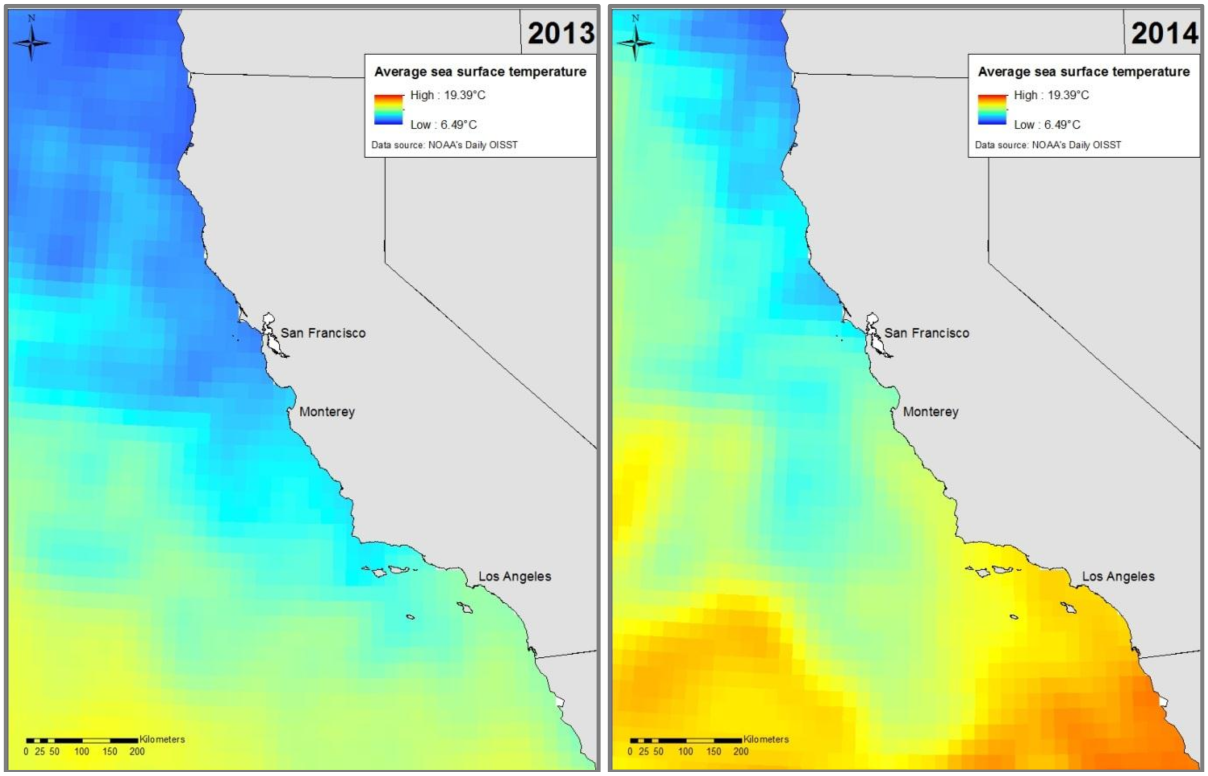


Figure 5. Average sea surface temperatures (SSTs) off the coast of California, 2013 and 2014 (data: http://gis.ncdc.noaa.gov/map/viewer/#app=clim&cfg=cdr&theme=cdr&layers=00001&node=gis).

fish landed were from manmade structures, such as piers. The tonnage and number of fish decreased from 2013, 83.6 % and 82.6% decreases, respectively.

Pacific Mackerel. In 2014, 5,420 t of Pacific mackerel were landed in California (table 1, fig. 2) generating over $1.2 million in ex-vessel revenue, and making it California's fifth largest volume fishery. This is a 32.8% decrease in volume and a 19.3% increase in ex-vessel revenue from 2013. Monterey area ports landed 243.4 t while landing nearly no Pacific mackerel in 2013. A shift in oceanic conditions, such as sea surface temperature, may have attributed to Pacific mackerel landings shifting northward (fig. 5).

Industry exported 2,994.5 t of mackerel product, valued at $2.6 million, mainly for human consumption, to 20 countries. The Philippines (1,074.3 t) and Egypt (447.5 t) received over 50% of this product.

Oregon reported landing 1,172.3 t of Pacific mackerel in 2014, with an ex-vessel revenue of $324,624. This is a 167% increase from the 2013 catch of 439.3 t. No exports were reported for Oregon.

Washington reported landing 544.6 t of Pacific mackerel in 2014, with an ex-vessel revenue of $155,337. There were no landings of Pacific mackerel in 2013. Washington exported 1,341.7 t of mackerel product, valued at $1.9 million, mainly for human consumption, to 15 countries. Ghana (247.3 t) and Malaysia (190.2 t) received over 50% of this product.

At the start of the 2014/15 season, which runs from 1 July to 30 June the following year, the PMFC set the HG at 29,170 t, including a 5,000 t set aside for incidental landings in other fisheries. Landings above the HG would be constrained by an incidental catch rate of 45% by weight when landed with other CPS.

The 2014 recreational Pacific mackerel catch as sampled from CRFS was 285.4 t (1,743,740 fish), a 79.3% increase (93.1% by number of fish) from 2013. The majority (49.5%, 863,230 fish) of fish landed were from manmade structures; 43.1% of fish were landed on commercial passenger fishing vessels (CPFVs).

Jack Mackerel. Jack mackerel has long been the smallest of the federal CPS finfish fisheries. It is a monitored species under the CPS FMP. Jack mackerel represented 3.2% of the total landings of the CPS finfish fisheries in California for 2014. Landings of jack mackerel totaled 784.4 t in 2014, with an ex-vessel revenue of $148,947 for California (table 1, fig. 2).

Oregon reported landing 800.4 t of jack mackerel, with an ex-vessel revenue of $146,577. This is a 549.7% increase from the 2013 catch of 123.2 t.

Washington reported landing 242.7 t of jack mackerel in 2014, with an ex-vessel revenue of $59,210. This is an increase of over 204.9% from the 2013 catch of 79.6 t.

The 2014 recreational jack mackerel catch as sampled from CRFS was 8.6 t (56,091 fish), a 101.7% increase (152.6% by fish) from 2013. A total of 31,224 fish were landed on manmade structures.

Northern Anchovy. Composed of three stocks, southern, central and northern, landings of northern anchovy in California have been reported since the early 1900s. Northern anchovies are only occasionally landed in Oregon and Washington (primarily used for live bait). The California fishery is harvested from the central stock, which ranges from San Francisco to northern Baja California. Currently, northern anchovy are a monitored species under the CPS FMP. Studies of scale deposits on the sea floor suggest that their abundance has historically been quite large. Now used for animal food, live bait, and human consumption, anchovy was used mainly in a reduction industry to produce oil and fish meal in the 1900s. From the 1900s to the late 1970s, northern anchovy was a major component of California's commercial CPS fisheries. During periods of low sardine abundance, anchovy landings have increased, hitting a peak in the mid-1970s at over 100,000 t. However, commercial landings of northern anchovy have remained relatively low since the 1980s due to market constraints. Presently, landings of northern anchovy are modest, averaging 7,877 t per year over the last 14 years.

Landings of northern anchovy in California for 2014 were 10,511 t with an ex-vessel revenue of greater than $1.6 million (table 1, fig. 2). When compared to landings in 2013, this represents a 75.0 % and 49.9% increase in volume and value, respectively. Nearly all (98.7%; 10,378.8 t) of California's 2014 northern anchovy catch was landed in the Monterey port area (table 2). Exports of northern anchovy product from California totaled 416 t for an export value of over $1.5 million. Seven countries received anchovy product from California; Australia received the majority at 77.0%.

In 2014, Oregon and Washington reported no landings of anchovy. Oregon did not report any anchovy exports in 2014. Washington exported 1.9 t of anchovy product to Canada, totaling $13,336 in revenue.

The 2014 recreational northern anchovy catch as sampled from CRFS was 4.1 t (227,759 fish), a 25.1% decrease (50.1% by fish) from 2013. The majority (91.6%) of fish landed were from manmade structures, and 6.5% were landed from CPFVs.

California Market Squid

In 2014, market squid (*Loligo (Doryteuthis) opalescens*) continued to dominate commercial landings of marine species in California, contributing about 64% of the total tonnage and 30% of total ex-vessel value of all species landed. Landings of market squid in 2014 decreased 2% compared to 2013 landings, from 104,370 t to 102,516 t (fig. 6). Ex-vessel value in 2014 decreased 3% compared to 2013, from $73.7 million to $71.8 million. California fish businesses exported 89,240 t of market squid to 40 countries for a value of $114 million in 2014 (http://www.st.nmfs.noaa.gov/commercial-fisheries/foreign-trade/). The majority (86%) was shipped to just 3 countries but most (73% of the total amount) went to China.

For the fifth season in a row, since the inception of the Market Squid Fishery Management Plan in 2005, market squid landings were projected to reach the seasonal catch limit of 107,048 t. By November 18, 2014, 97.2% of the catch limit had been landed. On this date, the seine sector of the squid fleet made a voluntary decision to stop fishing so that the remaining portion of the catch limit could be set aside for the brail sector. Neither the brail nor seine sector of the commercial fleet made directed landings of market squid after November 18, 2014, and the 2014/15 season ended without reaching the seasonal catch limit.

Commercial fishing for market squid is limited by fishery control rules set forth in the Market Squid Fishery Management Plan (MS FMP). Vessels are required to have a permit to commercially fish for market squid. In 2014, there were 75 market squid vessel (purse/drum seine), 34 light boat (attracting), and 44 brail (or dip net) permits issued. Of the 75 vessel permits issued, 64 vessels were active in the fishery with 52 vessels contributing 95% of the landings. Of the 44 brail permits issued, 11 brail vessels landed squid. Other fishery control rules include a seasonal catch limit that starts April 1 and ends March 31 of the following year, weekend closures, spatial closures, and lighting restrictions.

The geographic distribution of market squid landings in 2014 is particularly interesting. Although the fishery has its historical origins in Monterey Bay, it had been dominated by southern California landings in recent years (fig.7). Landings north of Point Conception have increased since 2010 and increased sharply in 2014. This sharp increase, paired with a sharp decrease in landings south of Point Conception, meant the fishery was no longer dominated by southern California in 2014. The Department's Commercial Fisheries Information System (CFIS) contains landing data back to 1980 and contains no record of directed squid landings north of the San Francisco Bay prior to 2014. The 2014/15 season represents the first time in recent history that directed fishing for market squid resulted in landings to the port of Eureka (2,174.8 t). A shift in oceanic conditions, such as sea surface temperature (SST), may have attributed to this northward shift of landings (fig. 5).

Market squid live less than a year and have been found in nearshore waters of the eastern Pacific Ocean from Baja California to the Gulf of Alaska. The population

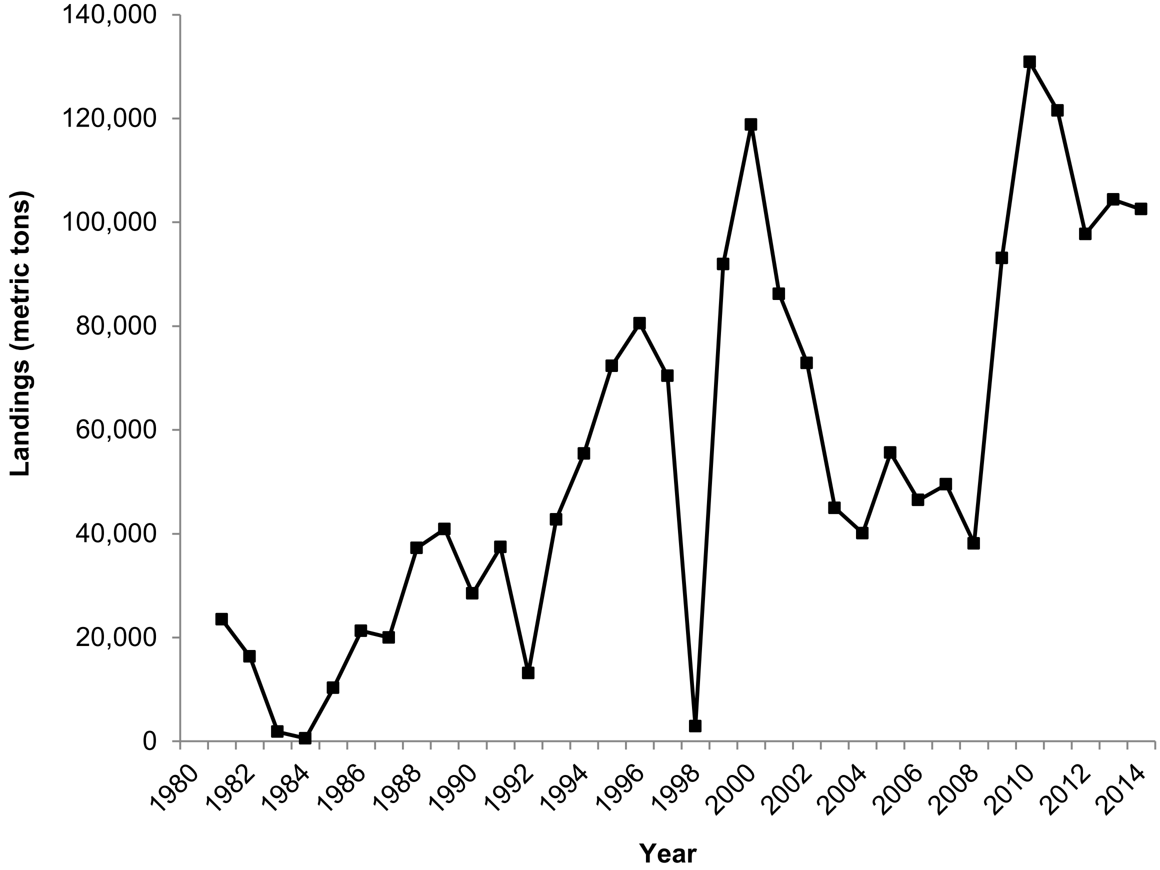


Figure 6. California commerical market squid (*Loligo (Doryteuthis*) opalescens) landings, 1981–2014.

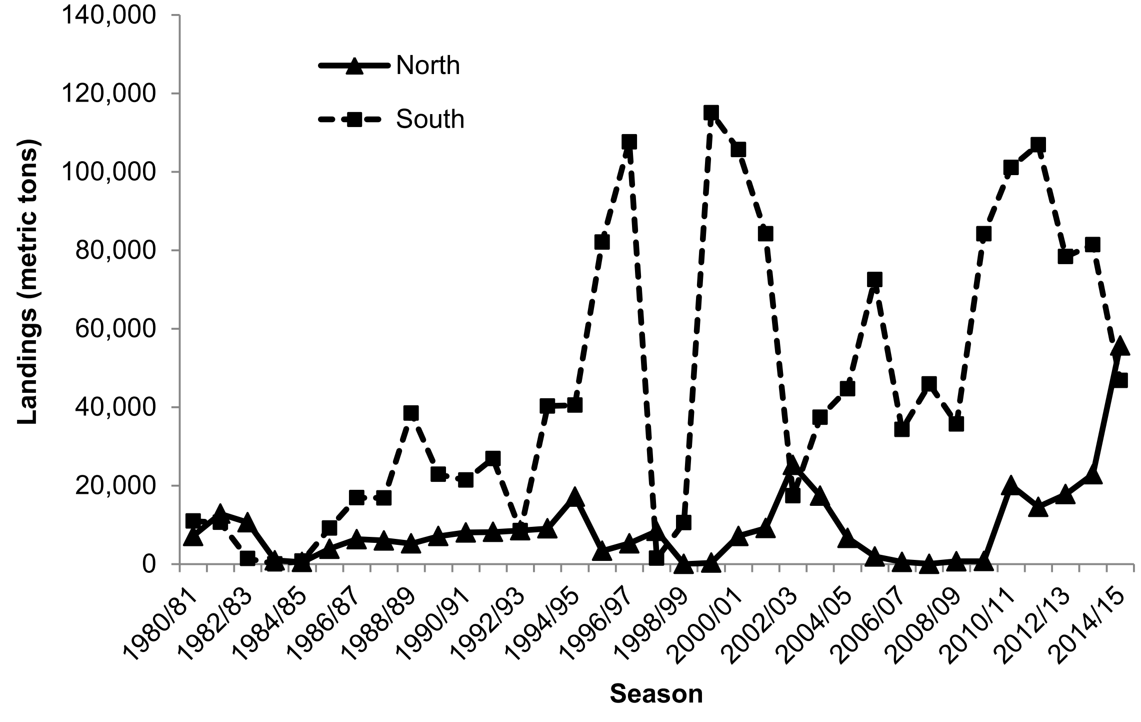


Figure 7. Comparison of market squid (*Loligo (Doryteuthis) opalescens*) landings for northern and southern fisheries by fishing season (1 April–31 March), from 1980/81 to 2014/2015 seasons.

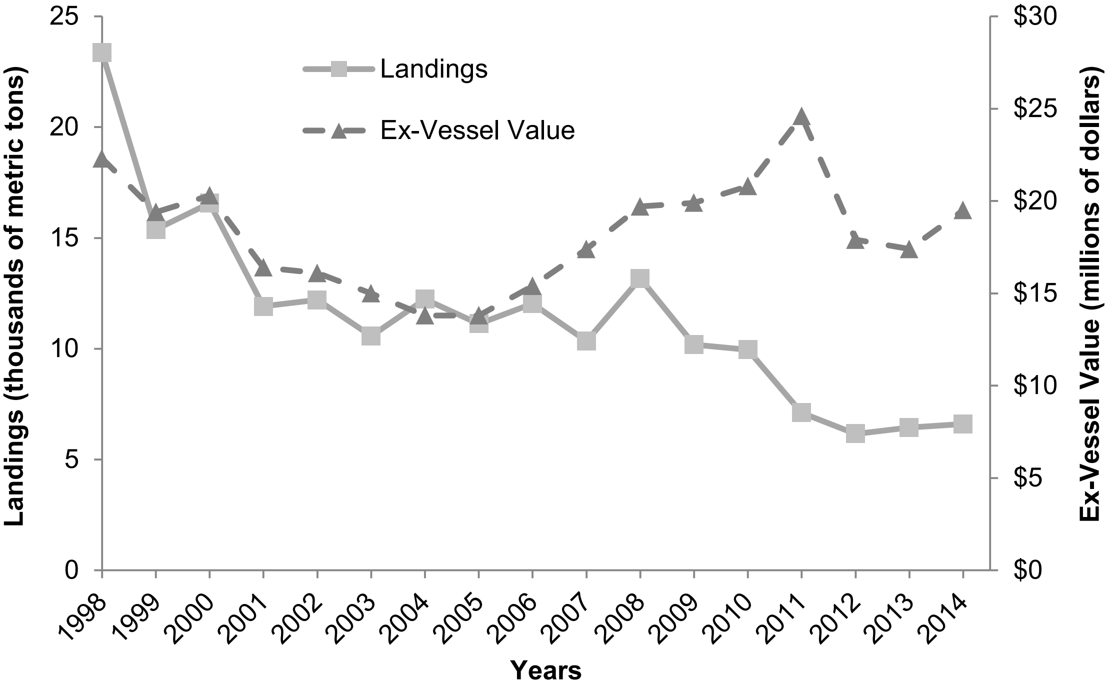


Figure 8. California commercial groundfish landings, 1998–2014.

appears to fluctuate widely in abundance in response to short-term oceanographic events, like the El Niño Southern Oscillation. Ecologically, they are considered important as forage for other species, including predatory fishes, marine mammals, and seabirds.

A live bait fishery exists for market squid, largely to supply recreational fishing in southern California. The live bait fishery is a low-volume, high-value endeavor, as recreational anglers are willing to pay up to $60 for a "scoop" of live squid, which averages 10 lbs.; as a comparison, the average price paid to the commercial fleet in 2014 was $0.32 per pound.

Groundfish

More than 90 species of bottom-dwelling marine finfish are included in the federally managed groundfish fishery. The species that comprise the groundfish fishery are diverse and complex; their primary distributions range from nearshore depths to deep offshore habitats. "Groundfish" species include all rockfishes in the Scorpaenidae family, flatfishes such as Dover sole (*Microstomus pacificus*) and petrale sole (*Eopsetta jordani*), roundfishes such as sablefish (*Anoplopoma fimbria*), and lingcod (*Ophiodon elongatus*), and various sharks and skates. These groundfish species are grouped into 39 federal management units, consisting of species or species groups, to help facilitate management measures that balance biological and economical goals.

Commercial Fishery. In 2014, California's commercial groundfish landings totaled 6,603 t, worth an estimated ex-vessel value of $19.5 million. This represents a 2.4% increase in landings from 6,443 t in 2013 and an increase in ex-vessel value of 12% from $17.3 million. During the last decade, groundfish landings declined by 46% (6,603 t in 2014 versus 12,243 mt in 2004); yet the ex-vessel value increased nearly 41% ($19.5 million in 2014 versus $13.8 million in 2004) (fig. 8). In 2014, the majority (71%) of groundfish was landed between the California/Oregon border and the Monterey Bay area and generated 52% of the total ex-vessel value of the fishery. By volume, trawl gear comprises 72% of the total statewide landings followed by hook and line and trap gear at 28%. While that 28% is low compared to trawl gear, hook and line and trap gear generated 41% of the total revenue generated by the fishery. The lower volume capacity of the hook and line gear accounts for the majority of total trips (89%) as compared to trawl gear (11%).

Landings of Dover sole, sablefish, thornyheads (*Sebastolobus altivelis* and *S. alascanus*), petrale sole, and chilipepper (*Sebastes goodei*) continued to be the top species by weight, with 1,897 t, 1,800 t, 989 t, 614 t and 276 t landed, respectively. These species comprised 84% of the groundfish landings.

Groundfish landings in 2014 were mostly comprised of flatfishes (41%), followed by roundfishes (29%), thornyheads (15%) and rockfish (10%). The "other" groundfish species category was comprised of grenadier (Macrouridae) which accounted for 61 t (table 3). Chilipepper was the top rockfish species by weight, with

TABLE 3
California commercial groundfish landings (in metric tons) and ex-vessel value in 2014 with comparisons to 2013. The top species by weight for the flatfishes and rockfishes are represented in the table.

	2014		2013		% change from 2013 (mt)	% change from 2013 ($)
	Harvest (mt)	Value ($)	Harvest (mt)	Value ($)		
Flatfishes						
Dover sole	1,897	$1,866,714	2,218	$2,143,990	–14%	–13%
Petrale sole	614	$1,644,155	470	$1,321,525	31%	24%
Arrowtooth flounder	75	$16,839	118	$26,824	–36%	–37%
English sole	59	$45,633	49	$39,777	20%	15%
Rex Sole	43	$38,219	45	$42,920	–4%	–11%
Sand sole	16	$36,136	15	$37,774	4%	–4%
Other flatfishes	14	25,811	28	$24,679	–49%	5%
Total Flatfishes	2,719	$3,673,507	2,944	$3,637,489	–8%	1%
Rockfishes						
Chilipepper	276	$455,998	322	$472,897	–14%	–4%
Blackgill rockfish	60	$142,603	72	$146,033	–17%	–2%
Bank rockfish	58	$119,993	52	$110,088	11%	9%
Black rockfish	40	$188,441	36	$159,878	12%	18%
Brown rockfish	26	$386,791	28	$422,334	–6%	–8%
Vermilion rockfish	27	$162,294	23	$142,335	15%	14%
Gopher rockfish	26	$436,526	23	$392,733	11%	11%
Other rockfishes	105	807,842	100	$751,094	5%	8%
Overfished species						
Bocaccio	15.2	$41,005	16.5	$39,700	–8%	3%
Canary rockfish	1.9	$2,984	1.6	$3,474	21%	–14%
Cowcod	0.2	$469	0.2	$191	11%	145%
Darkblotched rockfish	3.9	$8,208	4.2	$6,204	–6%	32%
Pacific ocean perch	0.04	$50	0.05	$56	–22%	–10%
Yelloweye rockfish	0.02	$34	0.01	$30	40%	12%
Total Rockfishes	638	$2,753,239	679	$2,647,047	–6%	4%
Roundfishes						
Sablefish	1,800	$8,964,857	1,375	$7,014,561	31%	28%
Lingcod	106	$514,508	64	$294,396	65%	75%
Cabezon	31	$402,236	29	$361,832	7%	11%
Kelp greenling	5	$60,085	5	$70,790	–15%	–15%
Pacific whiting	5	$223	4	$212	35%	5%
Total Roundfishes	1,947	$9,942,180	1,478	$7,741,790	32%	28%
Scorpionfish, California	2	$23,098	3	$28,399	–45%	–19%
Sharks & Skates	248	$204,975	172	$145,009	44%	41%
Thornyheads	989	$2,891,294	1,085	$3,114,120	–9%	–7%
Other Groundfish	61	$35,322	84	$68,466	–27%	–48%
Total Groundfish	6,603	$19,523,614	6,443	$17,382,320	2%	12%

*Petrale sole was declared overfished in 2009
Data Source: CFIS (CMASTR) Extraction Date: 04/28/2014

landings of 276 t worth an ex-vessel value of $455,998. Unlike high-volume, high-value species such as sablefish, nearshore rockfishes are generally a low-volume, high-value commodity in California—brown rockfish (*S. auriculatus*), gopher rockfish (*S. carnatus*), and grass rockfish (*S. rastrelliger*) were worth a combined ex-vessel value of $1,049,843 with landings of 26 t, 26 t and 11 t respectively. Restricted access and the live fish market are primarily responsible for the high market value of the nearshore fishery. In 2014 the top grossing nearshore species were grass rockfish, black-and-yellow rockfish (*S. chrysomelas*), and gopher rockfish; valued at approximately $21,100/t, $17,000/t and $17,000/t, respectively. By contrast, chilipepper (a non-nearshore rockfish) was valued at approximately $1,650/t.

Landings of overfished rockfish species, which accounted for <1% of the groundfish landings in 2014, decreased by 7.4% compared to 2013 (21.3 t versus 23 t). In both years the predominant species was bocaccio (*S. paucispinis*), which accounted for 71% and 73% of the total overfished rockfish species landings in 2014 and 2013, respectively. Management measures to protect overfished species have greatly reduced landings over the past decade.

Recreational Fishery. The Recreational Fisheries Information Network (RecFIN) Program stores recreational data from California, Oregon, and Washington. RecFIN incorporates data from two recreational fishery sampling programs in California—the Marine Recreational Fisheries Statistical Survey (MRFSS), which

TABLE 4
Comparison of recreational groundfish catch in California in 2014 and 2013 (does not include discards and only includes catch greater than 5 metric tons).

Species	2014 Harvest (mt)	2013 Harvest (mt)	% Change from 2013
Lingcod	572	433	32%
Black rockfish	340	363	–6%
Vermilion rockfish	206	211	–2%
Blue rockfish	134	106	26%
California scorpionfish	123	112	9%
Brown rockfish	120	82	48%
Pacific sanddab	107	86	25%
Copper rockfish	102	99	4%
Bocaccio	100	131	–24%
Yellowtail rockfish	60	56	7%
Gopher rockfish	55	41	34%
Cabezon	32	25	28%
Olive rockfish	32	20	56%
Squarespot rockfish	22	17	35%
Kelp rockfish	18	19	–8%
Widow rockfish	16	18	–8%
Canary rockfish	16	13	25%
Starry rockfish	15	24	–39%
Leopard shark	14	14	1%
Kelp greenling	13	14	–8%
Grass rockfish	12	10	26%
Chilipepper	11	7	46%
Black-and-yellow rockfish	10	6	68%
Greenspotted rockfish	10	11	–12%
China rockfish	10	10	3%
Speckled rockfish	9	16	–39%
Flag rockfish	9	14	–34%
Treefish	9	13	–28%
Honeycomb rockfish	6	9	–39%
Rosy rockfish	5	6	–18%
Other groundfish	31	27	15%
Total Groundfish	2,220	2,014	10%
Angler Trips			
Bottomfish Effort	950,801	925,682	3%

Data source: RecFIN
Date Extracted: 05/08/2015

operated from 1980 to 2003, and the California Recreational Fisheries Survey (CRFS) initiated by the Department in 2004. These data, which are available from 1980 to the present, represent the best available information on recreational catch in California. CRFS data indicate that California anglers targeting groundfish participated in an estimated 950,801 trips in 2014, a small increase (<3%) from 2013 (925,682 trips). The predominant gear type used in the California recreational groundfish fishery is hook and line.

An estimated 2,220 t of groundfish were taken by the recreational fishery in 2014 (table 4), which represents a 10% increase compared to 2013 (2,014 t). The top five species in 2014 were lingcod, black rockfish (*S. melanops*), vermilion rockfish (*S. miniatus*), blue rockfish (*S. mystinus*), and California scorpionfish (*Scorpaena guttata*), which accounted for approximately 62% of the groundfish catch by weight; in 2013, the same five species comprised 61% of the catch. In 2014, the majority (52%) of groundfish catches occurred in central California (Point Conception to Cape Mendocino), where lingcod was the most frequently encountered. In southern California (south of Point Conception), anglers took 36% of the groundfish catch, with vermilion rockfish being the most frequently encountered. Lastly, northern California (Cape Mendocino to the California-Oregon border) accounted for 12% percent of the catch, with black rockfish being the most frequent.

Commercial Nearshore Fishery Update. The state Nearshore Fishery Management Plan (NFMP) has been in place for more than twelve years, having been first adopted in October 2002 to meet the mandates of the Marine Life Management Act in addressing growing concerns regarding increasing participation in the nearshore fishery. The NFMP provides a framework for management of nineteen species including various rockfish and a number of species caught in association with them in nearshore habitat. A full review of steps taken to implement the NFMP since its inception is provided in a recently published paper by Wilson-Vandenberg et al. (2014).

To date, full stock assessments have been completed for half of the nearshore species, including blue, black, brown, China, copper, and gopher rockfish, as well as California scorpionfish and cabezon. The remaining species have been assessed with less intensive data methods (table 5). Many stocks are considered to be healthy while others are in the precautionary zone; none are considered overfished.

Regulations have been developed to prevent commercial harvest from exceeding the allowable limits. Season lengths, depth restrictions, gear restrictions, trip limits and a restricted access permit system have been implemented and have been successful at providing as much fishing opportunity as possible while keeping catches within allowable limits.

Commercial Nearshore Fishery. During development of the NFMP, a restricted access program was developed to address overcapitalization issues in the nearshore fishery and to keep catches within allowable limits. Three different species specific permits were developed for this fishery—a Nearshore Fishery Permit (NFP; also known as the shallow nearshore permit), a Deeper Nearshore Fishery Permit (DNSFP), and a Nearshore Fishery Bycatch Permit (bycatch permit). The NFP is divided into four regions (North Coast, North-Central Coast, South-Central Coast and South Coast) with area-specific capacity goals; capacity goals are North Coast = 14, North-Central Coast = 9, South-Central Coast = 20, and South Coast = 18. This permit can only be fished in the region for which it is issued. This permit is also transferrable, but two permits must

TABLE 5
The 19 nearshore species with relevant federal and state management and stock assessment information. Shallow and Deep permit types refer to the Nearshore Fishery Permit (NFP) and Deeper Nearshore Species Fishery Permit (DNSFP), respectively.

		NFMP		
Species	Managed by	Species by Permit	Last Assessed	Status[a]
Black rockfish (RF)	Fed/State	Deep	2007	healthy
Black-and-yellow RF	Fed/State	Shallow		
Blue RF	Fed/State	Deep	2007	precautionary
Brown RF	Fed/State	Deep	2013	precautionary
Calico RF	Fed/State	Deep		
China RF	Fed/State	Shallow	2013	healthy[b]
Copper RF	Fed/State	Deep	2013	healthy[b]
Gopher RF	Fed/State	Shallow	2005	healthy[b]
Grass RF	Fed/State	Shallow		
Kelp RF	Fed/State	Shallow		
Olive RF	Fed/State	Deep		
Quillback RF	Fed/State	Deep		
Treefish	Fed/State	Deep		
Cabezon	Fed/State	Shallow	2009	healthy[b]
CA scorpionfish	Fed/State	Shallow	2005	healthy
Kelp greenling[c]	Fed/State	Shallow	2011	
Rock greenling	State	Shallow		
CA sheephead[c]	State	Shallow	2004	
Monkeyface prickleback[c]	State	—[d]		

[a] Status of the stock is based on the Nearshore Fishery Management Plan (NFMP) 60-20 Harvest Control Rule

[b] indicates the northern portion of the stock was precautionary; the southern portion was healthy

[c] Stock status was not determined or the assessments were deemed inadequate for management

[d] No permit required. A commercial fishing license is required as it is for all 19 species

be purchased and one retired. The DNSFP can be fished coast-wide and is nontransferrable. The bycatch permit was issued to allow incidental take of shallow nearshore species with trawl or gill net gear only. This permit is not transferrable.

The restricted access program has greatly reduced the number of participants in the fishery. Between 1999 and 2002, the number of permits issued decreased from 1,127 to 505. The number of NFPs purchased in 2003 totaled 220 but has been reduced through transfers or non-renewal, to 150 permits in 2014, for an attrition rate of 32%. Despite the reduction in the number of NFPs, each region remains above its capacity goal. In 2014 the number of permits issued by region is as follows: North Coast = 16; North-Central Coast = 26; South-Central Coast = 52; and South Coast = 56.

The DNSFP was intended to act as a moratorium to prevent any further entrants into the fishery and does not have gear restrictions or a capacity goal. In 2003, 294 DNSFPs were issued; through attrition the number has been reduced 36% to 188 permits in 2014. In addition, a bycatch permit was created allowing for the incidental take of the nine shallow nearshore species with trawl or gill net gear only. In 2003, 97 individuals qualified for a bycatch permit but only 26 permits were issued. By 2014, the number of bycatch permits was reduced to 11 permits, yet only 3 of these permit holders were active (i.e., making at least one landing of shallow nearshore species).

Summary and Geographic Distribution of Landings. In the early 1990s, prior to implementation of the NFMP and restricted access program, coast-wide nearshore landings (shallow and deeper combined) totaled 445 t, with an ex-vessel value of $1.7 million. After implementation of the restricted access program and the DNSFP in 2003 the coast-wide shallow and deeper nearshore species landings totaled 230 t, with an ex-vessel value of $2.0 million. Eleven years later, in 2014, coastwide nearshore landings (shallow and deeper combined) decreased (6%) to 212 t compared to 2003; however, the ex-vessel value increased (25%) to $2.5 million (fig. 9).

While the fishery originated in the South and South-Central regions in the 1980s, it expanded northward, and between 2003 and 2014 catch has been more evenly distributed over all regions (fig. 10). The composition of catch varies by area in part due to the geographic distribution of each species and availability of other target species (table 6).

Many of the nearshore species are underharvested, meaning they are harvested at levels lower than permissible. While economic factors can affect harvest, protective measures implemented in the early 2000s to protect overfished rockfish are likely having the greatest impact. Canary and yelloweye rockfish are frequently found to co-occur with many nearshore species; as a result large areas of allowable fishing area were closed, which eliminated and/or reduced access to productive fishing

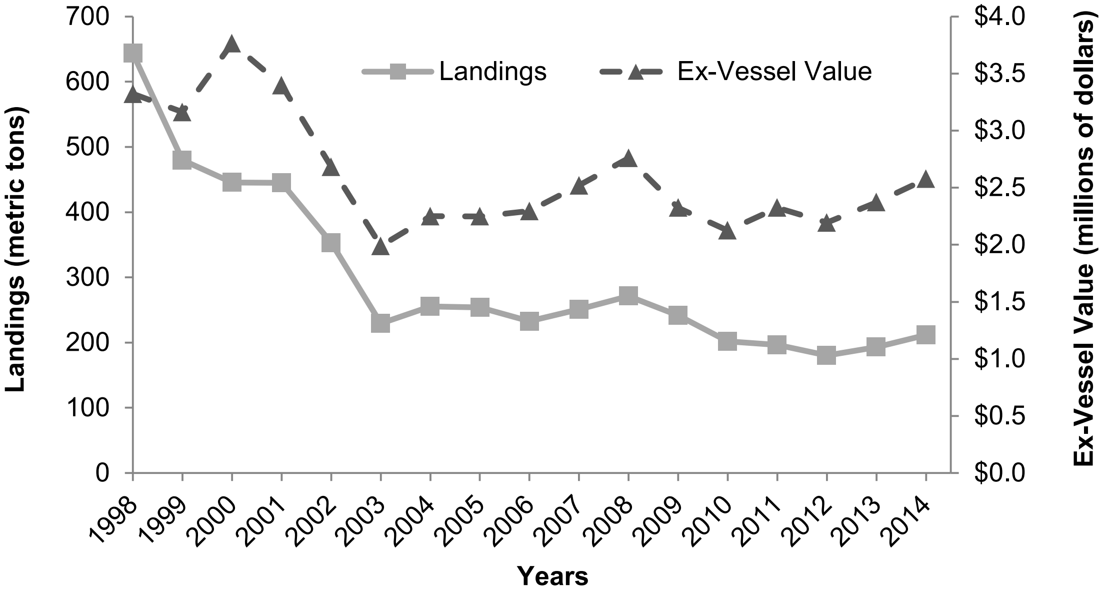


Figure 9. California commercial nearshore groundfish landings, 1998–2014.

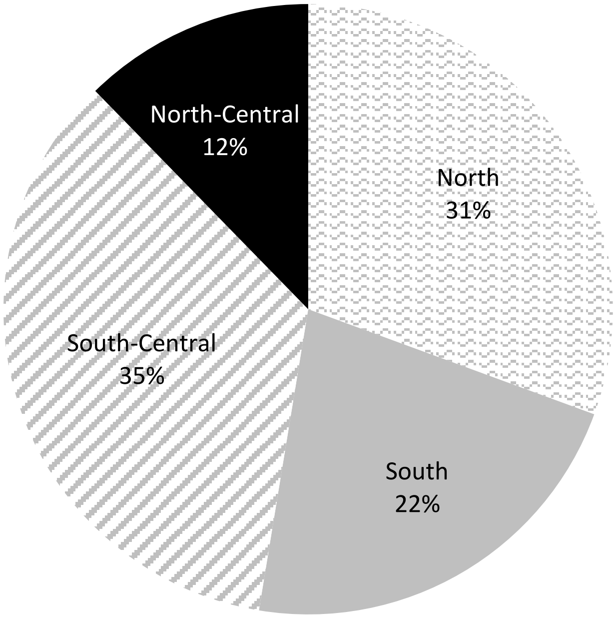


Figure 10. Commercial nearshore landings (shallow and deeper combined) by region, 2003–14.

TABLE 6

Nearshore species regional commercial landings composition, 2003–14. Data from California Department of Fish and Wildlife commercial landing receipts (CFIS).

Species/Group	North Coast Region	North-Central Coast Region	South-Central Coast Region	South Coast Region	Total All Regions
Deeper Nearshore Rockfish	94.80%	40.00%	32.80%	5.50%	46.70%
Shallow Nearshore Rockfish	1.60%	36.60%	42.30%	10.70%	22.20%
CA Sheephead	0.00%	0.00%	0.40%	69.70%	15.50%
Cabezon	3.10%	20.30%	22.50%	9.10%	13.30%
Greenlings	0.60%	3.00%	2.00%	0.00%	1.20%
CA Scorpionfish	0.00%	0.00%	0.00%	4.90%	1.10%
Monkeyface Prickleback	0.00%	0.00%	0.00%	0.00%	0.00%

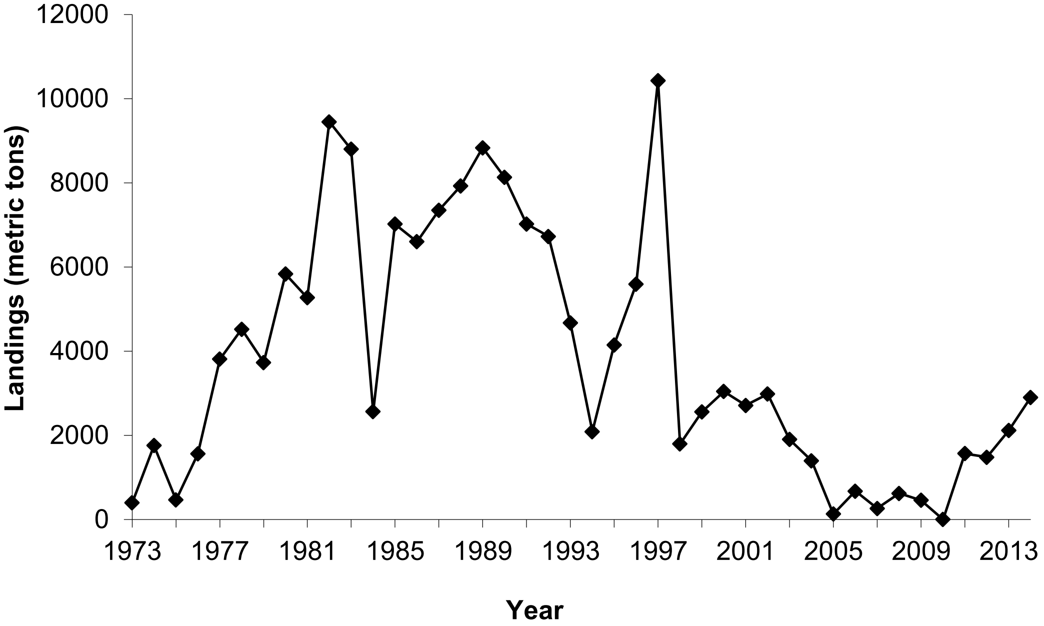


Figure 11. San Francisco Bay commercial Pacific herring (*Clupea pallasi*) sac roe, 1972–2014.

grounds. As canary and yelloweye rockfish continue to rebuild, additional opportunities such as higher trip limits or more access to deeper depths may be permitted.

Pacific Herring

Fishing effort for Pacific herring (*Clupea pallasi*) in 2014 continued at reduced levels when compared to historic landings for California. San Francisco Bay was the only active fishery during this reporting year. There has been no commercial fishing effort in Tomales Bay since 2007, Humboldt Bay since 2005, and Crescent City Harbor since 2002. During the 2014 sac roe season (January 2014–March 2014), the San Francisco Bay fleet landed 2,901.2 t, an increase over the 2013 landings (2,115.6 t) (fig. 11) and 93% of the 3,122.5 t quota.

The forecast base price for roe herring is a good indicator of the economic status of the fishery and determines whether fishermen will participate in the fishery. Ex-vessel prices for roe herring are set using a base price with an additional roe percentage point bonus. The base price is set per short ton of roe herring with a minimum roe percentage of 10%. Roe herring that are landed which exceed the minimum roe recovery level are given a bonus for each percentage point exceeding 10%. Ex-vessel prices in the herring sac roe fishery can vary greatly based on roe recovery rates. The 2014 base price for roe herring with 10% or greater roe recovery was \$200/short ton landed (\$220/t), with an additional \$20 paid for each percentage point above the 10% baseline. The average roe count for the 2014 season was 13.4% resulting in an ex-vessel value of \$268/short ton (\$295/t). Due to a decrease in base price, the statewide ex-vessel value of the herring sac roe fishery fell from over \$1.7 million in 2013 to \$857,064 in 2014.

The San Francisco Bay herring-eggs-on-kelp (HEOK) fishery landed 0 t during the 2014 season, however the fishery was active during the 2013 season, landing 35.7 t of HEOK product. Price paid for HEOK typically ranges from \$17.6–48.5/kg (\$8–22/lb) depending on the quality of the product.

During the 2014 season, the Department conducted spawn deposition surveys in San Francisco Bay to estimate the spawning biomass of the herring stock. The spawning biomass estimate for San Francisco Bay was 54,999 t, a 23.8% decrease over the previous season's estimate of 72,130 t. However, 2014 was the fifth consecutive year of increased biomass since the historic low in the 2009/10 season of 4,394 t and was above the long-term average biomass for San Francisco Bay (1979–2014) of 47,445.8 t. There were no spawning biomass estimates conducted in Tomales Bay, Humboldt Bay, or Crescent City for 2014.

The commercial herring fishery is closely regulated through a catch-quota system to provide for adequate protection of this important forage species. The Department conducts annual assessments of the spawning herring population in San Francisco Bay as part of its ongoing monitoring and management of the fishery. The Department also examines age structure, growth, general condition, and biological aspects of the catch. These data serve as the basis for establishing fishing quotas for the following season. The quota range is based on the determination of the Department's assessment of the stock status, utilizing the best science available. This includes,

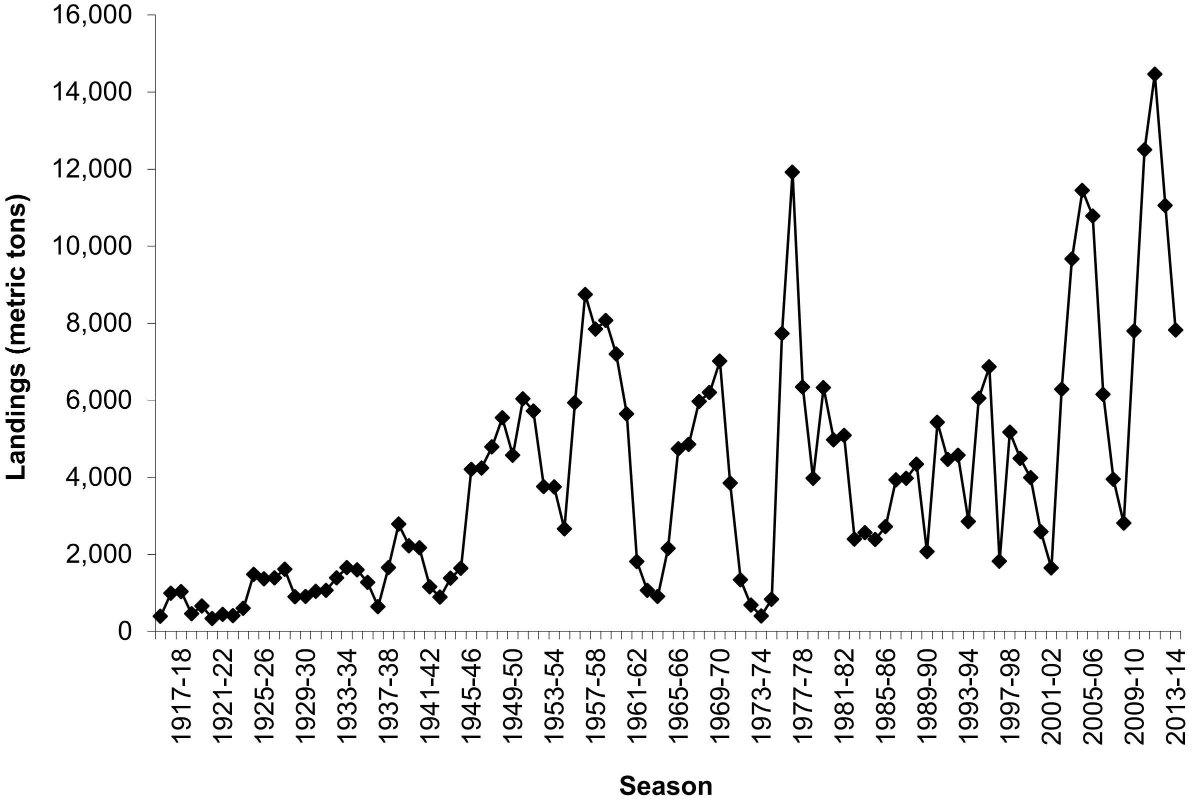


Figure 12. California commercial Dungeness crab (*Metacarcinus magister*) landings, 1915/16–2013/14.

but is not limited to, recent fishery-independent field surveys, commercial catch and age composition analysis, and environmental data. Quota recommendations for San Francisco Bay are primarily based on the most recent assessments by the Department of the size of the spawning population in San Francisco Bay. The recommendation also takes into account additional data collected each season, including ocean and bay conditions, growth rates of herring, strength of individual year-classes, and predicted size of incoming year-classes (i.e., recruitment).

In response to poor recruitment, indication of population stress, and/or unfavorable oceanographic conditions, harvest targets in recent years have been set at or below 10%. The San Francisco Bay fishery was closed during the 2009/10 season for the first time ever to allow for stock recovery following a record low biomass estimate of 4,394 t. After the one-year closure, harvest targets have been set at precautionary levels of approximately 5%. Since the 2004/05 season, harvest targets have allowed over 96% of the spawning biomass to return to the ocean after spawning in the bay. Based on accepted fishery management principles, these harvest targets are conservative and represent a precautionary approach to safeguard the population as forage and to provide a robust reproductive base to allow for stock rebuilding during years of low recruitment or abundance.

Dungeness Crab

The trap-based Dungeness crab (*Metacarcinus magister*, formerly *Cancer magister*) fishery spans the West Coast of North America from Alaska to central California. The California commercial fishery is regulated through the state legislature and is managed primarily on the basis of size, sex, and seasonal restrictions. Male crabs larger than 159 mm (6.25 in) carapace width (CW) are harvested commercially in California's two management areas, demarcated by the Sonoma/Mendocino county line. The commercial season in the central area, south of this line, begins November 15 and ends June 30, while it conditionally begins on December 1 and ends July 15 for the northern area, depending on the condition of the crab.

Mature males typically molt on an annual basis in the summer months and then begin gaining weight in their new shells. The timing of this molt varies, but the December 1 fishery opening along most of the West Coast usually results in adequately filled-out crab reaching the popular holiday markets. Commencing with the 1995/96 season the state legislature authorized an industry-funded preseason crab quality test to ensure crab meat adequately fills the new hardened shell on the target opening date. The test is conducted in concert with tests in Washington and Oregon. The states then mutually agree, through the Coastal Dungeness Crab Tri-State Committee, on whether to delay the opening

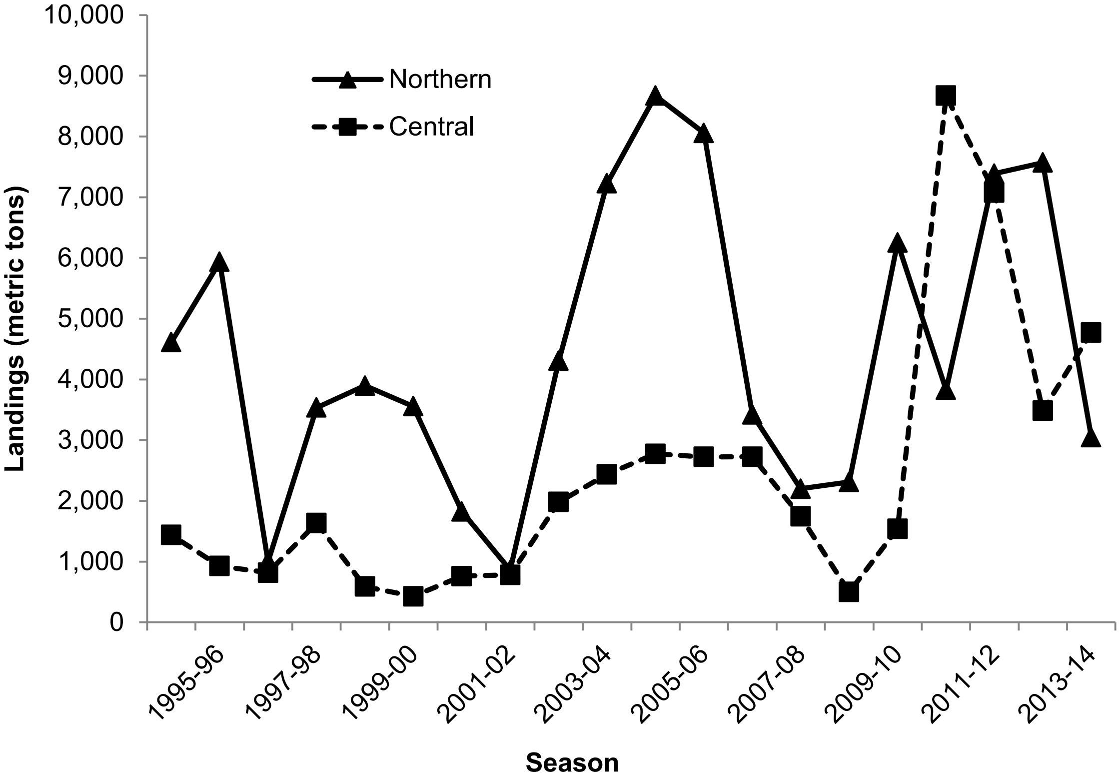


Figure 13. California commercial Dungeness crab (*Metacarcinus magister*) landings by management area, 1994/95–2013/14.

of the season in order to let the crabs reach a standard relative body weight. The 2013/14 season in the northern management area was not delayed and began on December 1 while the central management area is not subject to opening delays by statute.

The 2013/14 crab season brought in statewide landings of 7,822 t, resulting in $60.1 million in ex-vessel value received by the fishermen (fig. 12). The high value overall was in part due to the increasing average price per kilogram over the course of the season at $7.69/kg ($3.49/lb), compared to $6.29/kg ($2.85/lb) the previous season. Dungeness crab was California's second-most valuable fishery in ex-vessel value for the 2014 calendar year at $65.8 million, resulting from the high average price and high landings from the previous 2012/13 season (11,054 t). Typically, the northern area contributes the majority of total crab landed statewide, however for the 2013/14 season 61% of landings were reported from central area ports, between Bodega Bay and Morro Bay (fig. 13). This area has experienced a recent shift in higher than average landings for the past four seasons and set a record for the area in 2010/11 of 8,670 t, more than three times the current 20-year average of 2,390 t. Landings in the southern ports of the central management area, Santa Cruz to Morro Bay, set a record for the area during the 2013/14 season of 714 t, where landings have averaged 157 t for the past 20 seasons.

The recent 2013/14 season is the first to implement the Dungeness crab trap limit program, the primary goal of which is to cap the overall amount of traps that are fished in California. Vessels in the fleet are now subject to fish up to a maximum trap number dependent on their placement in one of seven trap allotment tiers. Placement was based on historical landings during a "window" period and vessels in the highest tier, Tier 1, are allowed a maximum of 500 traps while the lowest tier, Tier 7, is set at 175 traps. Tier 1 vessel permits contributed the most to the 2013/14 statewide total catch at 31%, and vessels in this tier landed on average 41 t, while Tier 7 vessels made up less than 6% of the total catch and averaged about 7 t.

Preliminary data from the 2014/15 season shows statewide landings exceeding 6,500 t (through February 2015), and like the preceding season the majority of these landings (80%) are reported from the central area. Although landings are trending lower than previous seasons, the record high average price of $7.99/kg ($3.63/lb) has contributed to over $50 million in ex-vessel value brought in by that date.

Legislation restricted access to commercial Dungeness crab fishing permits beginning in 1995. A limited entry permit system was then enacted by the legislature with the provision that most permits are transferable. Of the approximately 563 vessels with a 2013 commercial

Dungeness Crab Vessel Permit, 453 vessels made at least one landing in the 2013/14 season. With about 20% of the total permits not actively participating in the fishery, there is concern that, even with trap limits in place, an influx of traps by these latent permits in future seasons could contribute to overfishing and intensify overcrowding on fishing grounds.

In 2008, legislation created the Dungeness Crab Task Force (task force), an advisory group comprised of Dungeness crab fishers from the major fishing ports in the state, members from the Department, and non-governmental organizations. The task force was reinstated in 2012 with SB 369 and one of their many objectives is to evaluate the trap limit program. An initial report was submitted to the Joint Committee on Fisheries and Aquaculture this past January 2015, with a final report of recommendations due on January 15, 2017. Further evaluation of the trap limit program continues as the fishing industry undergoes another fishing season with trap limits in place.

Ocean Salmon

Ocean salmon fisheries in California primarily target Chinook salmon (*Oncorhynchus tshawytscha*). The retention of coho salmon (*O. kisutch*) has been prohibited in the commercial and recreational fisheries since 1993 and 1996, respectively. Pink salmon (*O. gorbuscha*) are taken occasionally in the fisheries, primarily in odd-numbered years. Each season, the Pacific Fishery Management Council (PFMC) and Fish and Game Commission (Commission) regulate California's ocean salmon fisheries to meet the conservation objectives for Klamath River fall Chinook (KRFC) and Sacramento River fall Chinook (SRFC) stocks as described in the Salmon Fishery Management Plan (FMP). In addition, the fisheries must meet the NMFS Endangered Species Act (ESA) consultation standards for listed stocks, including Sacramento River winter Chinook (endangered), Central Valley spring Chinook (threatened), California Coastal Chinook (threatened), Central California Coast coho (endangered), and Southern Oregon/Northern California coho stocks (threatened).

In 2014, California ocean salmon fisheries north of Point Arena were primarily constrained by the NMFS consultation standards for California Coastal Chinook which limits the KRFC age-4 ocean harvest rate to a maximum of 16%. California ocean salmon fisheries south of Point Arena were primarily constrained by the NMFS consultation standards for Sacramento River winter Chinook, which restricts season opening/closing dates, imposes minimum size limits, and sets an age-3 ocean impact rate cap (15.4% in 2014) based on the last three years of spawner escapement.

Commercial salmon fisheries south of Point Arena opened May 1 and closed south of Pigeon Point (Monterey-south management area) on August 13. All other areas south of Point Arena (San Francisco management area) closed on September 30, with the exception of an October 1–15 (Monday through Friday) fishery between Point Reyes and Point San Pedro. In the Fort Bragg management area between Horse Mountain and Point Arena, the fishery opened June 19 through September 30. The fishery was closed statewide during the first two weeks of July and during the last two days of August. The Klamath Management Zone (KMZ), including Crescent City and Eureka ports, opened on September 12 with a 4,000 Chinook quota and daily bag and possession limit of 20 Chinook.

Commercial fisheries in the four major port areas (KMZ, Fort Bragg, San Francisco and Monterey-south) had 342 combined days open to fishing in 2014 compared to 410 days open during the 2013 season. An estimated 166,500 Chinook salmon (1,011 t) were landed during the 2014 commercial season (fig. 14) in 14,200 days fished. The average weight per fish was 6.08 kg (13.4 lbs). The average price was $12.19/kg ($5.54/lb), with a total ex-vessel value of the fishery estimated at $12.3 million. Approximately 600 Chinook were landed out of the KMZ's 4,000 Chinook quota.

The 2014 recreational fishing season increased 14 days compared to 2013, for a season total of 743 days open in each of the four management areas combined. The recreational fishery opened in the Fort Bragg, San Francisco, and Monterey-south areas on April 5 while the KMZ opened on May 10. All fisheries remained open through the summer until closing on September 8 (KMZ), October 6 (Monterey-south), and November 10 (Fort Bragg and San Francisco).

In 2014, an estimated 74,700 Chinook were landed (fig. 15) in 120,300 angler days, a decrease in both catch and effort compared to 2013. Approximately 480 coho were landed illegally during 2014, presumably by anglers who misidentified their salmon as Chinook. The bag limit was two salmon per day of any species except coho and anglers were required to use no more than two single-point, single-shank barbless hooks when fishing for salmon. The possession limit regulation was changed for the 2014 season to state that no more than two daily bag limits may be possessed when on land. On a vessel in ocean waters, no person shall possess or bring ashore more than one daily bag limit. The minimum size limit ranged from 20–24 inches (508–610 mm) TL to protect the generally smaller-sized ESA-listed endangered Sacramento River winter Chinook.

In fall 2014, SRFC exceeded the conservation goal of 122,000–180,000 hatchery and natural area adult spawners for the fifth consecutive year. Nearly 211,700 SRFC adults and 25,400 jacks (age-2 fish) returned to spawn in the Sacramento River basin. Likewise, KRFC surpassed

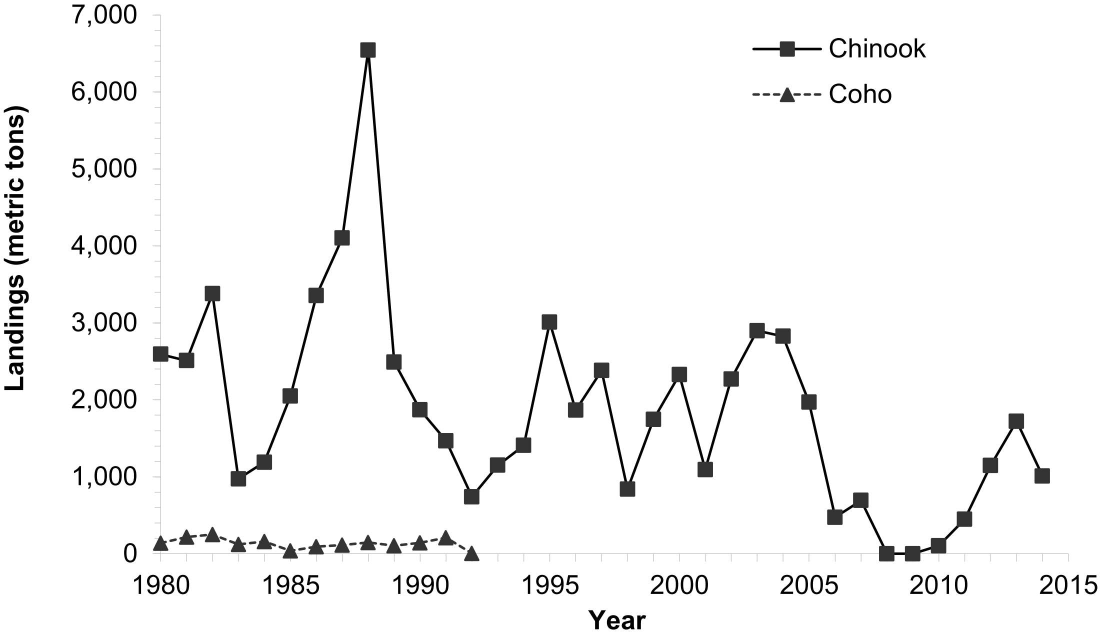


Figure 14. California commercial landings of ocean salmon, 1980–2014.
Note: Commercial fishery landings of coho salmon have been prohibited since 1993 to protect ESA-listed California coastal coho salmon stocks.

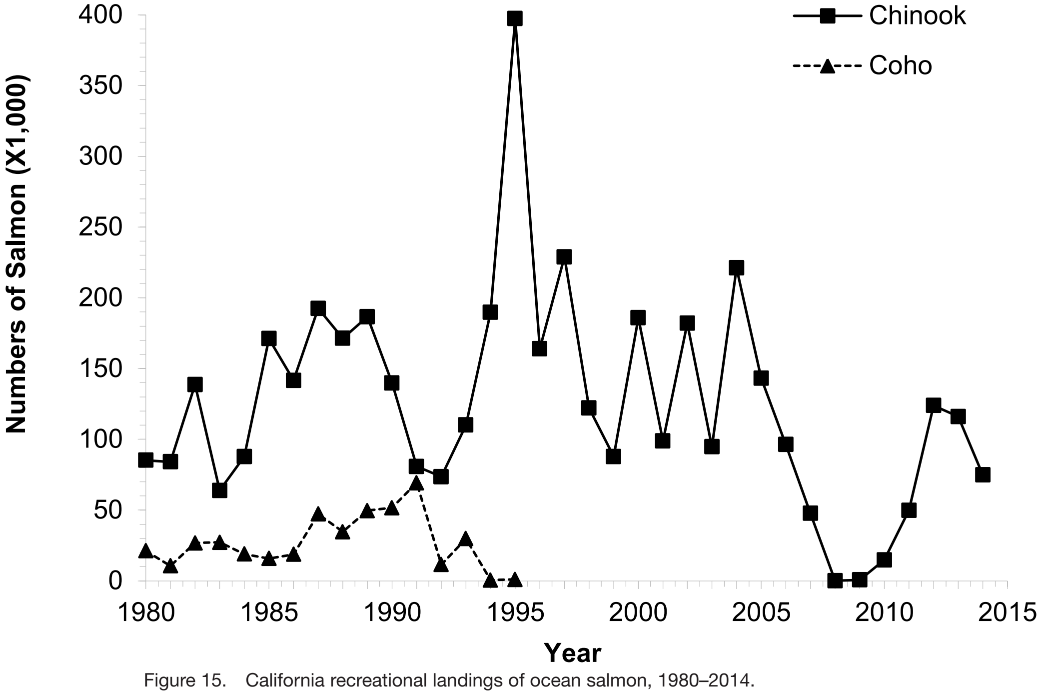


Figure 15. California recreational landings of ocean salmon, 1980–2014.
Note: Recreational fishery landings of coho salmon have been prohibited since 1996 to protect ESA-listed California coastal coho salmon stocks.

the conservation objective of at least 40,700 natural area adult spawners, with 95,300 returning to the Klamath-Trinity Basin in fall 2014.

The 2015 ocean abundance forecasts for SRFC and KRFC are higher than their respective 2014 projections. The Sacramento Index of ocean abundance forecast for 2015 is 652,000 SRFC, while the KRFC ocean abundance projection is 423,800 without additional ocean or in-river fishing. However, protections in addition to NMFS guidance for ESA-listed endangered SRWC were deemed prudent when developing the 2015 ocean salmon fishing seasons. As a result of the drought's continuing detrimental effects on SRWC and based on the best available data, the PFMC adopted more stringent

Figure 16. Surf smelt fisherman with throw net (Photo credit Ken Oda, CDFW).

Figure 17. Night smelt fisherman setting net (Photo credit Kristine Lesyna, CDFW).

Figure 18. A-frame dip net (Photo credit Kristine Lesyna, CDFW).

recreational and commercial management measures, such as higher minimum size limits, reduced days open, and a new sub-management area south of Pt. Sur. These restrictions are expected to provide additional protection to SRWC.

True Smelts

The family Osmeridae is comprised of approximately 11 genera and 30 species. These "true smelts" are small, soft-rayed, schooling fishes with an adipose fin and are found in marine, estuarine, and freshwater habitats in the Northern Hemisphere. They range from Pt. Arguello, California, to the Gulf of Alaska. The related family Atherinopsidae (silversides) includes jacksmelt, topsmelt, and grunion. Members of the true smelts occurring in California waters are delta smelt (*Hyposmesus transpacificus*), eulachon (*Thaleichthys pacificus*), longfin smelt (*Sprinichus thaleichthys*), night smelt (*Sprinchus starksi*), surf smelt (*Hypomesus pretiosus*), whitebait smelt (*Allosmerus elongatus*) and a nonnative, the Wakasagi (*Hypomesus nipponenisis*).

Historically, most of California's Osmerids contributed to sport, commercial, and tribal fisheries; however, only surf and night smelt support these fisheries today. Surf and night smelt, though small in size, are a popular local food fish. Surf smelt are typically headed, gutted, and pan fried due to their relative large size while night smelt are fried whole—"fries with eyes" flavor. Surf and night smelt are also sold by fish wholesalers to aquariums as food for fish, birds, and mammals. Anglers use Osmerids for bait targeting a range of gamefish including striped bass, California halibut, rockfish, lingcod, and redtail surfperch.

Most commercial and recreational Osmerid fishermen use cast nets (Hawaiian throw nets) and/or A-frame dip nets (figs. 16–18). Two-person beach seines ("jump nets") were once popular and are currently legal gear, but the use of beach seines has waned recently in favor of cast nets by recreational fishermen targeting surf smelt. Cast nets are most effective when thrown at visible schools of fish. Fishermen wait until they spot surf smelt appearing in the wash and immediately throw their nets at schooling fish. Cast nets are also readily available, relatively inexpensive, and with practice can be effective.

A-frame dip nets are still used for targeting night smelt throughout their range. The webbing, approximately 3/8 inch measured stretched, is sized to minimize gilling the catch. The net frame is placed seaward into the substrate then the net is tilted up and the catch is tumbled down the throat of the net into the bag. A-frame nets that are handmade have become increasingly difficult to source with ageing of fishery participants but are still widely used.

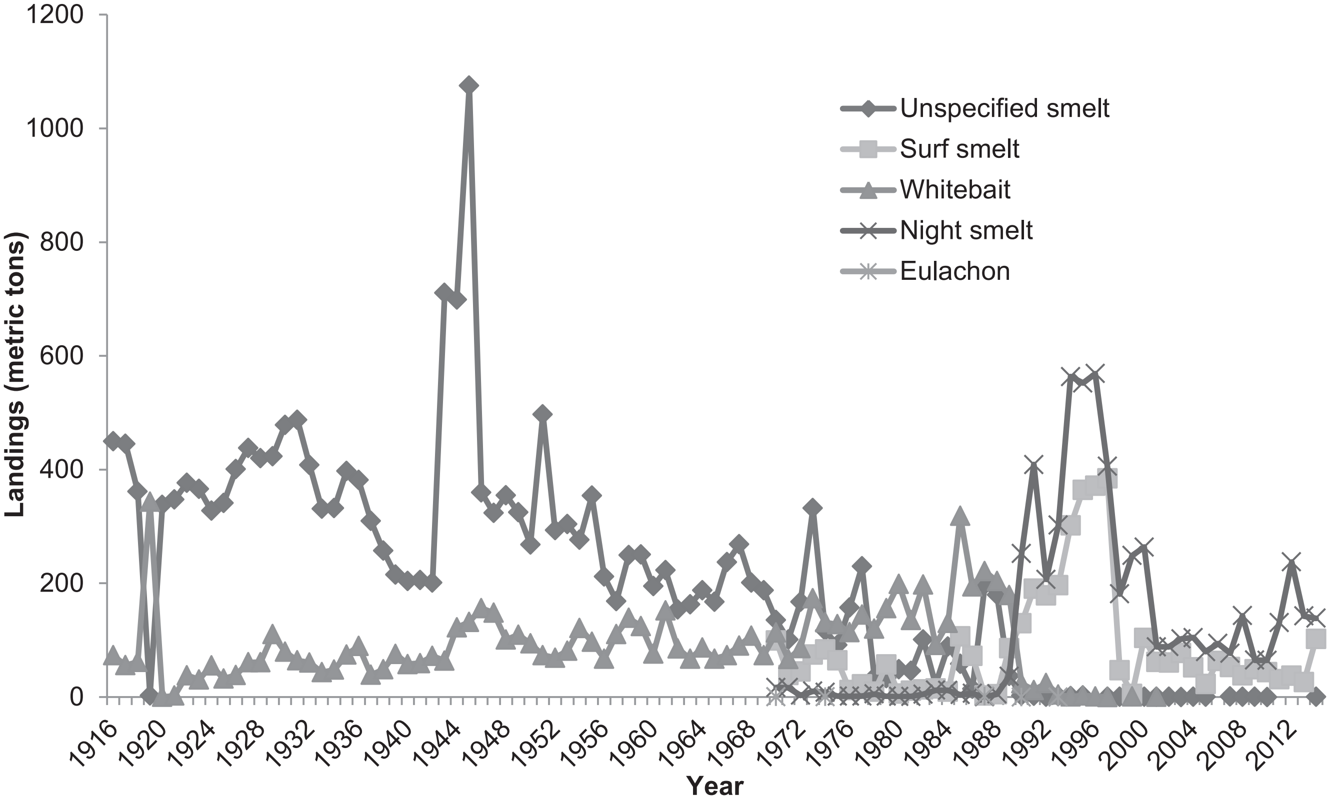


Figure 19. Annual commercial statewide smelt landings, 1916–2014.

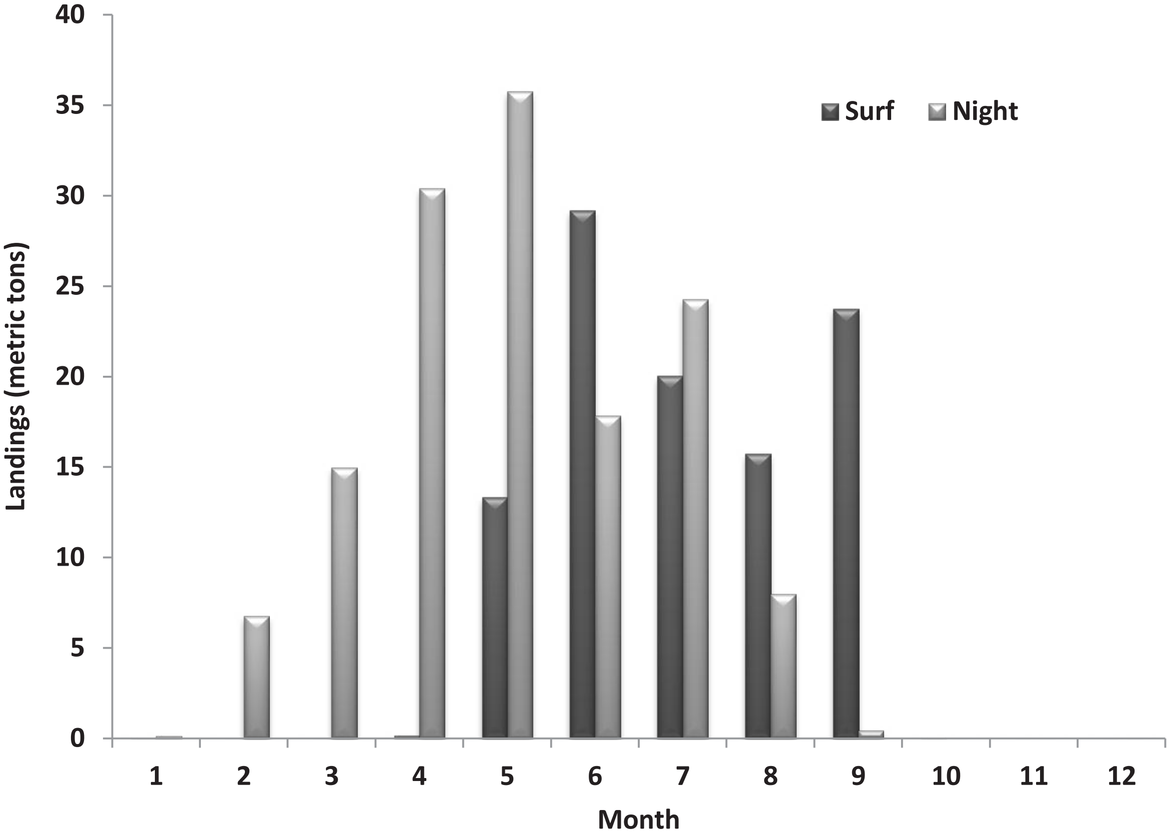


Figure 20. Commercial night smelt (*Sprinchus starksi*) and surf smelt (*Hypomesus pretiosus*) landings by month, 2014.

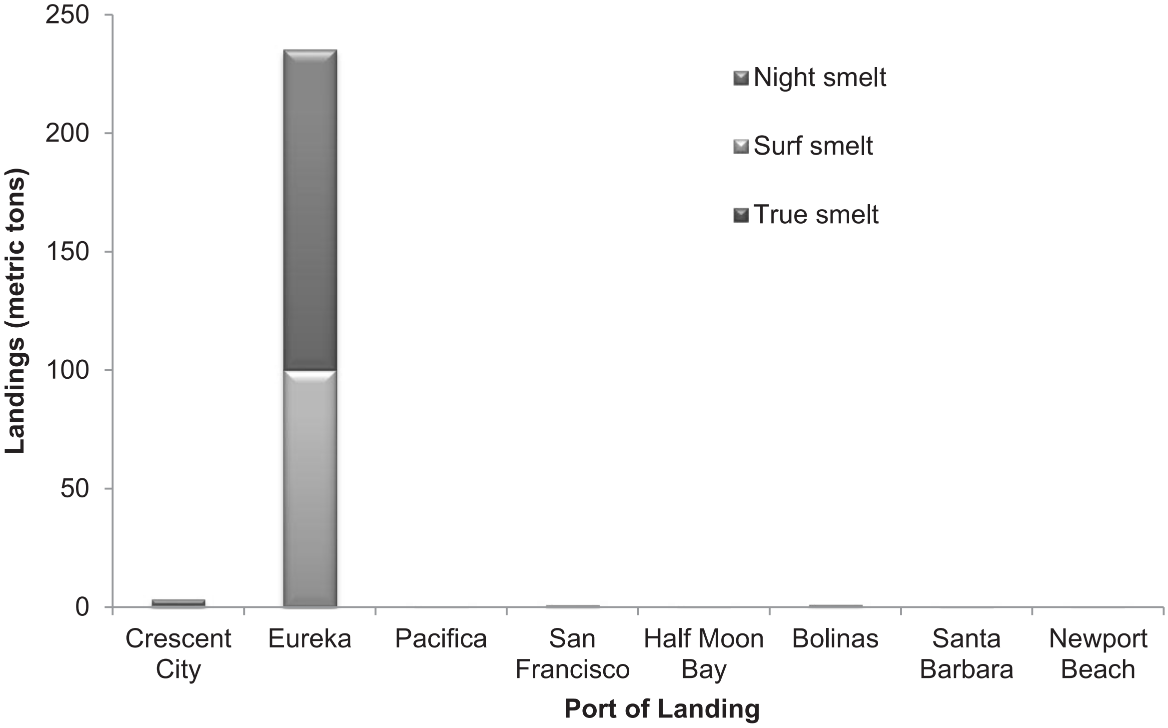


Figure 21. Statewide Osmerid landings by port, 2014.

Commercial landing records for all Osmerid and Atherinopsid species from 1916 through 1969 were recorded as "smelt" and "whitebait smelt." "Smelt" was comprised of surf smelt, but may have also included silversides—jacksmelt, topsmelt, and grunion, depending on the individual fish buyer and region. "Whitebait smelt" was primarily night smelt and similarly sized but less abundant Osmerids including whitebait, longfin smelt, and delta smelt.

After 1969, the "smelt" category was replaced by the "true smelt" and "silversides" market categories to capture Osmerids and Atherinopsids, respectively. True smelt included all Osmerids except whitebait and night smelt; however it is important to note that whitebait was the only Osmerid market category preprinted on receipt books provided to fish buyers to record catch. Therefore, it appears likely that whitebait included other Osmerid species including surf smelt and night smelt. Market categories were created for silversides (unspecified Atherinopsids) including jacksmelt, topsmelt, grunion, night smelt, and surf smelt.

Over time, true smelt and whitebait landings steadily declined as the use of night smelt and surf smelt market categories on fish receipts increased. The decline in true smelt and whitebait landings is attributed to phasing out these market categories as receipt books were replaced rather than changes in species abundances. Use of night smelt and surf smelt market categories was initiated in 1970. In 2014, the true smelt market category composed less than 0.07% of the total Osmerid landings and whitebait landings dropped to zero. Currently, receipt books have preprinted categories for night smelt and surf smelt as well as jacksmelt.

From 1977 to 2014, the combined commercial catch of the Osmerid market categories, primarily night smelt and surf smelt, ranged from 102.5 t in 2005 to 941.4 t in 1996 (fig. 19). Ex-vessel value of the landings ranged from $43,500 in 1971 to $608,000 in 1995. In 2014, night smelt landings totaled 138.5 t with an ex-vessel value of $169,000; surf smelt landings totaled 102.2 t with an ex-vessel value of $157,000. Fish processors paid an average of $1.37/kg ($0.62/lb) and $1.28/kg ($0.58/lb) for night smelt and surf smelt respectively, in 2014. The last commercial eulachon landing was recorded in 1974.

Commercial landings of night smelt and surf smelt indicate peaks in April–May and June–July, respectively (fig. 20). Night smelt begin spawning in late winter while surf smelt begin appearing in the spring. Both species are found on the same beaches but are fished at different times of the day—surf smelt are also called "day fish" or "day smelt" and are caught typically during daylight hours while night smelt are fished at dusk. Landings of both species are often caught on the same fishing trip.

Over 97% of the 2014 statewide commercial Osmerid harvest was landed in Eureka with the remainder landed in the ports of Crescent City, San Francisco, and Half Moon Bay (fig. 21). Landings reported from

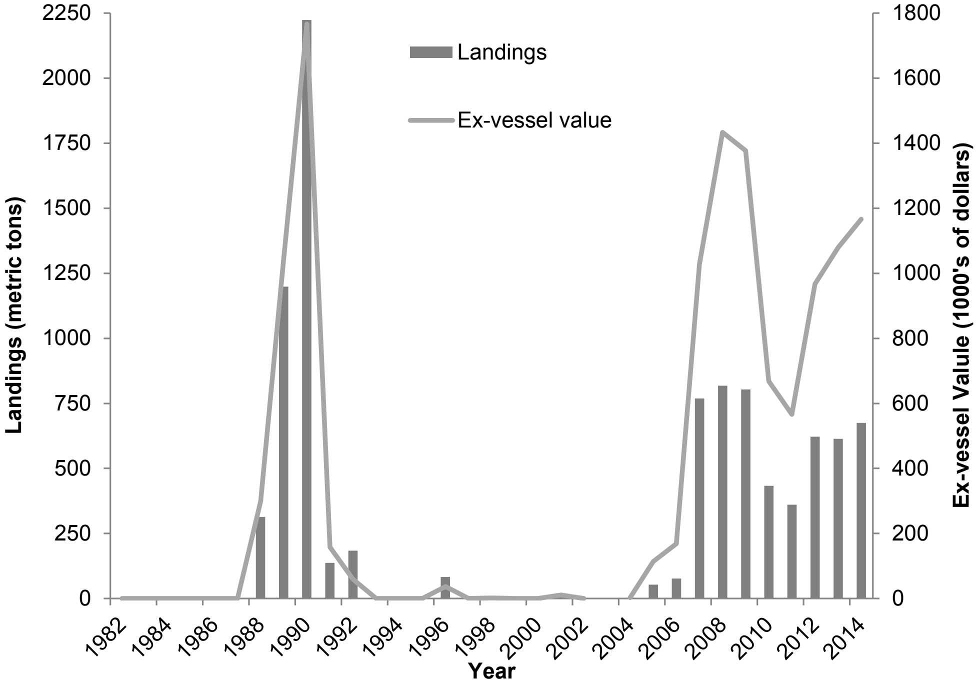


Figure 22. California commercial landings of Pacific hagfish (*Eptatretus stoutii*), 1982–2014

Santa Barbara and Newport Beach as Osmerids may be Atherinopsids.

Historical recreational landings data on Osmerids is extremely limited. An estimated 181 t of unspecified smelt were taken in 1958 based on the results of a Department of Fish and Game recreational fishing survey. Subsequent MRFSS and CRFS estimates ranged from 5 t in 2000 to 199 t in 1984 for surf smelt. Night smelt recreational landing estimates have been sporadic. Recent estimates are unavailable due to safety concerns and logistical issues related to night time data collection and assignment of the Osmerids as a low priority species. Results of the MRFSS ranged from 0.01 t in 1982 to 16 t in 1980. Recreational estimates of annual surf smelt take have varied widely, most likely because this species is rarely encountered in the Department's recreational fishery surveys. Eulachon was listed as a threatened and endangered species by NOAA in March 2010 resulting in the closure of California's sport fishery in 2012 to conform with federal regulations.

Hagfish

Pacific hagfish (*Eptatretus stoutii*) are a member of the Myxinidae (hagfishes) family. Members of this family are cartilaginous, lack eyes and jaws, and have a single nostril with several barbels. The most notable characteristic of hagfishes are the series of mucus-producing "slime" glands along each side of the fish's body. This thick, sticky, protein-based mucus, in the presence of water, converts into a jelly like slime. Produced when agitated, this slime may act as a defense mechanism. Pacific hagfish (hagfish) prefer muddy substrate in depths from 9–732 m. Considered scavengers, hagfish feed upon dead fish and marine mammals, or any other animal matter they can find. Knowledge of maturation and fecundity is limited although studies indicate that females attain sexual maturity between 325 and 340 mm TL, and are between 7 and 12 years. Hagfish fecundity is low with a female hagfish producing 20–30 eggs per reproductive cycle. Reproductive cycle length is unknown, since viable female hagfish may contain eggs that are of various stages of maturity.

Prior to 1988, hagfish landings in California were nonexistent. However, hagfish imports were in great demand by South Korea due to a localized depletion of two related species, brown hagfish (*Paramyxine atami*) and inshore hagfish (*Eptatretus burgeri*). In 1988, a Korean hagfish importer recruited San Francisco and Monterey fishermen to target hagfish for export to South Korea. Statewide landings and fishing effort expanded in 1989 leading to 1,199 t of landed hagfish (fig. 22). By 1990, hagfish landings from Eureka to San Diego resulted in a record high of 2,223.5 t. Hagfish were euthanized with the fish anesthetic MS222 to prevent captured fish from sliming and biting each other. Landed in fresh-dead condition, hagfish were then frozen, and shipped for use in the Korean leather goods market. Due to Korean processing laws and the use of MS222, imported hagfish were used for their skin only and the flesh was discarded. In the latter part of 1990, Korean demand for

California-caught hagfish decreased due to unexplained blemishes, holes, and marks on the skins. Due to these imperfections, hagfish from California became less desirable and South Korean importers took an interest in hagfish exported from British Columbia. Ex-vessel price declined in 1990, but fleet efficiency allowed for the continuation of the California fishery. Ex-vessel price continued to drop in subsequent years, leading to reduced effort and participation.

From 1993 to 2004, annual landings exceeded 20 t in only one year (1996) and averaged 8.9 t. Fishing effort and catch began to increase in 2005 as hagfish were exported in live condition for human food at a greater ex-vessel price, with 54 t landed and a rise again in 2006 with 77 t landed. In addition to resurgence in Korean demand, displaced commercial fishermen were looking for other sources of income, which by 2008 resulted in the highest landings since 1990 of 818 t, valued at $1.43 million. Landings remained high in 2009 with 803 t, valued at $1.38 million. In 2010, while some displaced fishermen returned to their respective fisheries, new fishermen began entering the fishery. From 2010 to 2014, landings were more consistent, averaging 541 t per year (range from 361 to 675 t).

As of 2015, California fishermen face heavy competition in the Korean import market. South Korean hagfish importers also purchase hagfish from Washington, Oregon, and from Korean-sponsored fishermen in Mexico. Hagfish from Washington and Oregon are on average larger than California hagfish and Mexican fishermen are selling hagfish at low market prices. Despite the adversity faced by California fishermen, South Korean import demand of hagfish remains consistent, resulting in regular landings by California fishermen. In 2014, five port complexes and 33 vessels contributed to a landings total of 675 t at an ex-vessel value of $1.17 million. The top three port complexes were Eureka, Morro Bay, and Bodega Bay.

Hagfish may be taken commercially using bucket traps or Korean traps primarily in the depth range of 55–185 m, although fishing occurs out to 370 m. A bucket trap consists of a 5-gallon bucket with a self-closing plastic cone fixed to the bucket lid. The plastic cone acts as a one-way entrance into the trap. Buckets have many drilled holes to allow water flow and possible escapement of small hagfish. Bucket traps are fished on a central ground line with a single vertical line and marker float. Korean traps (currently not used in California) are small, elongated plastic cylinders no greater than 15.24 cm (6 in) in diameter and no more than 60.96 cm (24 in) long. Korean traps employ the same type of plastic cone for an entrance; however, trap holes are smaller and prefabricated. Vessels are limited to 500 Korean traps or 200 bucket traps. No species other than hagfish may be possessed or sold when Korean or bucket traps, or hagfish, are on board the vessel. All traps must have a destruct device, and time-released buoys (pop-ups) are prohibited. Only a general trap permit is required to participate in this open access fishery. Traps are baited with fish, squid, or fish carcasses.

Prior to January 2015, there was no restriction in California on minimum trap hole diameter. In 2013, as part of a collaborative project between the Department and industry to determine the influence of hole diameter in bucket traps on average size of retained hagfish, fishery participants were interviewed to determine what hole diameters were being used. The two common hole diameters were 12.7 mm (1/2 in) and 14.3 mm (9/16 in). Based on this knowledge, the Department conducted a fishery-independent hagfish study in Monterey Bay in 2013, using bucket traps with four different hole diameters, including the two above. Traps with 14.3 mm holes saw a resource benefit of a 10% reduction in retained immature hagfish compared to traps with 12.7 mm holes. Because of this work, a new regulation was developed by the Department and adopted by the Fish and Game Commission (Commission). Effective in January 2015, it is required that all holes in hagfish traps, except for the entrance, be no less than 14.3 mm in diameter.

In 2013, two commercial fishermen requested Experimental Gear Permits from the Commission to use individually floated, 151.4 L (40 gal) barrel traps. The fishermen suggested that the proposed gear might reduce negative gear interactions with other benthic fisheries and reduce dead loss of hagfish from crowding. Pending favorable evaluation, this gear could offer hagfish fishermen a third alternative for the take of hagfish. In addition to onboard observations, Department staff evaluated this gear through logbooks and laboratory dissection of hagfish retained from observed trips. Evaluation of this experimental gear concluded in April 2015 with a regulation proposal expected for August 2015.

Since late 2007, the Department's Northern/Central Finfish Research and Management Project (Project), formerly the State Finfish Management Project, has monitored hagfish fishing activity through dock sampling and laboratory dissection. Due to the difficulty in measuring live hagfish, Project staff use average count per kg from sampled landings to document changes in average size of hagfish. Specimens are collected and examined for length, weight, sex, and maturity.

Deep Water Visual ROV Surveys of MPAs and Surrounding Nearshore Habitat

In December 2012, California implemented the largest scientifically designed network of Marine Protected Areas (MPAs) in the United States, following an MPA

Figure 23. The ROV *Beagle* being launched off Campus Point State Marine Conservation Area.

design and siting process led by the California Department of Fish and Wildlife (Department). This design process spanned eight years across four coastal regions, including the central coast region (2004–07), north central coast region (2007–10), south coast region (2008–12), and the north coast region (2009–12). Regional MPA baseline monitoring programs began in each of the four coastal regions shortly after each implementation. These programs are administered through a partnership among the Ocean Science Trust, Ocean Protection Council, California Sea Grant, and the Department. The research is conducted by scientists from various research institutions, agencies, and nongovernment organizations. Deep water visual surveys have been an important component of each of these regional programs. The purpose of this report is to highlight the Department's work conducting deep water (20–300 m) visual surveys along California's coast inside and outside MPAs using a remotely operated vehicle (ROV). These Department led surveys are separate but complimentary to the regional baseline monitoring programs (including other ROV surveys) and substantially increase the geographic coverage of deep water monitoring throughout the statewide network.

Even before the Marine Life Protection Act and the implementation of California's redesigned MPA network, the Department has been at the forefront of efforts to use ROVs for subtidal ecosystem monitoring. In 1999, Department scientists began developing techniques for using ROVs for MPA monitoring and in 2001 completed the first extensive baseline survey of an MPA in California using an ROV at Punta Gorda Ecological Reserve on the remote rugged coast near Cape Mendocino. Since then, the Department has successfully completed substantial surveys in all four of California's MPA regions. Data gathered from these surveys, on the abundance and distribution of fish and invertebrates, have provided much needed characterization of the baseline ecological condition of California's vast deep water habitats.

In January 2014, the Department initiated new ROV expeditions to explore deep water habitats in each of the four MPA regions. These quantitative surveys occur both inside and outside California's MPAs, at locations previously identified using bathymetric data collected by the California Seafloor Mapping project (CSMP). The CSMP created high resolution maps of predicted rocky habitat which has provided the information necessary to identify index sites for continued monitoring. Within these index sites the project characterizes ecological conditions by quantifying and describing the abundance and distribution of fish and invertebrate species. For these expeditions the Department is contracting with its longtime partner Marine Applied Research and Exploration (MARE) who is providing the ROV *Beagle* (fig. 23) as well as extensive operational and data processing expertise.

Three deployments were successfully completed in 2014 beginning a three year statewide survey. In January 2014, surveys were completed between Point Conception and Santa Barbara with additional survey sites at Anacapa and Santa Cruz Islands. In June 2014, the sec-

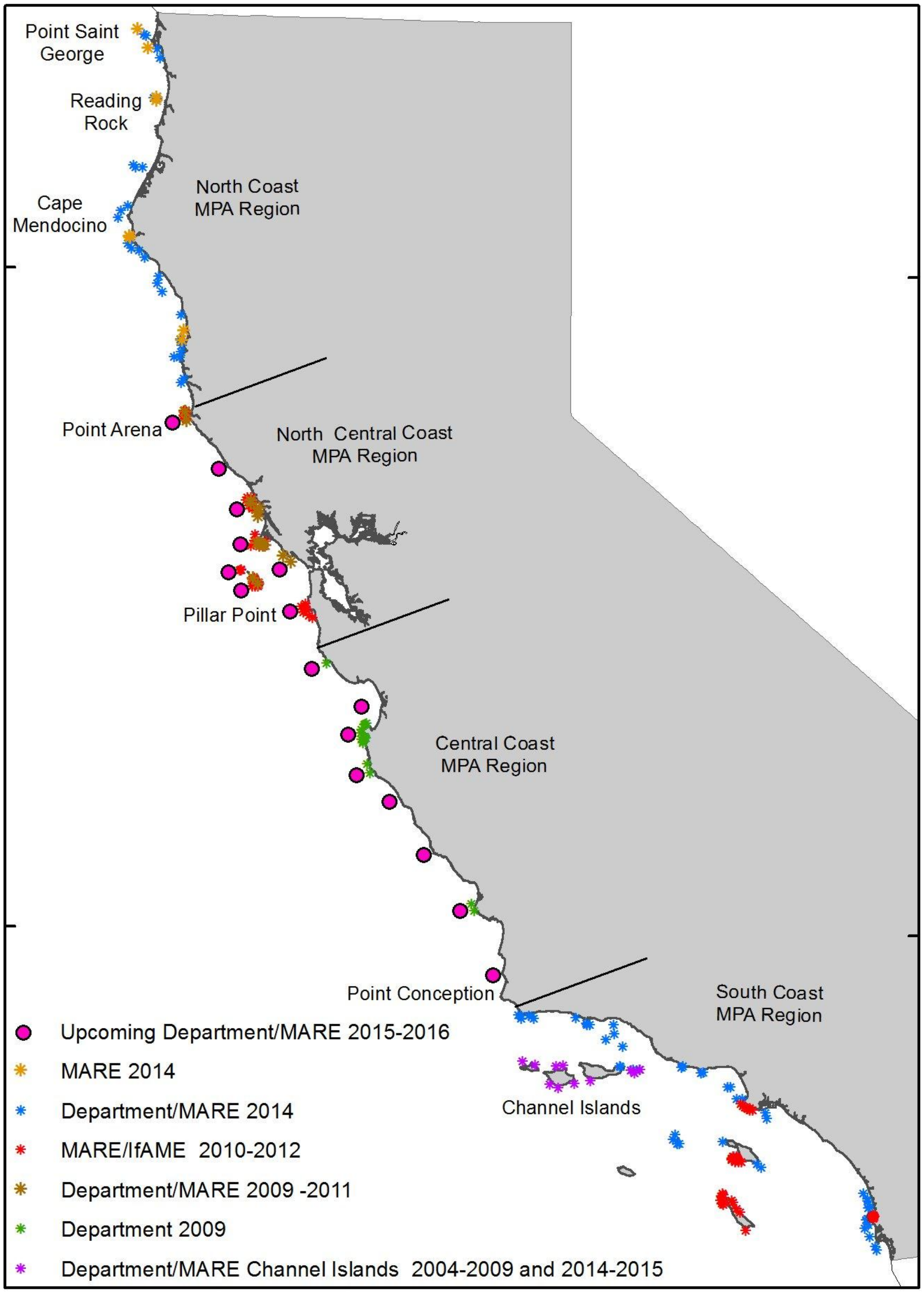
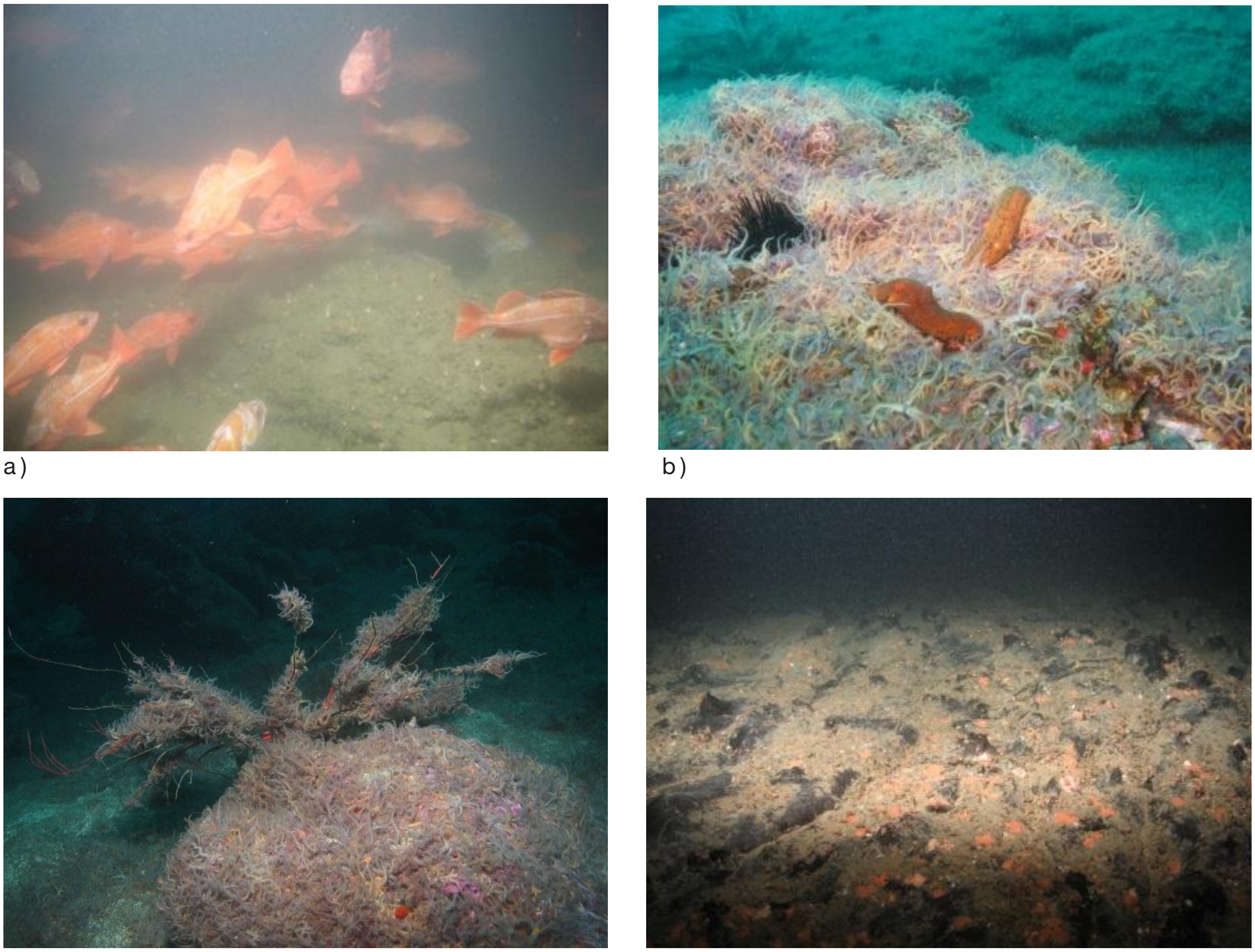


Figure 24. Map of ROV survey areas visited during 2014, historic survey sites (Department, MARE, and IfAME), and sites planned for 2015–16.

ond deployment surveyed the remainder of the south coast region from Point Dume to San Diego, including sites at Santa Barbara and Catalina Islands. In September and October 2014, a third deployment surveyed deep habitat within the north coast MPA region from Crescent City to Albion. Throughout all 2014 ROV surveys, additional sites outside MPAs were also visited. These sites allow the Department to further expand on ROV data for habitat characterization and species distributions, while also providing reference sites to allow comparisons to MPA sites over time (fig. 24).

Surveys completed in 2014 collected video and still imagery from 81 distinct sites. Twenty MPAs were visited including eleven state marine reserves (SMRs) and nine state marine conservation areas (SMCAs), two of which are designated as no-take. Over 200 km of video strip transects were performed resulting in 108 hours of video. Along these transects over 15,000 high resolution still



a)
b)
c)
d)

Figure 25. Selected photos taken during surveys of the South Coast MPA region: a) vermilion and copper rockfish (*Sebastes miniatus, S. caurinus*) aggregations at Campus Point SMCA, b) warty sea cucumbers (*Parastichopus parvimensis*) at Anacapa Island SMR, c) brittle stars and dying gorgonian coral at Anacapa SMR, and d) natural tar deposits at Point Conception SMR.

images were captured. At the date of this writing much of this imagery is still being processed for habitat classification, species identification, and spatial referencing.

The first two deployments of 2014 revealed interesting features of southern California MPAs. In Point Conception SMR, areas that were thought to be rocky habitat (as characterized by the CSMP) were found to be natural tar deposits (fig. 25d). Subsequent examination of the ROV imagery and bathymetric maps indicate that these tar deposits (also called tar mounds or tar volcanoes) may cover over 3 km^2 of seafloor within and near the SMR. Scattered throughout these tar mounds, small areas of less viscous tar were observed oozing from the seafloor along with bubbles of methane gas. Fish and invertebrates were less abundant in and around these deposits and biodiversity appears to be lower compared to nearby sites with rocky habitat.

Dense aggregations of rockfish, predominantly vermillion, copper, and flag rockfish (*Sebastes miniatus*, *S. carinus*, and *S. rubrivinctus,* respectively) were observed at several locations inside and outside of Campus Point SMCA and Point Conception SMR (fig. 25a). We suspect these aggregations may be spawning related as multiple fish were observed with bulging abdomens which may indicate gravid females.

An undocumented bed of geoduck clams (*Panopea generosa*) was discovered inside Naples SMCA. Using the location identified by the ROV, Department divers later confirmed this by collecting geoducks from the area and other nearby areas. A handful of locations in southern California waters were known to have beds of subtidal geoduck clams and recent explorations by Department divers continue to find more locations. This bed is one of the first documented on the mainland coast and appears to extend deeper (>40 m) and contains densities higher than beds observed in other areas.

A portion of the first southern California deployment was focused on exploring areas of sea cucumber trawl

TABLE 7
Preliminary densitities (number of individuals/100 m^2 of overall ROV survey transect area without taking into account habitat type) of giant red and warty sea cucumbers (*Parastichopus californicus* and *P. parvimensis*) observed at Anacapa Island, mainland sites (Campus Point and Santa Barbara), and trawl ground sites. No surveys were performed in study area and depth combinations without values.

Study Area—Species	Density (Number of Individuals / 100 m^2)										
Anacapa Is.—Warty	16.4	5.5	4	0.7	0	0	0	0			
Anacapa Is.—Giant Red	0	0	0	0	0.3	4.6	9.4	1.7			
Mainland—Giant Red	0	0.1	0.4	0.7	0.8	19.3	6	2.3			
Trawl Grounds—Giant Red									1.9	0.1	0.3
Depth Range (meters)	42297	20–30	30–40	40–50	50–60	60–70	70–80	80–90	90–100	100–110	110–120

grounds to examine densities and habitat of the giant red sea cucumber (*Parastichopus californicus*) in areas where there is high fishery effort. Giant red sea cucumbers were observed in high densities in Campus Point SMCA and in deep areas of Anacapa SMR (table 7). Densities in the deeper (90–120 m) trawled areas were lower than in the mainland sites and deep (40–80 m) portions of Anacapa. Rocky habitats in shallower waters of Anacapa Island sites were also surveyed for the warty sea cucumber, *P. parvimensis* (fig. 25b), which is the target of a commercial dive fishery. Warty sea cucumbers were found in high densities in the shallower (10–40 m) areas of the Anacapa Island SMR and SMCA. These surveys documented sea cucumber densities during the winter period which is generally a period of very low catch rates for the trawl and dive fisheries. These surveys are the first to try to document seasonal changes of abundance in deep areas (40–100 m) of MPAs where abundance is not affected by fishing. Distribution and abundance data collected on these commercially fished sea cucumbers are providing much needed information that will aid the Department's management of these expanding and valuable fisheries.

In and around the Anacapa SMR and SMCA dense beds of brittle stars (Ophiouroids) cover vast areas of sandy and rocky habitats forming mats up to 10 cm thick over the substrate in depths from roughly 15–40 m. A noticeable increase in area covered and density was observed in the January surveys compared to Department surveys in 2004–09. In the same areas many gorgonian corals appear to be dead or dying compared to what was seen in previous surveys (fig. 25c). The Department is working with MARE to further investigate these findings and quantify the increase of brittle stars and decrease of gorgonian corals.

The second deployment in southern California looked at mainland areas between San Diego and Point Dume as well as sites at Santa Catalina Island and Santa Barbara Island. Some of these sites targeted low-relief, sparse rocky areas that are surrounded by vast areas of sandy habitat along the mainland coast. Although scattered across large areas, these low-relief habitat patches may be important to fish populations in nearshore waters of southern California where rocky habitat is less prominent than in central and northern California.

Rockfish abundance and size was greater in north coast areas than southern California. Juvenile and adult lingcod (*Ophiodon elongates*) were abundant in both north and south surveys, although increased size and abundance was evident in the north (fig. 26b). Patchy distributions of fish were observed with some areas surprisingly devoid of common species. This patchiness was most common in areas with large, expansive low-relief, rocky reef areas. The north coast's complex and dynamic habitats that are swept by strong ocean currents, large waves, and receive increased sedimentation from rivers, may be influencing these patchy distributions. For example, greater fish abundance and more invertebrates were observed on the northern side of Reading Rock offshore of Orick, (fig. 26b). Inside Reading Rock SMR, on the south side of the actual sea stack, very few fish and sparse invertebrate growth was observed in rocky habitats covered with fine sediment (fig. 26a). River mouths adjacent to Reading Rock (Klamath River and Redwood Creek) deposit large volumes of sediment into the surrounding waters during winter storms. Local winds and currents may be washing away this sediment from the north side of Reading Rock creating the differences observed. Similar areas of sediment impacted reefs were observed at sites around Point Saint George Reef and Crescent City.

The Department's efforts compliment other deep water ROV survey efforts in California waters using the same or similar equipment and methods. Researchers at MARE and Institute for Applied Marine Ecology (IfAME) at California State University, Monterey Bay collaborated to examine the deep habitats of several MPAs as part of the baseline monitoring projects in the north central (2010–11) and south coast (2011–12) MPA regions. The current Department survey builds off these surveys and fills in data gaps by visiting MPAs and outside reference areas that have not been surveyed, as well as revisiting some MARE/IfAME sites.

In the south coast, Department surveys coincided with a MARE-led project focused on revisiting the Channel

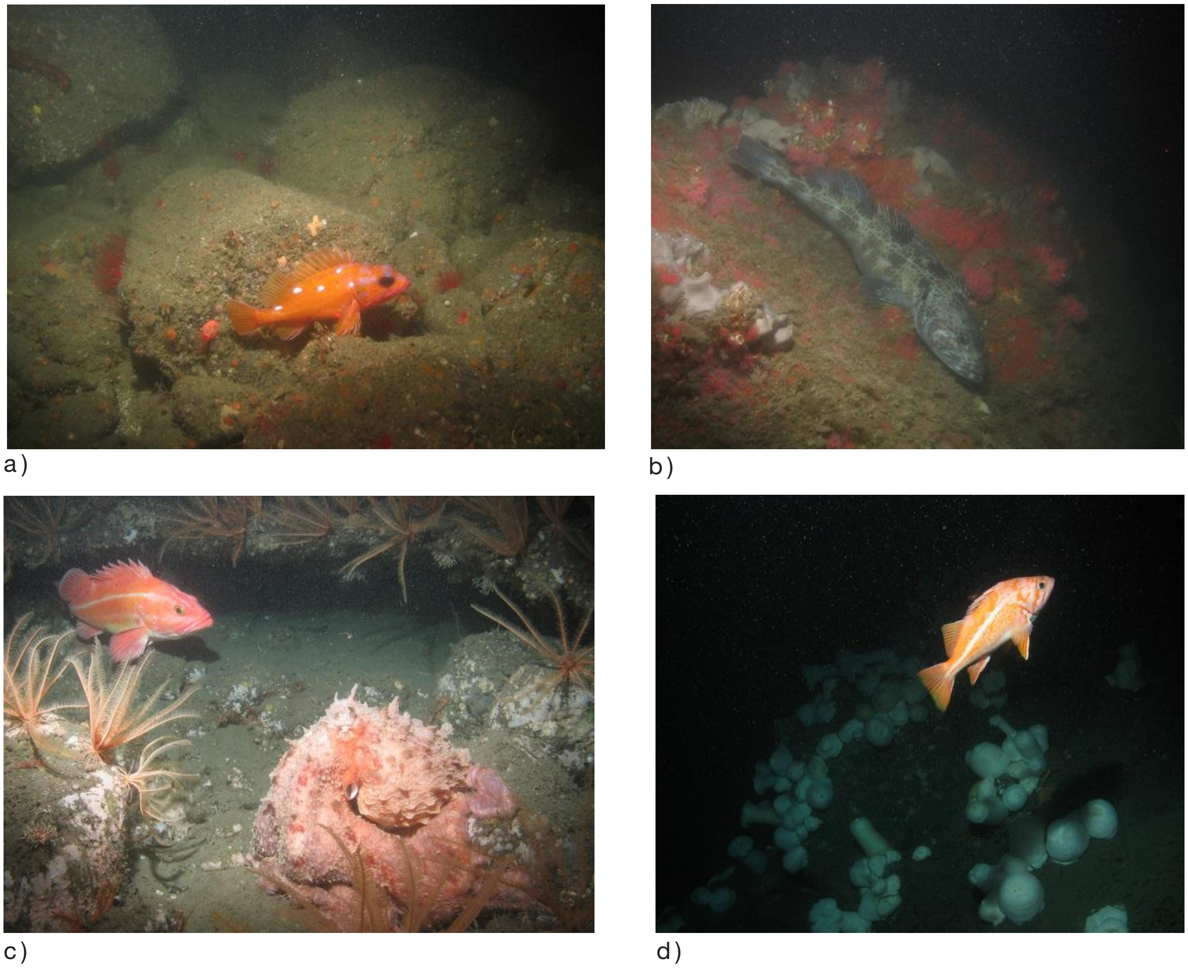


Figure 26. Selected photos taken during surveys of the North Coast MPA region: a) rosy rockfish (*Sebastes rosaceus*) in sediment impacted rocky habitat of Reading Rock SMR, b) lingcod (*Ophiodon elongates*) in rocky habitat less impacted by sediment outside of Reading Rock SMR, c) yelloweye rockfish (*Sebastes ruberrimus*) and giant Pacific octopus (*Enteroctopus dofleini*) at Sea Lion Gulch SMR, and d) a canary rockfish (*Sebastes pinniger*) at Sea Lion Gulch SMR.

Islands sites previously surveyed from 2004-09. These surveys are looking for potential ecological changes that arose 10 years after MPA implementation. Similarly, in 2014 the Department combined its statewide survey project with MAREs north coast MPA baseline project. During this four week long joint research cruise aboard the RV *Miss Linda*, MARE and the Department each visited four MPAs completing 52 km and 58 km of transects, respectively. Additionally, the Department surveyed another seven locations within the region, focusing on prominent rocky habitat areas. This collaborative partnership provided much greater coverage of deep water habitats than was possible in any of the previous regional baseline monitoring programs.

In 2015 and 2016, researchers will revisit MPAs in the north central coast MPA region where both MARE/IfAME and the Department surveyed in 2009–11. Similarly, researchers will revisit sites in the central coast region, originally surveyed by the Department in 2007–09, and fill in data gaps while visiting additional MPAs and reference sites that were not part of the first surveys. When complete this effort will result in unprecedented coverage of nearshore deep water habitats across the entire coastline of California (fig. 24).

After completion of data processing and summary analysis, technical reports of each ROV deployment will be made available. Each report will summarize the abundance of fish and invertebrates, and will provide a characterization of habitats and stereographic sizing of select fish species. An in-depth analysis of the statewide data set by Department scientists may include investigations on distributions of managed species inside and outside MPAs, size structure of select fish species, descriptions of unexplored deep water habitats, and other findings that emerge from this extensive data set. Particular attention has been placed on directing survey effort both inside and outside MPAs, and in rockfish conservation areas where rocky habitats important to the overfished yelloweye and canary rockfish (*Sebastes ruberrimus* and *S. pinniger*) are found (figs. 26c–26d). Analysis of survey data will examine distribution, habitat preference, and size structure of these protected species. Analyses will also focus on areas within the north coast region where frequent encounters of these protected species by recreational anglers impose restrictive fishing seasons, depth restrictions and catch limits. Department scientists are also exploring collaborative partnerships to analyze the extensive data set that will result from these surveys. The data sets will be made available to researchers, and will likely provide opportunities to study many species of fish and invertebrates in relation to MPA effectiveness and fishery management.

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STATE OF THE CALIFORNIA CURRENT 2014–15: IMPACTS OF THE WARM-WATER "BLOB"

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ABSTRACT

In 2014, the California Current (~28°–48°N) saw average, or below average, coastal upwelling and relatively low productivity in most locations, except from 38°–43°N during June and July. Chlorophyll-*a* levels were low throughout spring and summer at most locations, except in a small region around 39°N. Catches of juvenile rockfish (an indicator of upwelling-related fish species) remained high throughout the area surveyed (32°–43°N). In the fall of 2014, as upwelling ceased, many locations saw an unprecedented increase in sea surface temperatures (anomalies as large as 4°C), particularly at 45°N due to the coastal intrusion of an extremely anomalous pool of warm water. This warm surface anomaly had been building offshore in the Gulf of Alaska since the fall of 2013, and has been referred to as the "blob." Values of the Pacific Decadal Oscillation index (PDO) continued to climb during 2014, indicative of the increase in warm coastal surface waters, whereas the North Pacific Gyre Oscillation index (NPGO) saw a slight rebound to more neutral values (indicative of average productivity levels) during 2014. During spring 2015, the upwelling index was slightly higher than average for locations in the central and northern region, but remained below average at latitudes south of 35°N. Chlorophyll *a* levels were slightly higher than average in ~0.5° latitude patches north of 35°N, whereas productivity and phytoplankton biomass were low south of Pt. Conception. Catches of rockfish remained high along most of the coast, however, market squid remained high only

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[1]Details on sampling protocols are available in previous reports and at http://www.nwfsc.noaa.gov/research/divisions/fe/estuarine/oeip/ka-hydrography-zoo-ichthyoplankton.cfm.

within the central coast (36°–38°N), and euphausiid abundance decreased everywhere, as compared to the previous year. Sardine and anchovy were nearly absent from the southern portion of the California Current system (CCS), whereas their larvae were found off the coast of Oregon and Washington during winter for the first time in many years. Waters warmed dramatically in the southern California region due to a change in wind patterns similar to that giving rise to the blob in the broader northeast Pacific. For most of the coast, there were intrusions of species never found before or found at much higher abundances than usual, including fish, crustaceans, tunicates and other gelatinous zooplankton, along with other species often indicative of an El Niño. Thus species richness was high in many areas given the close juxtaposition of coastal upwelling-related species with the offshore warm-water intrusive or El Niño-typical taxa. Thus the California Current by 2015 appears to have transitioned to a very different state than previous observations.

INTRODUCTION

This report reviews the oceanographic and ecosystem responses of the California Current system (CCS) between spring 2014 and summer of 2015. Biological and hydrographic data from a number of academic, private, and government institutions have been consolidated and described in the context of historical data (fig. 1). The various institutions have provided data and interpretations of the data in response to an open solicitation for contributions; these contributions are acknowledged in the author list. These data are summarized and synthesized here, in the spirit of providing a broader description of the present condition of the CCS. All data are distilled from complex sampling programs covering multiple spatial and temporal scales into simple figures that may not convey the full complexity of the region. As a consequence, we focus on the findings of the data and limit our descriptions of the methodology to only that which is required for interpretation. More complete descriptions of the data and methodologies can be found through links to the individual survey programs. The survey designs are dissimilar and each has unique limitations restricting a common interpretation within the CCS. Therefore, this report should be considered a first examination for instigating more focused exploration of potential drivers of the ecosystem dynamics.

This report focuses on data highlighting the conditions during 2014–summer 2015, with a particular emphasis on the conditions associated with several offshore regions of anomalously warm water, the northernmost commonly referred to as the blob (Bond et al. 2015). Similar to last year's report, we have moved some of the physical supporting data from this document to an online supplement (www.calcofi.org/ccpublications/state-of-the-california-current-live-supplement.html). The goal is to create a "live" State of the California Current (SOTCC) web page resource, where information can be rapidly obtained for the most recent, up-to-date state of the CCS. Thus, several long-term time series of physical and biological data that have traditionally been found within this document have been replaced by a table stating only their current state, along with a link to the appropriate web page. As in past reports, we begin with an analysis of large-scale climate modes and upwelling conditions in the California Current. Following, the various observational data sampling programs are reviewed to highlight the links between ecosystem structure, processes, and climate. Lastly, a short discussion of the most recent conditions within the CCS and the impacts of the blob are discussed.

TABLE 1
List of CCS indices, their current status, and link to live supplement (e.g., S1 = Supplement Figure 1; www.calcofi.org/ccpublications/state-of-the-california-current-live-supplement.html).

Index	Current State	Trend	Implication	Link
PDO	Positive	Increasing	Warming	S1
NPGO	Negative	Decreasing	Low Productivity	S1
ENSO (MEI)	Positive	Increasing	El Niño	S1
Upwelling Anomaly	Positive	Neutral	Moderately Productive in the North	Figure 2, S2
Cumulative Upwelling	Neutral	Neutral	Moderately Productive to the North	Figure 3, S3
SST Anomaly	Positive	Increasing	Warm Surface Waters	Figure 4,7, S4, S5, 40
Wind Anomaly	Anti-Cyclonic	Increasing Anti-Cyclonic	Warm Coastal Surface Waters	Figure 4, S4
Temperature-Salinity, CalCOFI	Warmer and Saltier at N Coastal, Surface	NA	Change in Transport	S7
Mixed-Layer Salinity, CalCOFI	Positive Anomaly	Decreasing	NA	Figure 11
Mixed-Layer NO_3, CalCOFI	Negative Anomaly	Neutral	Decreased Productivity	Figure 12
Nitricline Depth, CalCOFI	Negative Anomaly	Decreasing	Decreased Productivity	Figure 12
Integrated Chlorophyll *a*, CalCOFI	Negative Anomaly	Increasing	Decreased Productivity	Figure 12
Chlorophyll *a* Profiles, CalCOFI	Low in Surface waters	NA	Decreased Productivity	S8
Chlorophyll *a*	Patchy	Increasing	Low to Mean Productivity	Figure 5

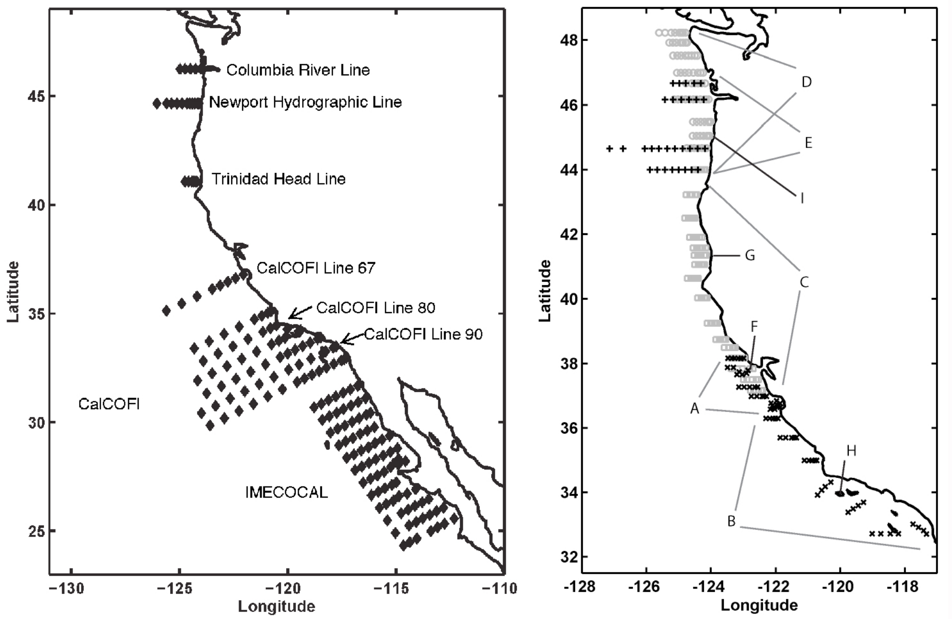

Figure 1. Left: Station maps for surveys that were conducted multiple times per year during different seasons to provide year-round observations in the Califor¬nia Current system. The CalCOFI survey (including CalCOFI Line 67) was occupied quarterly; the spring CalCOFI survey grid extends just north of San Francisco. The IMECOCAL survey is conducted quarterly or semiannually. The Newport Hydrographic Line was occupied biweekly. The Trinidad Head Line was occupied at biweekly to monthly intervals. Right: Location of annual or seasonal surveys, including locations of studies on higher trophic levels, from which data was included in this report. Different symbols are used to help differentiate the extent of overlapping surveys. A. SWFSC Fisheries Ecology Division (FED) midwater trawl survey core region (May–June) B. SWFSC FED midwater trawl survey south region (May–June). C. SWFSC FED salmon survey (June and September) (grey squares). D. NWFSC salmon survey (May, June, and September). E. NOAA/BPA pelagic rope trawl survey (May through September). F. Southeast Farallon Island. G. Castle Rock. H. San Miguel Island. I. Yaquina Head Outstanding Natural Area.

NORTH PACIFIC CLIMATE INDICES

The warm phase in the North Pacific that started in the beginning of 2014 continued through the summer of 2015 (Supplemental fig. S1). The Pacific Decadal Oscillation index (PDO; Mantua et al. 1997) experienced the highest positive value in December 2014 since June 1997. From January 2014 to June 2015 the PDO values were positive—the longest sustained period of positive values since the summer of 2002. The positive values of the PDO can be attributed to the excessively warm sea surface temperature (SST) anomalies experienced first in the northeast Pacific in winter of 2013, which then expanded along the west coast of North America to Baja California, Mexico, during 2014 and 2015 (Bond et al. 2015). The North Pacific Gyre Oscillation (NPGO; Di Lorenzo et al. 2008) index was positive from April 2007 through October 2013, indicating strong circulation in the North Pacific Subtropical Gyre. At the end of 2013 the NPGO switched from the positive values experienced over the previous seven years to negative values. Except for small positive NPGO values in May, October, and November of 2014, the NPGO has remained in a negative state through the summer of 2015. As of June 2015 the multivariate El Niño Southern Oscillation (ENSO) index (MEI; Wolter and Timlin 1998) reached the largest positive value since the strong 1996–98 El Niño. Large positive values of the MEI indicate an El Niño event and NOAA's Climate Prediction Center (http://www.cpc.ncep.noaa.gov) advises that the current El Niño will continue into the winter of 2016.

Upwelling in the California Current

Monthly means of the daily upwelling index (Bakun 1973; Schwing et al. 1996) indicated strong upwelling for the entire year of 2013 especially north of 36°N (fig. 2). Upwelling in 2014 was near the long-term mean for all latitudes, except for a pulse of strong upwelling in June for latitudes between 36° and 42°N. The normal downwelling conditions that occur during the winter at the northern latitudes were reduced in January 2015 due to increased upwelling winds between 33° and 39°N (figs. 3, 4, and S5). For the rest of 2015 upwelling was slightly above the long-term mean for latitudes north of 33°N.

The cumulative upwelling index (CUI) is the cumulative sum of the daily upwelling index starting January 1 and ending on December 31. The CUI provides an estimate of the net influence of upwelling on ecosystem structure and productivity over the course of the year (Bograd et al. 2009). The highest values of

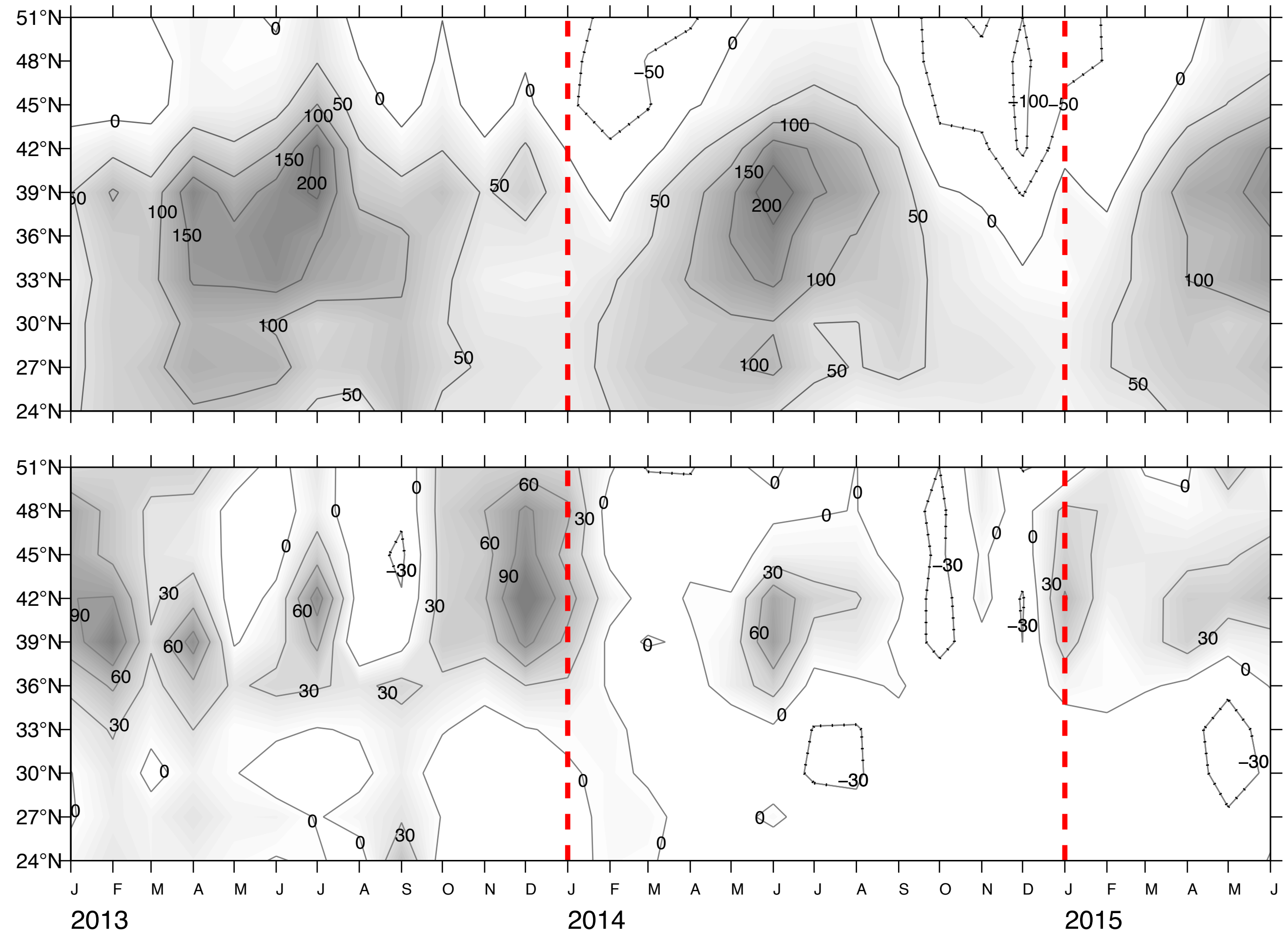

Figure 2. Monthly means of daily Bakun Upwelling Index (top) and anomalies (bottom) for January 2012–July 2015. Shaded areas denote positive (upwelling-favorable) values in upper panel, and positive anomalies (generally greater than normal upwelling) in lower panel. Anomalies are relative to 1967–2014 monthly means. Units are in m^3 s^{-1} per 100 km of coastline. Daily upwelling index data obtained from http://pfeg.noaa.gov/products/PFELData/upwell/daily.

the CUI for the entire record (1967–2015) occurred in 2013 for latitudes north of 39˚N. Upwelling during 2014 was near the long-term mean for the first half of the year (fig. 3). However, after June the CUI from 39 to 44˚N was higher than the long-term mean, but south of 33˚N the CUI was lower than the long-term mean. Through June 2015, the CUI has been near the long-term average for all latitudes except those between 42˚ and 48˚N. Upwelling winds for these latitudes increased and remained high starting at the beginning of February. Defining the spring transition as the date of the minimum CUI value in the first 151 days of the year it is evident from the strong upwelling in the late winter and early spring that the spring transition date occurred earlier in the year for locations in the north. For example, the spring transition at 42˚N was 32 days earlier than the climatological spring transition date of March 16.

North Pacific Climate Patterns

Basin-scale examinations of SST and surface wind vectors allow for the interpretation of the spatial evolution of climate patterns and wind forcing over the North Pacific related to trends in the basin-scale and upwelling indices (fig. S1 and fig. 4). SST anomaly values during July and December of 2014 were generally positive with the largest positive anomalies occurring in the Bering Sea, Gulf of Alaska, and along the west coast of North America down to Baja Mexico. This broad region of persistently high SST anomalies has been termed the blob (Bond et al. 2015), and has been associated with observations of unusual species distributions (described in the Regional Ecosystem Indicators section). The largest positive SST anomalies (over 4.5˚C) were located at the entrance of the Gulf of California during July 2014. During the summer and fall of 2014 negative SST anomalies occurred in the region of the Subarctic Frontal Zone, with values lower than –2.5˚C during July 2014. A cyclonic wind anomaly was associated with this region of negative SST values. Positive SST anomalies persisted into 2015 with large positive anomalies in the same locations as those in 2014, with the exclusion of the Bering Sea where the anoma-

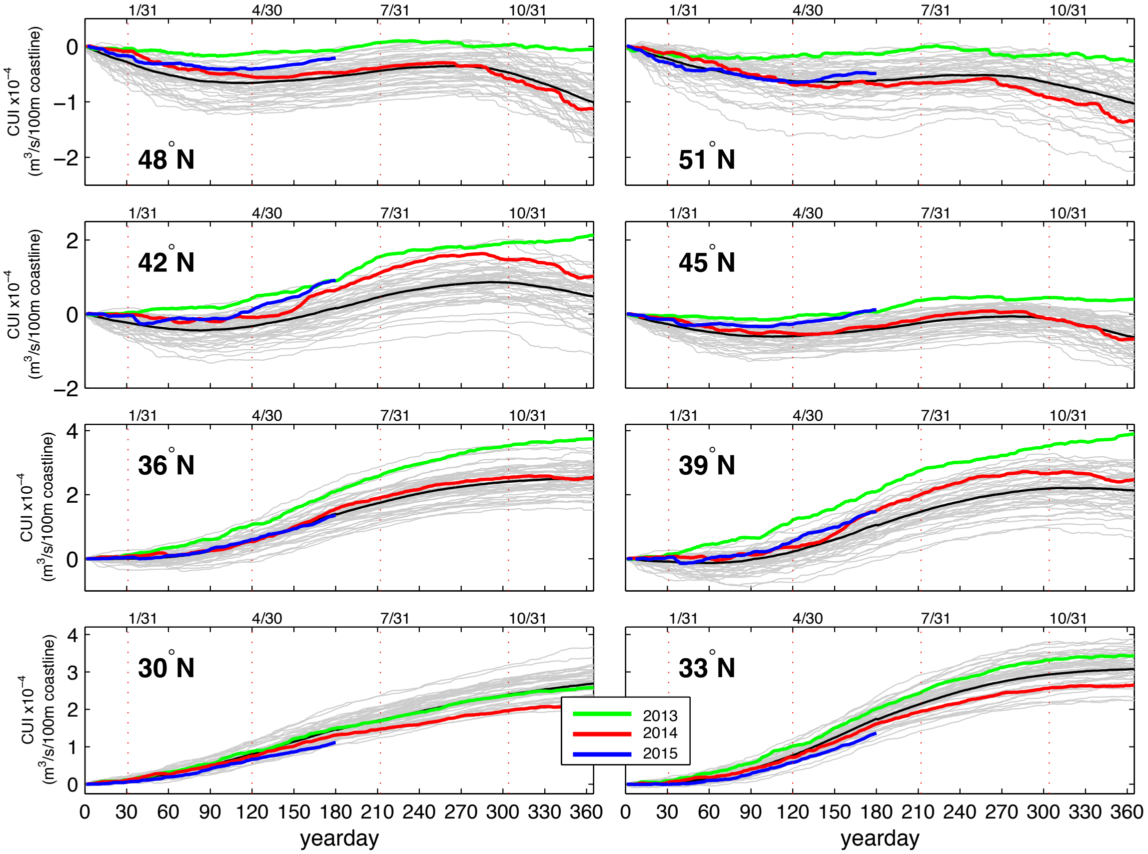

Figure 3. Cumulative upwelling index (CUI) from January 1 calculated from the daily Bakun Upwelling Index at locations along the West Coast of North America for 1967–2013 (grey lines), the mean value for the period 1967–2011 (black line), 2013 (green line), 2014 (red line), and 2015 (blue line). The red dashed vertical lines mark the end of January, April, July, and October.

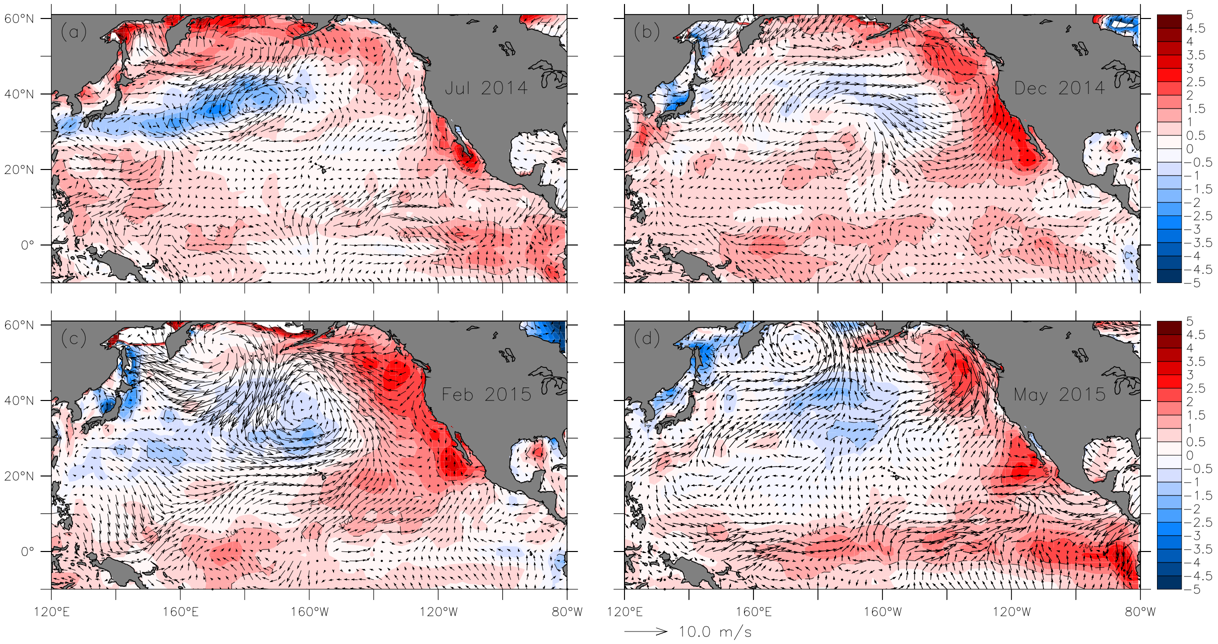

Figure 4. Anomalies of surface wind velocity and sea surface temperature (SST) in the North Pacific Ocean, July 2014, December 2014, February 2015, and May 2015. Arrows denote magnitude and direction of wind anomaly (scale arrow at bottom). Contours demote SST anomaly. Shading interval is 0.5°C and contour intervals of ±1 and 2°C are shown. Negative (cool) SST anomalies are shaded blue. Wind climatology period is 1968–96. SST climatology period is 1950–79. Both SST and wind data are from NCEP/NCAR Reanalysis and were obtained from http://www.esrl.noaa.gov.

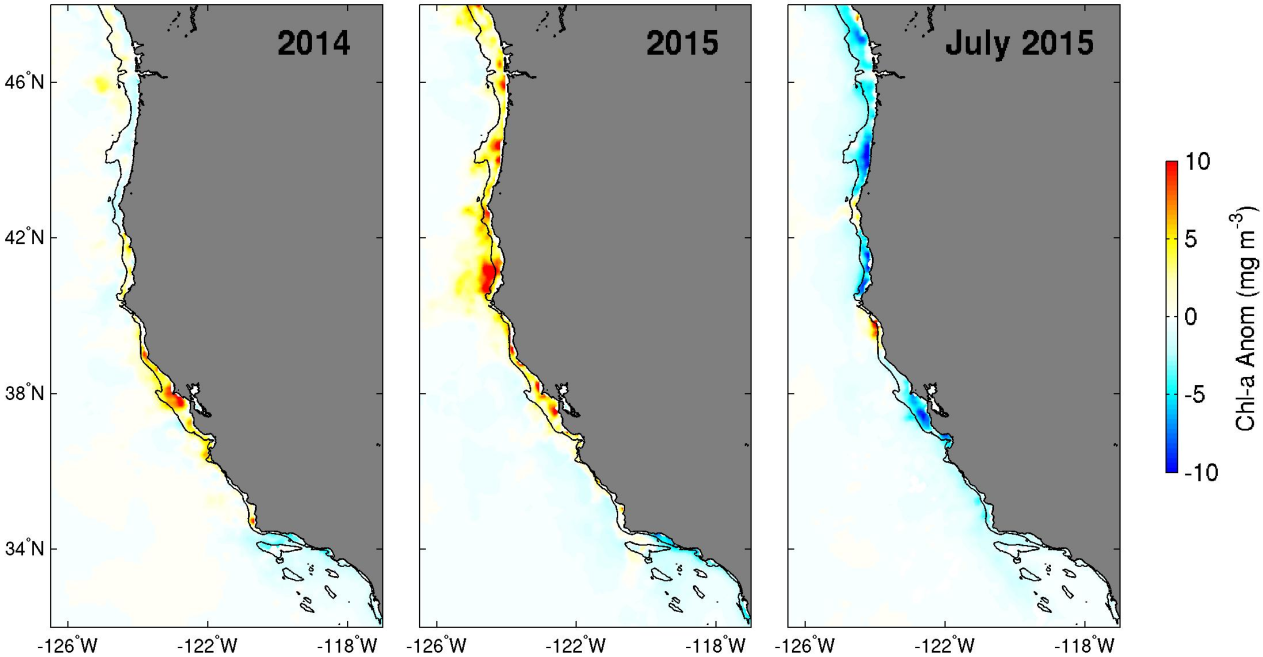

Figure 5. Chlorophyll *a* anomalies from Aqua MODIS for: spring (March–May) of 2014 (left panel), spring (March–May) of 2015 (center), and July 2015 (right panel). Monthly anomalies were averaged onto a 0.1˚ x 0.1˚ grid and the climatology was based on the time period from 2002-15. The data were obtained from http://coastwatch.pfel.noaa.gov/.

lies were considerably cooler, but still positive, by May 2015. While the SST anomalies throughout the CCS were extremely warm, the upwelling-favorable alongshore winds in the winter and spring of 2015 were unusually strong (fig. S5). In May 2015 these wind anomalies were the strongest in the north around Washington and Oregon, but the winds lessened in central and southern California. The wind anomalies in the western and central equatorial Pacific indicate strong winds blowing from the west to the east, which might be an indication of westerly wind bursts that could strengthen the current El Niño conditions (Hu et al. 2014).

Coastal Sea Surface Temperature

Daily SST as measured by National Data Buoy Center (NDBC) buoys showed unusually warm SST values from August 2014 to June 2015 for locations throughout the CCS (fig. S5 and fig. 40). The highest deviations from the climatological cycle happened in the late summer and fall of 2014, with some days having temperatures more than 4˚C above the long-term mean. Starting in the spring of 2015 the SST values "cooled," but they were still greater than the climatological mean with only a slight drop below for locations between Bodega Bay and Stonewall Bank. The meridional winds during the warm SST period were not unusually weak in magnitude or overly downwelling producing (+ values). The decrease in SST values seen in the central CCS during the spring of 2015 corresponded with an extended period of upwelling producing winds (– values).

Sea Surface Chlorophyll *a*

During spring 2015, sea surface chlorophyll *a* levels, as measured by remote sensing, were higher than average for most of the CCS, excluding the Southern California Bight (fig. 5), likely as a result of the favorable upwelling during this period as compared to the previous year. By summer 2015, sea surface chlorophyll *a* levels were anomalously low in most places, except for a few small patches along the central coast (centered near 38˚ and 42˚N; fig. 5), again reflecting the patterns seen in upwelling across the region.

REGIONAL ECOSYSTEM INDICATORS

Northern California Current: Oregon (Newport Hydrographic Line[1])

The winter of December 2013–March 2014 was quite mild with no large southwesterly storms, resulting in a lack of deep mixing. Bottom waters at midshelf (station NH-5) were colder than normal (fig. 6; second coldest December since the start of the time series in 1997). Beginning in spring of 2014, waters over the Oregon shelf were unusually warm and fresh, with temperatures comparable to those observed during the 1998 El Niño coupled with salinities comparable to those observed in 2003 (fig. 6).

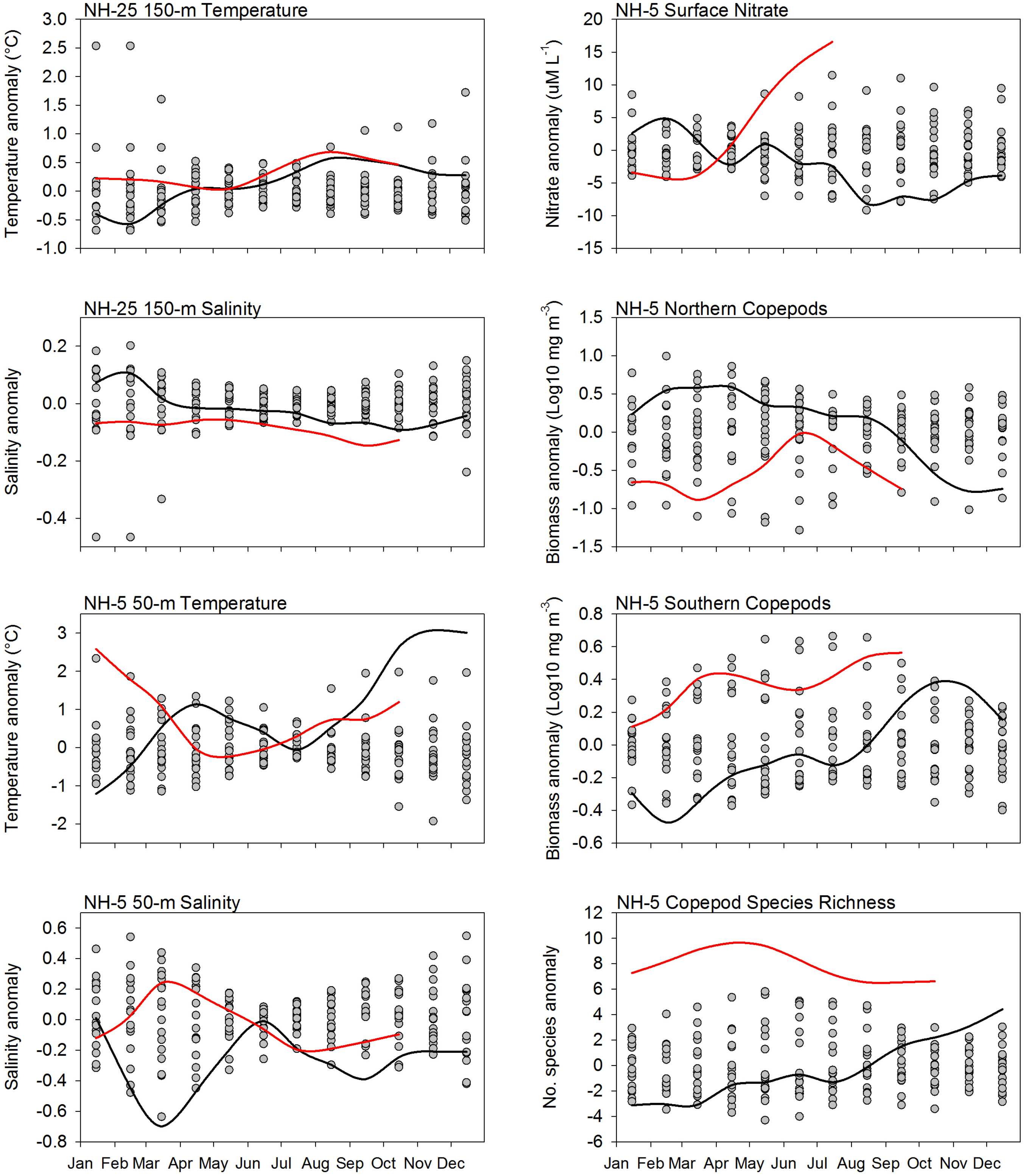

Figure 6. Time-series biophysical plots (Red line = 2015, Black line = 2014, dots = pervious years). Time series plots of local physical and biological anomalies from 1997–present at NH-25 (Latitude: 44.6517°N Longitude: 124.65°W) NH-5 (Latitude: 44.6517°N Longitude: 124.1770°W) along the Newport Hydrographic Line. Temperature and salinity from 150 m and 50 at NH-25 and NH-5 respectively, $NO_2 + NO_3$ from the surface, and copepod biomass and species richness anomalies are integrated over the upper 60 m. All data were smoothed with a 3-month running mean to remove high frequency variability.

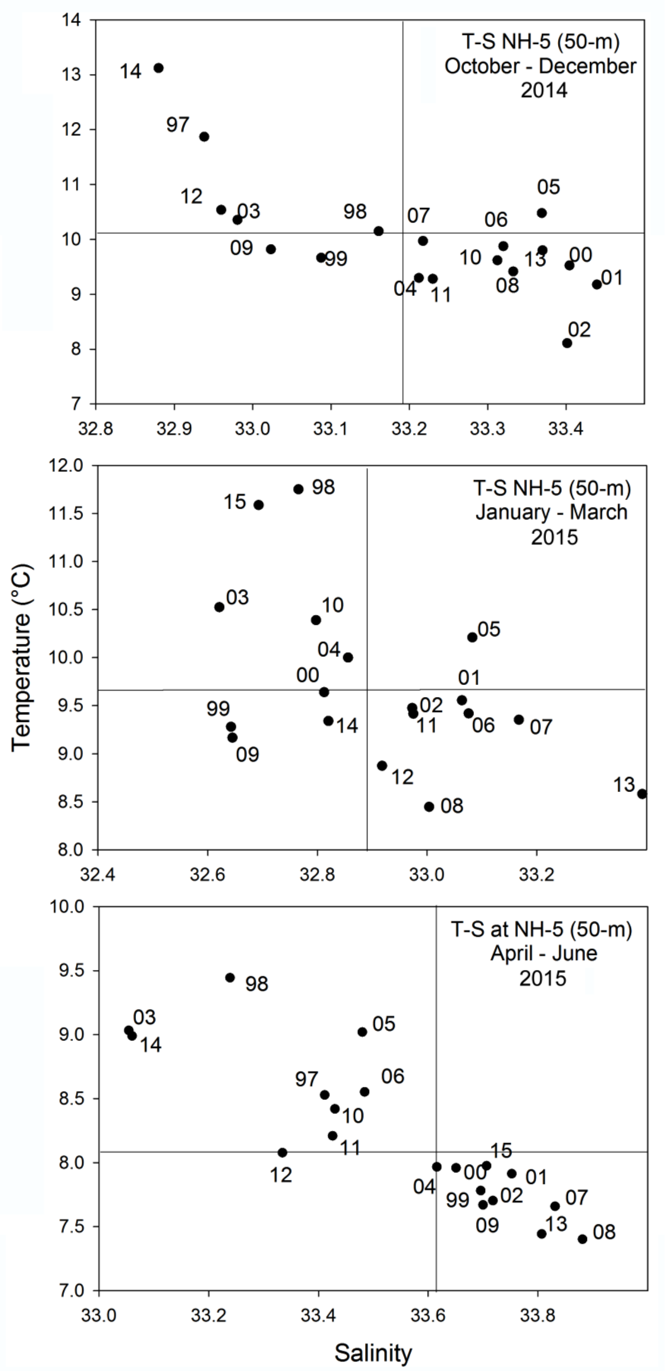

Figure 7. Seasonal mean temperature and salinity at 50 m depth at station NH-5 (Latitude: 44.6517°N Longitude: 124.1770°W) along the Newport Hydrographic Line for October through December 2014 (top panel), January through March 2015 (middle panel), and April through June (bottom panel). Note changes in scale on both temperature and salinity axes. Numbers next to points indicate year of observations.

Upwelling off Oregon was delayed in 2014 (spring transition per CUI on 10 May, or 26 days later than average), and ended 3 weeks earlier than average (20 September 2014), yet total upwelling during this shortened season was near average. As upwelling declined, unusually warm offshore waters rapidly arrived on the shelf, marked by a dramatic increase in SST (peak at 19.4°C, or 4.5°C above normal on 14 September at NDBC Buoy 46050; see fig. 40 for extended history at this location). These waters were warm, fresh, and nutrient-poor (figs. 6 and 7). Deep (50 m) waters on the shelf during the fall and into the winter (October through December, 2014) were the warmest and freshest observed over the past 20 years (comparable to the 1997–98 El Niño), yet deep (150-m) water on the slope during this period was only slightly warmer and fresher than average (fig. 7). This differs substantially from conditions during the 1997–98 El Niño when deep water on the shelf and slope was very warm and fresh (fig. 7).

During spring and summer of 2014, the biomass of northern copepods was moderately high and the biomass of southern copepods and the copepod species richness were relatively low (fig. 6). With the arrival of warm blob waters in late September, the copepod community immediately changed from a lipid-rich "cold water-/upwelling" assemblage to a lipid-poor "warm-water" assemblage, with concomitant decreases in the biomass of northern copepods and increases in the biomass of southern copepods and species richness. Copepod biomass anomalies are comparable to those observed during the 1997–98 El Niño, despite the stronger temperature and salinity anomalies observed in 2014–15. Copepod species richness, however, was the highest observed in the 20-year time series, far exceeding the number of species observed during the strong El Niño event in 1997–98. This increase in species richness reflects the occurrence of at least 17 copepod species that have not previously been (or only rarely) observed in the northern California Current, which is consistent with an unusual and distant source for the waters that arrived in late 2014.

Trinidad Head Line, Northern California

Conditions off northern California in early 2014 reflected a winter marked by weak but consistent northerly winds and relatively mild storm activity, followed by a transition to more intense upwelling-favorable winds that triggered a substantial (>10 µg chlorophyll *a* L^{-1}) phytoplankton bloom over the shelf in late spring to midsummer, peaking in June (fig. 8). Throughout much of 2014, bottom waters on the shelf were warm relative to conditions typically observed at a given time of year. By late summer and early fall, however, midshelf bottom waters were consistently warmer, fresher, and more oxygenated than had been previously reported. A second phytoplankton bloom was observed during late summer and early fall (September), as upwelling winds weakened and became more variable, and stratification increased over the shelf. The arrival of blob waters in the fall followed a transition to increasingly frequent southerly wind events and was marked by strong warm-

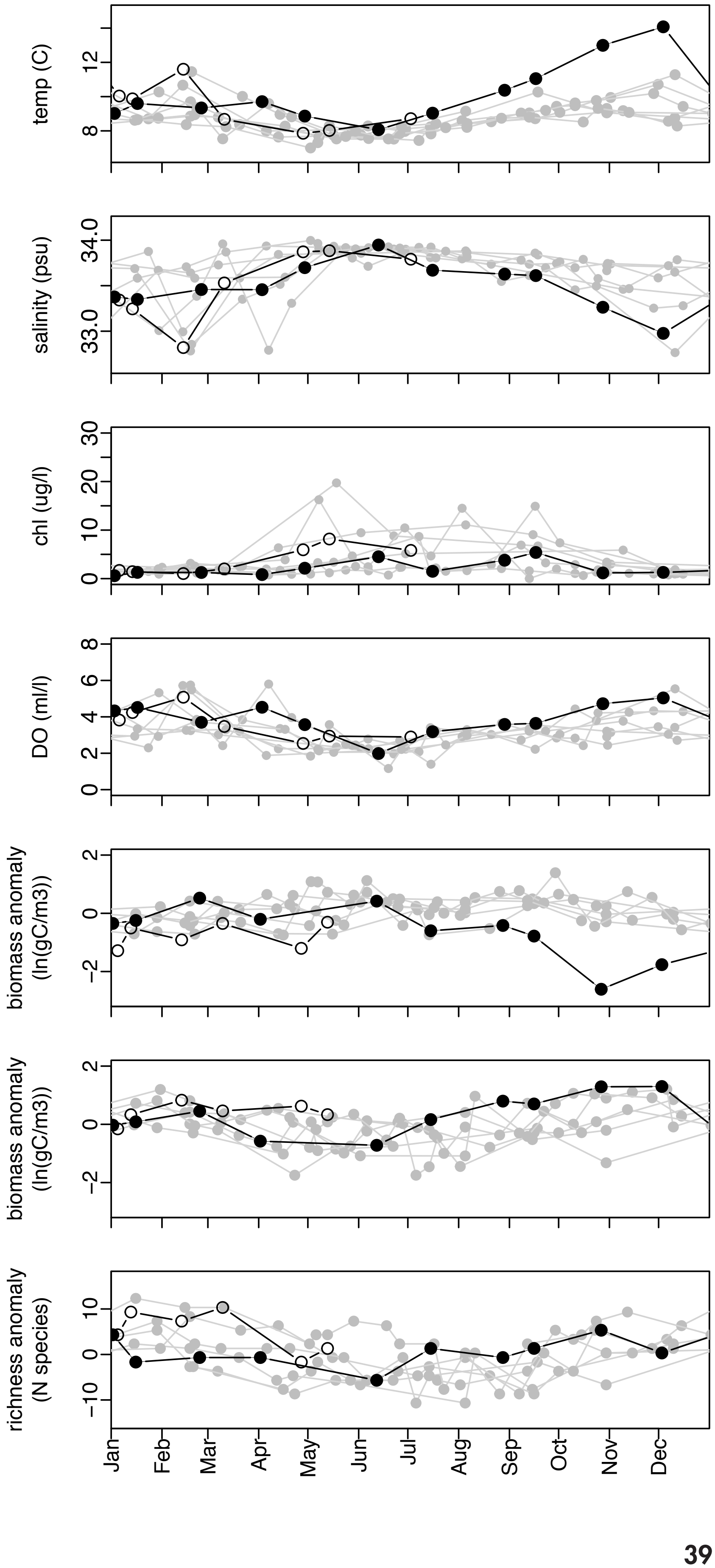

Figure 8. Hydrographic and ecosystem indicators at mid-shelf along the Trinidad Head Line (station TH02; 41°03.5'N, 124°16'W, 75 m depth). Panels from top to bottom show near-bottom (68 m) temperature, near-bottom (68 m) salinity, mean chlorophyll *a* concentration over the upper 30 meters of the water column, near-bottom (68 m) dissolved oxygen concentrations, biomass anomalies for northern copepod species, biomass anomalies for southern copepod species, and species richness anomalies. All assemblages are defined following Hooff and Peterson (2006), and all anomalies are calculated using means from the full time series (2006–15). For all plots, grey symbols indicate historical observations (2006–13), filled circles indicate observations during 2014, and unfilled symbols indicate observations in 2015.

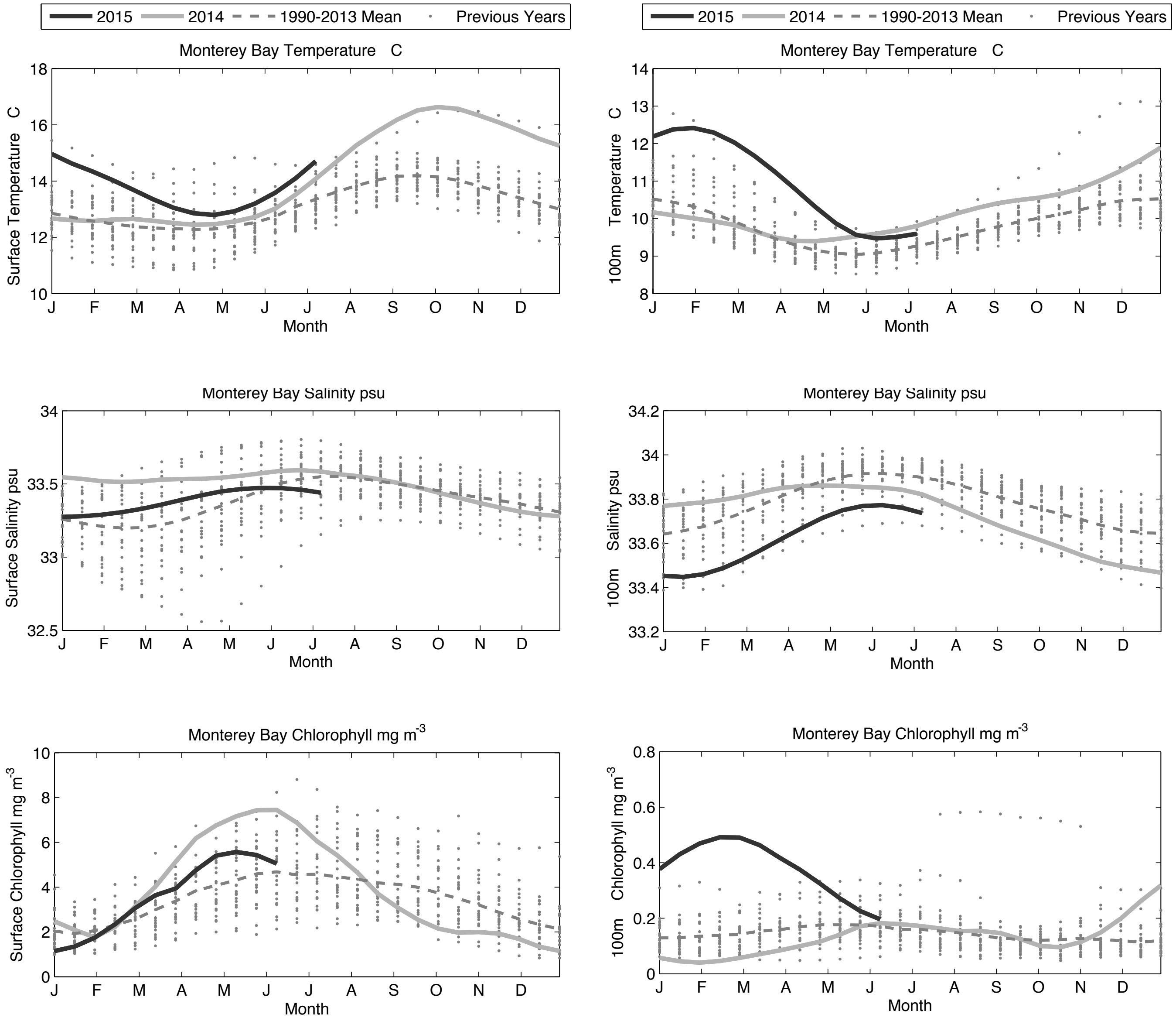

Figure 9. Temperature (top panels), salinity (middle panels) and chlorophyll *a* concentration (bottom panels) at the surface (left-hand column) and at 100 m (right-hand column) observed at the M1 mooring in Monterey Bay, CA.

ing over the shelf in the fall and the decline of the late summer bloom (fig. 8). Coastal waters responded to mild upwelling and storm events during early 2015, and more intense upwelling during spring and summer 2015, yet surface waters often remained relatively strongly stratified throughout the spring and summer. In spring 2015, there was a much stronger phytoplankton bloom (>17 μg chlorophyll *a* L^{-1}). Phytoplankton and water samples collected during spring 2015 confirmed a strong domoic acid event off northern California, and *Pseudo-nitzschia* sp. has remained common into summer 2015.

The copepod community observed off northern California experienced strong shifts in community composition related to changes in hydrographic conditions. Early in 2014, the biomass of copepods with northern biogeographical affinities was similar to past observations, but began to decline in July and dropped dramatically in fall 2014 (fig. 8). Biomass of southern copepods increased during the late summer and fall and remained consistently high through the end of 2014. This pattern of depressed biomass of northern copepods and elevated biomass of southern copepods has persisted through spring 2015. The decline of northern taxa is especially apparent when northern neritic species (including the normally abundant *Pseudocalanus mimus*) are considered separately (data not shown), with strong negative biomass anomalies for the nearshore neritic assemblage persisting through spring 2015. Copepod species richness has

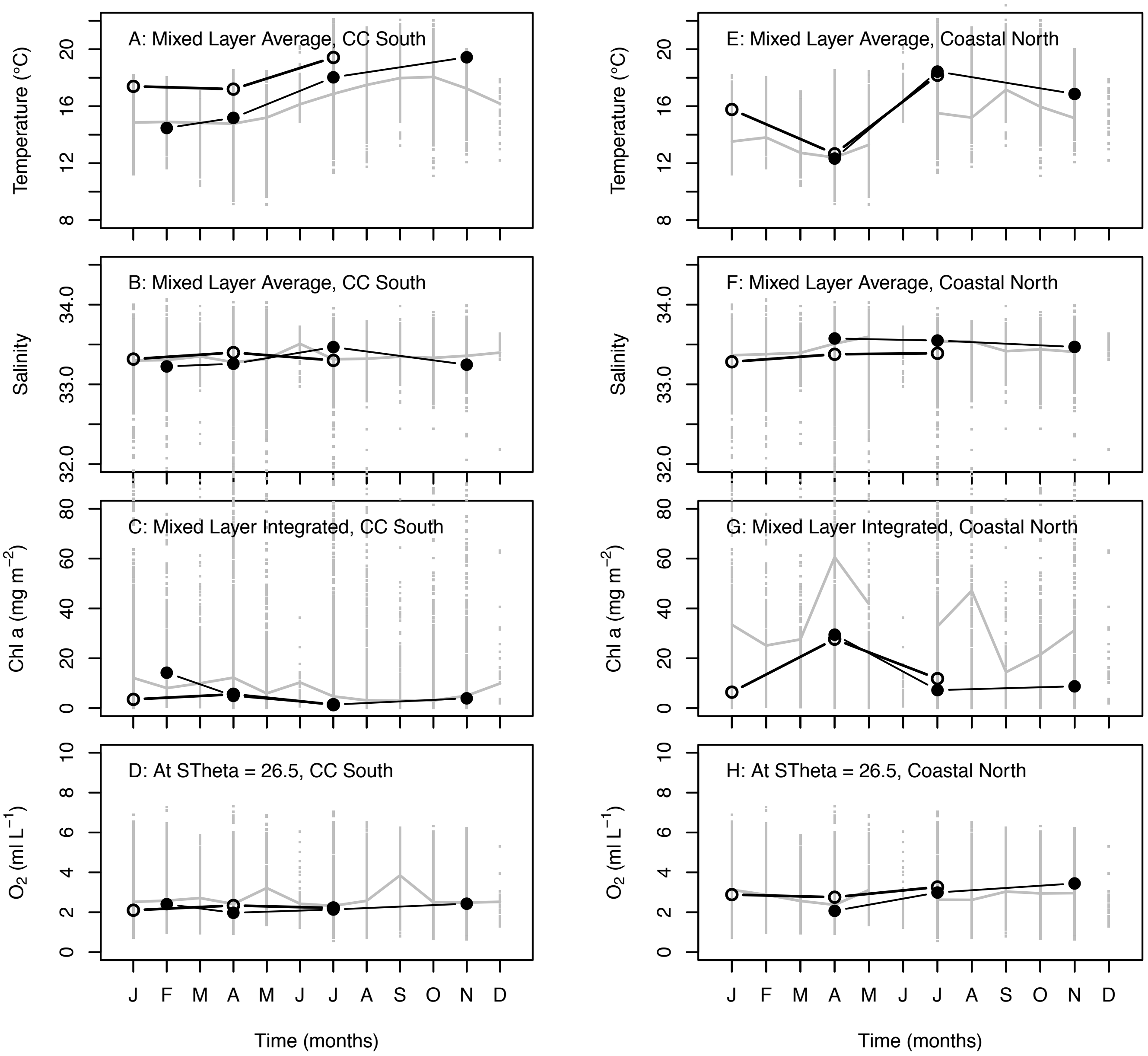

Figure 10. Average mixed layer temperature (A and E), average mixed layer salinity (B and F), integrated mixed layer chlorophyll *a* (C and G), and average O$_2$ concentration at the σ_θ 26.5 kg m^{-3} isopycnal, from the southern coastal region of the CalCOFI grid (CC south, left-hand column) and the north coastal region of the CalCOFI grid (coastal north, right-hand column). Grey dots show averages for individual cruises from 1984–2013, grey line shows climatological monthly average (1984–2013), line with open symbols shows 2015, and line with closed symbols is 2014. Note, the Feb 2014 cruise was cancelled partway through the cruise due to engine failure, thus there were no samples from the coastal north region.

been consistently high relative to previous years during summer and fall 2014, and again in early 2015 (fig. 8). During this period, several species of southern or offshore copepods have been observed for the first time in the Trinidad Head Line record. Similar patterns are observed in the euphausiid community along the Trinidad Head Line, with substantial declines in *Thysanoessa spinifera*, greater prevalence of offshore species, and the observation of several life history stages of *Euphausia recurva*, a euphausiid that typically occurs well to the south or offshore.

MBARI, M1 Mooring, Central California

Temperatures in Monterey Bay at the surface were some of the highest recorded during fall 2014 since 1990, whereas surface salinities remained near the climatological average during this time period (fig. 9). This contrasts with the rapid warming and freshening seen off Oregon due to the advective intrusion of the blob at that location. Chlorophyll *a* was high at the surface during spring 2014, but declined during the fall. 2015 saw a shift to a fairly different state than previously seen. Chlorophyll *a* values were as high as ever recorded in the subsurface during the spring, as were subsurface temperatures. However, salinity was also anomalously low, and temperatures anomalously high in the subsurface, suggesting at these depths, there was an intrusion of a different water mass. Surface properties during 2015 were similar to the climatological average.

CalCOFI Surveys, Southern California

The updates to this report are based on four cruises in July and November of 2014 and January and April of 2015. These cruises are part of the CalCOFI program (Ohman and Venrick 2003). Each cruise covers 66 stations off southern California (fig. 1) i.e., the CalCOFI domain, a region that encompasses the southern California Current (sCCS), the Southern California Bight (SCB) and, partially, the coastal upwelling region at and north of Pt. Conception and the edge of the North Pacific Gyre (CalCOFI Lines 90 & 93, Stations 100 to 120). At each station a CTD cast and various net tows are carried out. This report focuses on the hydrographic, chemical, and simple biological data derived from ~20 depths, between the surface and ~515 m, bottom depth permitting. Data from net tows are not available at the present time. For a by-month comparison among years (fig. 10), we divide up the CalCOFI domain following Wells et al. (2013). The first subregion "CC south" denotes the area landward of the main core of the California Current, south of Pt. Conception; essentially the Southern California Bight (CalCOFI lines 87–93, and stations 60–90). The second region "coastal north" denotes the nearshore, upwelling-dominated region from Pt. Conception north to Pt. San Luis (lines 77–80, and stations <60). The third region "edge of North Pacific Gyre" is to the south and offshore, influenced by the subtropical gyre (defined by lines 90–93, and stations 100–120). Within each of these regions, we compared cruise-averaged mixed-layer temperature, salinity, integrated chlorophyll *a*, and oxygen at the σ_θ 26.5 kg m^{-3} isopycnal versus their respective climatological monthly means (based on 1984–2013).

In 2014, within CC south, average mixed-layer (ML) temperatures and salinity were similar to the climatological monthly means (figs. 10A and B, S6), although ML temperatures increased in the fall cruise to >2˚C above the mean. ML temperatures were also higher (~ 2˚C) in the fall in 2014 in the coastal north region (fig. 10E). Integrated chlorophyll *a* in the CC south was similar to the mean during all cruises, except the early springtime (figs. 10C, S9). In contrast, chlorophyll *a* was anomalously low in the coastal north region during all of 2014, with values typically half their climatological value (fig. 10G). Oxygen at the σ_θ 26.5 kg m^{-3} isopycnal was also similar to the mean in both regions for all of 2014 and 2015 (fig. 10D).

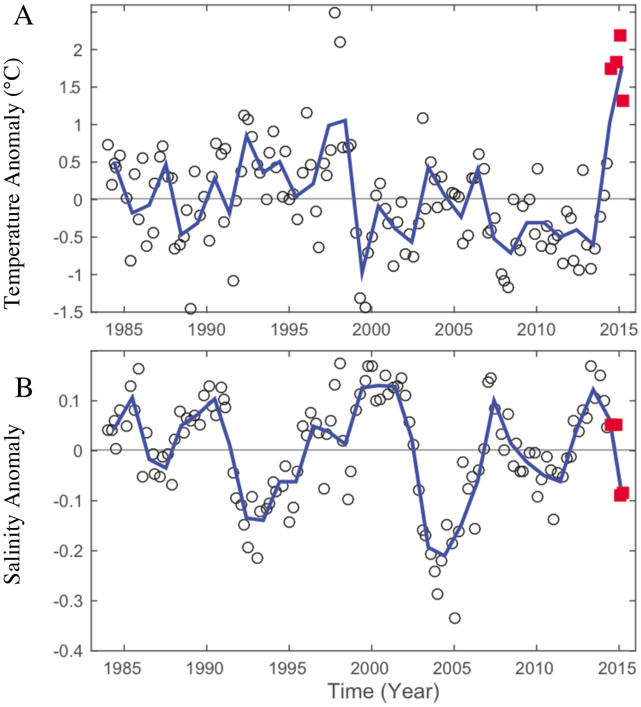

Figure 11. Cruise averages of property anomalies for the mixed layer (ML) of the CalCOFI 66 station standard grid for 1984 to 2015. A: ML temperature; B: ML salinity. Data from individual CalCOFI cruises are plotted as open circles; data from the four most recent cruises, 201407 to 201504, are plotted as solid red squares. Thin solid blue lines represent annual averages, grey horizontal lines the climatological mean, which is zero in the case of anomalies. Anomalies are based on the 1984 to 2012 time period.

In 2015, within the CC south region, ML temperatures were on average >3˚C warmer than the climatological mean from winter through spring (fig. 10A). ML temperatures in the north coastal region were warmer than average in the winter, and summer, but not the spring cruise, as there was some limited upwelling in that region during that time (figs. 10E and 2). Chlorophyll *a* was again approximately half that of the climatological mean for both the south and north coastal regions during the 2015 cruises (figs. 10C and G).

For time series analysis (figs. 11 and 12), observations were averaged over all 66 stations covered during a cruise. Anomalies (fig. 11) were calculated comparing these averages with respect to the 1984–2012 time period. The mixed-layer depth is calculated using a density criterion and is set either to 10 m or to the half-way point between the two sampling depths where the sigma-theta gradient first reaches values larger than 0.001 kg m^{-3} per meter, whichever is larger. The nitracline depth is defined as the depth where concentrations of nitrate reach values of 1 µM, calculated from measurements at discrete depths using linear interpolation. Methods used to collect samples and analyses carried out on these samples are described in detail at calcofi.org/methods. Regressions of time series were

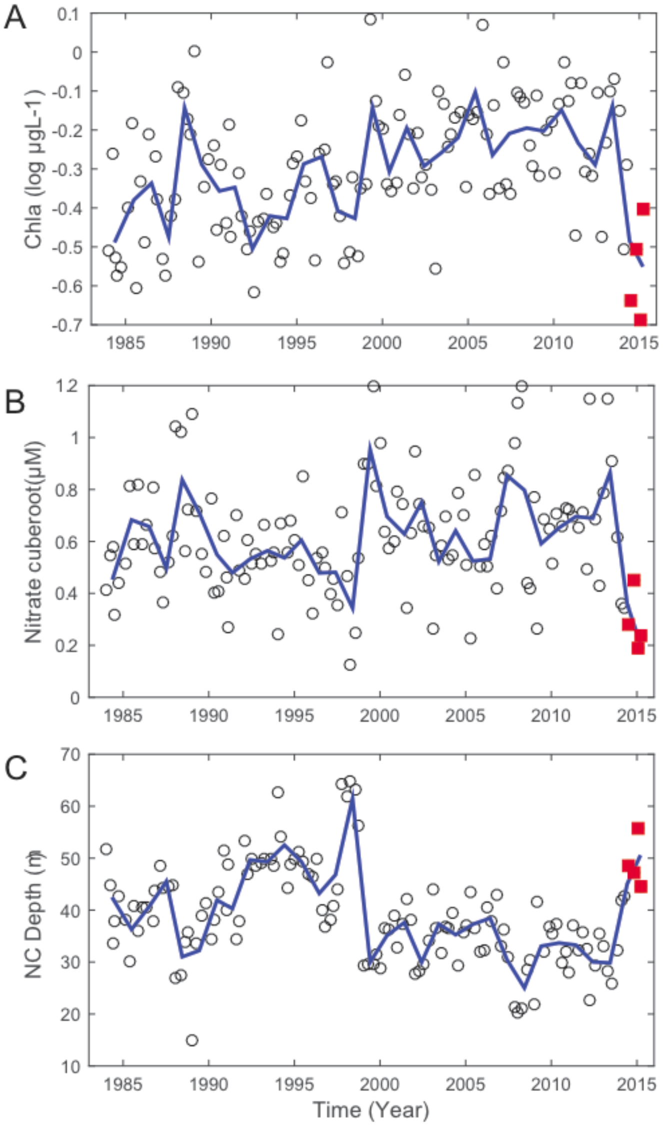

Figure 12. Cruise averages of properties for a depth of 10 m for the CalCOFI standard grid. A: The log10 of chlorophyll *a*, B: the cube root of nitrate, and C: nitracline depth. Data are derived and plotted as described for Fig. 11.

carried out in MATLAB's System Identification toolbox, which follows Ljung (1999).

Over the last 12 months ML temperatures off southern California were as high as those observed during the 1998 El Niño (fig. 11A), a clear expression of the Southern California Warm Anomaly (SCWA; geographically distinct from the NE Pacific blob). Significant near-surface (10 m) warm relative anomalies (which are standardized anomalies and therefore dimensionless) were first observed during the spring of 2014 along the continental shelf break (figs. 36A and B), on the order of 1.5 standard deviations larger than the long-term mean. The winter 2014 cruise did not cover the whole CalCOFI grid, only Lines 93 and 90. Relative temperature anomalies along Line 90 (see below) had values of 0.8 units during this cruise, compared to values of 1.7 during the spring cruise. The relative anomalies intensified in the summer of 2014 in the SCB and were particularly strong SW off Pt. Conception (fig. 36C), reaching values of 4 units. It is unlikely that these high anomalies are entirely due to the in situ warming of the surface layer. Upwelling during July and August of 2014 was unusually low at 33°N (fig. 2); thus the "absence" of cold water, often present off Pt. Conception due to upwelling (e.g., fig. 36C), contributed to the extremely large anomalies during the summer of 2014. By the fall of 2014 large positive anomalies were observed throughout the study domain and these reached highest values during the winter of 2015 (fig. 36E), when the average relative temperature anomaly was 2.2 with values at individual stations ranging from 1.2 to 3.7 units. During the spring of 2015 relative anomalies were still very strong in the California Current proper and in the southern part of the study domain. The decrease in ML salinity (fig. 11B) over the last 12 months is primarily due to decreased salinity in the California Current region; relative changes of ML salinity in coastal and offshore areas were not as large (fig. S7). Similar patterns, i.e., salinity changes primarily driven by the waters of the CCS, were observed during the 2012 salinity minimum (Wells et al. 2013). Spatial distributions of these properties for the individual cruises can be found at calcofi.org/publications.

Plots of ML chlorophyll *a* and ML nitrate (NO_3) vs. time are difficult to interpret because distributions of the data are skewed. This can be avoided using a log-transform for the chlorophyll *a* data and a cube-root transform for the NO_3 data (the latter to effectively deal with zero values of nitrate). Such transformations will place heavy emphasis on the variability of these parameters when their values are low. Values of ML log chlorophyll *a* during the SCWA were the lowest observed during the 1984 to 2015 time period (fig. 12A). Cruise averages of cube-root NO_3 during the SCWA were almost as low (fig. 12B). Annual ML chlorophyll *a* and nitrate averages show great coherence over time, and significant correlations (Autoregressive Exogenous, ARX [1 2 0] model) at lags of zero ($p < 0.01$) and one ($p < 0.01$) year. This correlation suggests that, during the SCWA, phytoplankton biomass was controlled by the availability of NO_3 or a nutrient co-varying with NO_3. Similar conclusions have been reached for low phytoplankton biomass during strong El Niño events in the southern California Current system (Hayward 2000). Low ML concentrations of NO_3 are likely controlled by stratification, as a comparison of cube-root NO_3 and nitracline depth (NC depth, fig. 12B, C) shows.

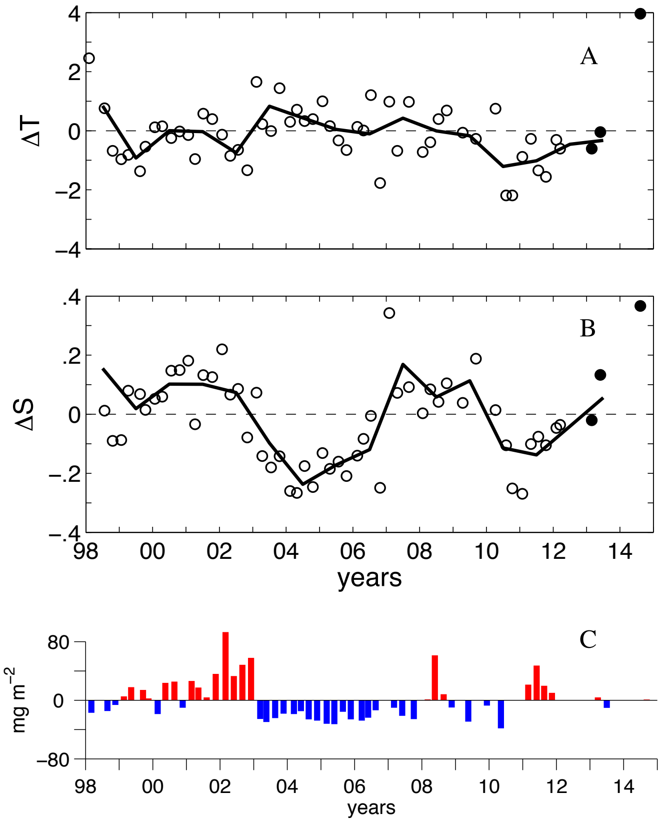

Figure 13. A) Mixed layer temperature (°C), and B) salinity (g kg^{-1}) anomalies off the Baja California Peninsula (IMECOCAL grid). Each symbol represents the average anomaly for each cruise conducted. Data from the 2013 and 2014 surveys are plotted as solid symbols. The thick solid line indicates annual average. C) Time series of 0–100 m integrated chlorophyll-*a* anomalies for the IMECOCAL region. Each bar represents the anomaly of a single cruise.

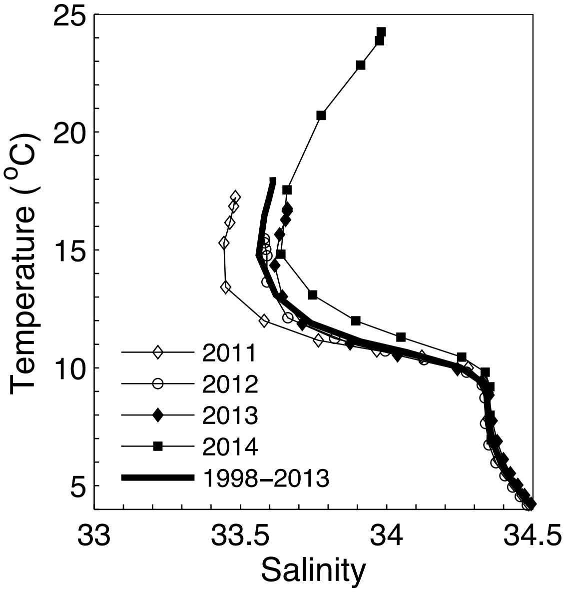

Figure 14. Annual mean T-S curves for the period 2011–13 of the IMECOCAL region. The curve labeled 2014 refers to the cruise mean values of summer 2014. The long-term mean (1998–2013), is indicated by the thick line. Each data point indicates one standard depth, from the surface to 1000 m.

IMECOCAL Surveys, Baja California

During 2014, a single summer cruise occupying a total of 85 hydrographic stations was conducted off the Baja California Peninsula by the IMECOCAL program (fig. 1). Contrasting to near normal mixed-layer temperatures in the previous year, summer 2014 depicted the presence of water up to 4°C warmer relative to the long-term mean (fig. 13A). Following the same regional trend, mixed-layer salinities also showed larger than normal values, with anomalies of ~0.4 g kg^{-1} (fig. 13B). As suggested by the temperature-salinity diagram (fig. 14), the influence of warmer and saltier waters during summer 2014 was apparently restricted to the upper 50 m. Below this depth, the TS curve follows closely the 1998–2013 climatological mean and the near-normal conditions observed during 2012 and 2013. The warming of the mixed-layer depicted in figures 13 and 14 was most conspicuous for latitudes south of Punta Eugenia, where near-surface warmer waters were evident since early 2014, and where the largest temperature and salinity anomalies (>5°C and ~0.7 g kg^{-1}, respectively) were observed near shore (data not shown). Dynamic height anomaly calculations indicated poleward alongshore flows in the southern region, typical for the summer season (Durazo 2015). As is commonly observed during warm events (Durazo and Baumgartner 2002), these flows were not evident north of Punta Eugenia. Water-column integrated phytoplankton chlorophyll *a* (0–100 m) continued with near normal conditions observed in previous years, with negligible anomalies in 2014 (fig. 13C).

REGIONAL PATTERNS IN FISH SPECIES

Northern California Current, Newport Line

Ichthyoplankton samples were collected from 3–4 stations representing coastal (<100 m in depth), shelf (100–1000 m), and offshore (>1000 m) regions along both the Newport Hydrographic (NH; 44.65°N, 124.35–125.12°W) and Columbia River (CR; 46.16°N, 124.22–125.18°W) lines off the coast of Oregon between June 15 and July 20 in 2007–14 (for complete sampling methods, see Auth 2011). In addition, post-larval (i.e., juvenile and adult) fish were collected using a modified-Cobb midwater trawl (MWT). MWT collections were made at 4–6 evenly-spaced, cross-shelf stations representing coastal, shelf, and offshore regions along nine half-degree latitudinal transects between 42.0° and 46.0°N latitude in the northern California Current region during June–July in 2011–15 (although no sampling was conducted in 2012).

The ichthyoplankton community in the central-northern coast of Oregon in June–July 2014 was simi-

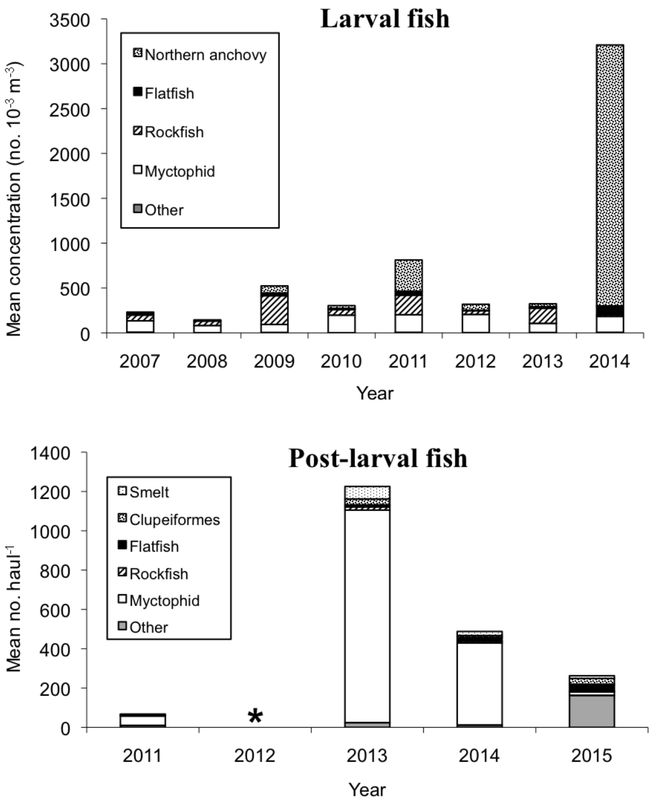

Figure 15. A) Mean concentrations (no. 10^{-3} m^{-3}) of the dominant larval fish taxa collected during June–July in 2007–14 along the Newport Hydrographic (NH; 44.65°N, 124.35–125.12°W) and Columbia River (CR; 46.16°N, 124.22–125.18°W) lines off the coast of Oregon. B) Mean catches (no. $haul^{-1}$) of the dominant post-larval fish taxa collected during June-July in 2011–15 along nine half-degree latitudinal transects between 42.0 and 46.0°N latitude in the northern California Current region. * = no samples were collected in 2012.

lar to the average community structure found in the same area and season during the previous seven years in terms of composition and relative concentrations of the dominant taxa, with the exception of the unusually high concentration of northern anchovy, which dominated the ichthyoplankton at a mean concentration that was >16x higher than that of the next highest taxon, myctophids (fig. 15A). Larval northern anchovy and flatfish in 2014 were found in concentrations >8x and >2x higher, respectively, than those of the next highest year in the time series, 2011, while larval rockfish were found in concentrations >2x lower than the next lowest year in the eight-year time series, 2012.

The post-larval fish community in the northern California Current in June–July 2015 differed from the community structure found in the same area and season in 2011–14 primarily due to the low numbers of myctophids found in 2015, which normally are the dominant taxon in the fish community, and the increased abundance of "other" taxa relative to previous years, which is an indicator of increased diversity in 2015 (fig. 15B). The abundance of flatfish in 2015 was the highest of the four-year time series, while that of rockfish was the lowest. The abundances of smelt and clupeiformes in 2015 were about average for the time series.

Northern California Current, Oregon and Washington Coast

Biomass of available fish prey for out-migrating juvenile salmon in 2015 is predicted to be above average based on the winter ichthyoplankton biomass index (Daly et al. 2013) primarily due to an anomalously high biomass of northern anchovy and rockfish larvae. This winter (January to March) biomass of fish larvae that salmon prey upon was the fourth highest in the last 18 years (fig. 16). The biomass of fish larvae in late winter provides an index of juvenile fish that are the common prey of juvenile salmon when they enter the ocean in spring and summer. Due to the anomalously warm ocean conditions during the winter of 2014–15, which typically predict lower salmon survival of early ocean migrants, we are uncertain about the accuracy of the current prediction for salmon returning in 2016 and 2017. The overall composition of winter ichthyoplankton that are important prey for salmon in 2015 was most closely aligned with 2004 and 2005, both poor outmigration survival years. While the biomass in 2015 predicts returns of spring Chinook salmon to Bonneville Dam at slightly over 200,000 adult fish, the ichthyoplankton composition based on axis ordination scores predicts 93,000 adult fish returning in 2017, which is the largest discrepancy in these two predictors over the 18 years of the survey. Warm winter ocean conditions observed in both 2014, and especially early 2015, indicate poor returns of adult salmon in the next few years. Also noteworthy in the winter ichthyoplankton collections for 2015 were that: 1) three new offshore taxa were collected, 2) there were larvae present at all sampling stations, 3) and there were high concentrations and biomass of Pacific sardine larvae in February and March from NH–01 (most inshore station) to NH–25 (most offshore station), all of which had not occurred prior to 2015 (fig. 15A). While northern anchovy larvae have previously been collected in January–March along the NH line (in March 1998 and 2003), their 2015 biomass was over 100 times greater than in any previous year, and as with the Pacific sardine larvae, northern anchovy larvae were present all across the shelf from inshore to offshore stations (NH–01 to NH–25; Auth et al. in prep).

Catch per unit effort (CPUE, number per km trawled) of most juvenile salmonids during this survey was lower than average compared to the 16 previous June surveys 1998–2013 (fig. 17). Catches of yearling Chinook salmon (*Oncorhynchus tshawytscha*) in June 2014 were ninth of the 17 years of sampling, and catches of yearling coho salmon (*O. kisutch*) were ranked 10 out of

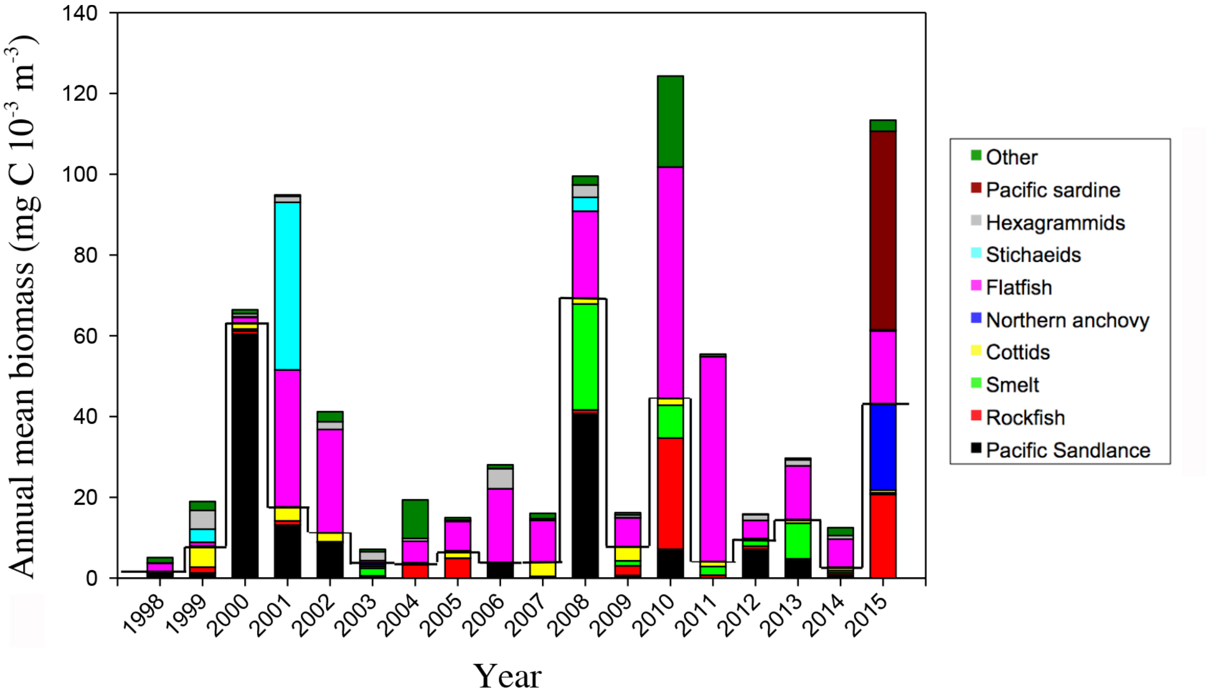

Figure 16. Annual mean biomass (mg C 10^{-3} m^{-3}) of the five important salmon prey taxa (below solid line) and five other dominant larval fish taxa (above solid line) collected during winter (January–March) in 1998–2015 along the Newport Hydrographic (NH) line off the coast of Oregon (44.65°N, 124.18–124.65°W). Figure expanded from one presented in Daly et al. (2013).

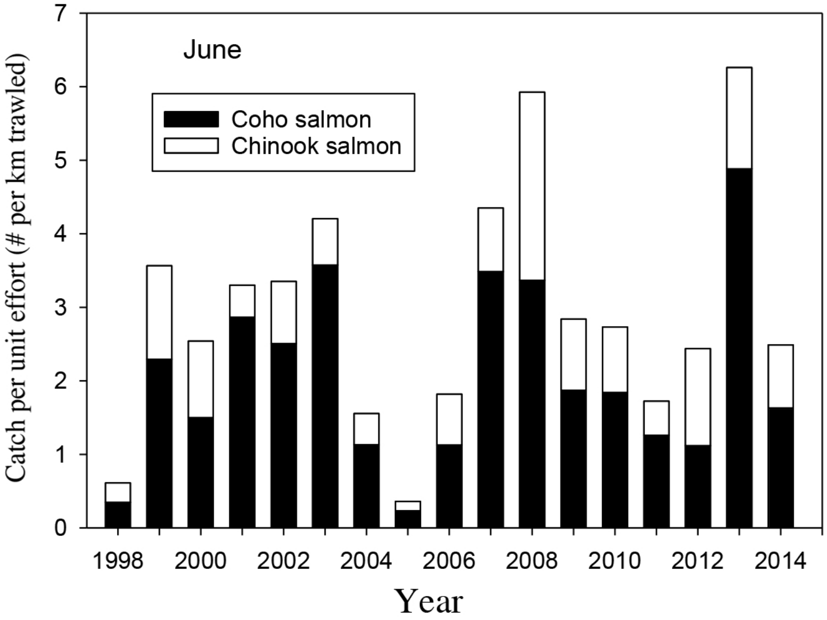

Figure 17. June salmon catch (catch per unit effort, CPUE, number per km trawled). Catches of juvenile coho (black bars) and Chinook (white bars) salmon off the coast of Oregon and Washington in June from 1998–2014.

17 years. The abundance of yearling Chinook salmon during June surveys has a significant and positive relationship to spring Chinook jack counts at Bonneville the following spring. The abundance of yearling coho salmon during these surveys also has a significant and positive relationship to coho smolt to adult survival. Thus, catches of yearling salmon in June may be a good indicator of first year ocean survival of yearling Chinook and coho salmon.

Pelagic fish and invertebrate catch data were collected by the NWFSC-NOAA Bonneville Power Administration survey surface trawls on standard stations along transects between La Push, WA, and Newport, OR, in June from 1999 to 2015. All tows were

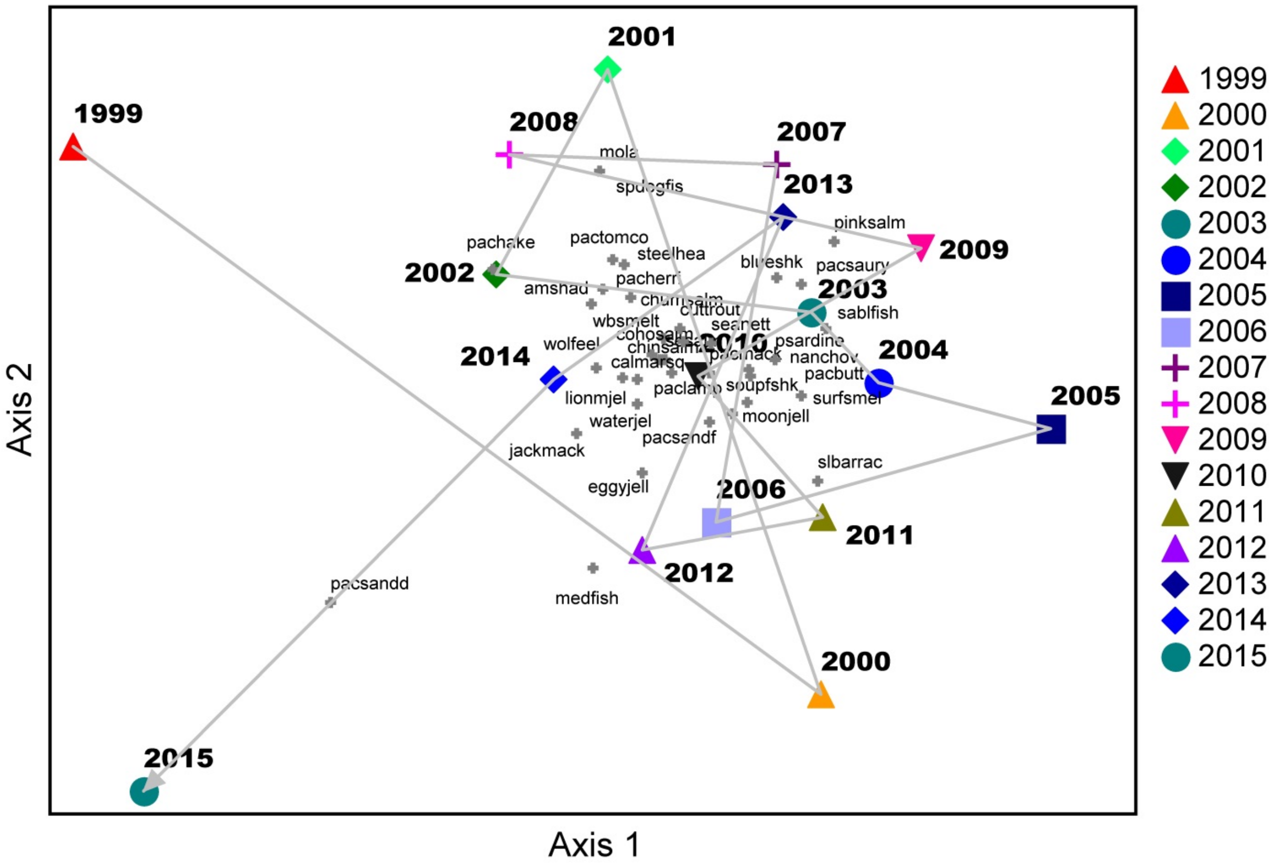

Figure 18. Nonmetric multidimensional scaling plot of the 36 most commonly-occurring taxa from the NWFSC-NOAA June pelagic fish surveys from the Northern California Current. Shown are the individual years as symbols, which are connected by a progressive vector and an overlay of the taxa that contribute to the variation seen in the plot. Final stress of the ordination was 13.898.

made during the day at predetermined locations along transects extending off the coast to the shelf break (Brodeur et al. 2005). We restricted the data set to stations that were sampled more than 9 years over the sampling time period. Numbers of individuals were recorded for each species caught in each haul and were standardized by the horizontal distance sampled by the towed net as CPUE (#/km^2 towed; units are calculated as the width of the trawl opening, 0.03 km, multiplied by the distance towed, in km. Height of the trawl gear was not measured during every cruise, and was thus not used in these calculations, but is estimated at 0.02 km). Yearly abundance data were obtained by averaging the standardized CPUE data across stations for each species sampled during the June surveys. We restricted the species data to the 36 most abundant species captured in this data set over the 17 years sampled. We applied a log(x+1) transformation to the species x year data set (36 species x 17 years), on which we ran a nonmetric multidimensional scaling (NMS; Kruskal 1964) ordination to describe the similarity of each year's community in species space.

The resulting NMS ordination explained 87.4% of the total variability in the first two dimensions, with NMS axes 1 and 2 explaining 64.1% and 23.3% of the variability, respectively. Although the community for 2014 had lower axis 1 scores than most of the previous years of sampling, it was not extreme, particularly compared to 2015 (fig. 18). The community of fish and invertebrates in June 2015 had the lowest value for axis 2 and the second lowest (slightly less than 1999) for axis 1. Although the main taxa most indicative of the relationship was Pacific sanddabs (*Citharichthys sordidus*), other taxa were more abundant than normally found in previous June cruises including jack mackerel (*Trachurus symmetricus*), California market squid (*Doryteuthis opalescens*), and several jellyfish taxa (water jellyfish, *Aequorea* sp.; egg yolk jellyfish, *Phacellophora camtschatica*). Several of the forage fish species typically found in these surveys, such as Pacific herring (*Clupea pallasi*), northern anchovy (*Engraulis mordax*), and smelts (family Osmeridae) and most salmonids were found in much lower abundances in 2015 than previous years. Large gelatinous zooplankton taxa have been quantified in large pelagic surface trawls off Oregon and Washington every June since 1999 (see Suchman et al. 2012 for collection methods). The normally dominant Scyphozoan species, *Chrysaora fuscescens*, has shown a decrease in abundance since the El

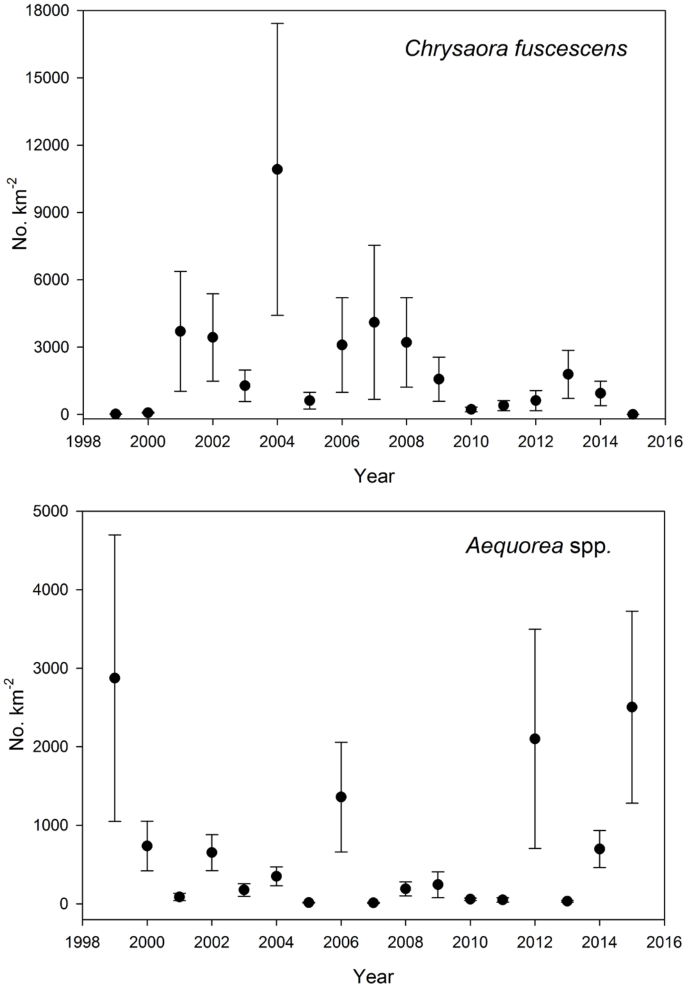

Figure 19. Catches of the dominant jellyfish taxa in pelagic surveys off the coast of Washington and Oregon in June from 1999 to 2015. Data are the means and standard deviations of the catch per km^2 of (a) *Chrysaora fuscescens* and (b) *Aequorea* spp. in the entire survey area.

Niño of 2010 and, in fact, was found in the lowest abundance of the time series in June 2015 (fig. 19), occurring in less than 25% of the stations sampled, mostly at the nearshore stations (<15 km from shore). The smaller Hydromedusae, *Aequorea* sp., is generally found in much lower densities at the offshore stations (Suchman et al. 2012) but was by far the numerically dominant taxa in 2015. Other offshore and/or southern species such as the large scyphozoan, *Phacellophora camchatica*, the pleustonic *Velella velella*, and colonial salps (*Salpa* and *Thetys*) were found during the warm ocean conditions that occurred in 2015 leading to a gelatinous faunal composition that resembled that of an El Niño year.

Ecosystem indicators for the Central California Coast, May–June 2014

The Fisheries Ecology Division of the SWFSC has conducted an annual midwater trawl survey for pelagic juvenile (young-of-the-year, YOY) rockfish (*Sebastes* spp.) and other groundfish off of central California (approximately 36° to 38°N) since 1983, and has enumerated most other pelagic micronekton encountered in this survey since 1990 (Ralston et al. 2013; Ralston et al. 2015). The survey, conducted in late spring (May–June), expanded the spatial coverage to include waters from the US/Mexico border north to Cape Mendocino in 2004. The primary objectives are to estimate the abundance of YOY rockfish and other groundfish for stock assessments and fisheries oceanography studies, but the survey also quantifies trends in the abundance and composition of other components of the micronekton forage assemblage (including other juvenile fishes, krill, coastal pelagic species, and mesopelagic species), as well as the collection of oceanographic information (CTD casts, continuous data on surface conditions and productivity, and acoustic data) and seabird and marine mammal abundance data. The results here include time series of anomalies of some of the key species or groups of interest in this region since 1990 (core area; fig. 1, right-hand panel, letter A) or 2004 (expanded survey area), and an update of a principal component analysis (PCA) of the pelagic micronekton community in the core area developed by Ralston et al. (2015), all of which have also been reported in earlier SoCC reports. The data for the 2015 survey are preliminary, and corrections have been made in catch data for previous years, which have resulted in very slight changes to overall abundance trends.

The standardized anomalies from the mean of the log (x+1) catch rates are shown by year for six key YOY groundfish and forage groups (fig. 20), including all YOY rockfish, market squid (*Doryteuthis opalescens*), krill (primarily *Euphausia pacifica* and *Thysanoessa spinifera*), YOY Pacific sanddab (*Citharichthys sordidus*), Pacific sardine (*Sardinops sagax*) and northern anchovy (*Engraulis mordax*). The 2015 data generally show a continuation of the very high catches of juvenile rockfish and Pacific sanddab (fig. 20; top left and middle right) in the core, southern and northern California areas (fig. 1, right-hand panel, letters A, B, and C, respectively); in fact in both the core and southern areas mean catches were the highest observed in the entirety of the time series. However, the abundance of krill (fig. 20; middle left) was at or below average levels for all regions, and the abundance of adult Pacific sardine and northern anchovy (fig. 20; bottom panels) remained very low as well (although larval catches for both species were at high or record levels in most areas). The abundance of market squid continued to remain very high in the core area, although catches were lower in the southern region where the bulk of the market squid fishery takes place (fig. 20; top right). Catches of octopus, lingcod (*Ophiodon elongates*), Pacific hake (*Merluccius productus*), and several other groundfish were also high. North of Cape Mendocino, catches of

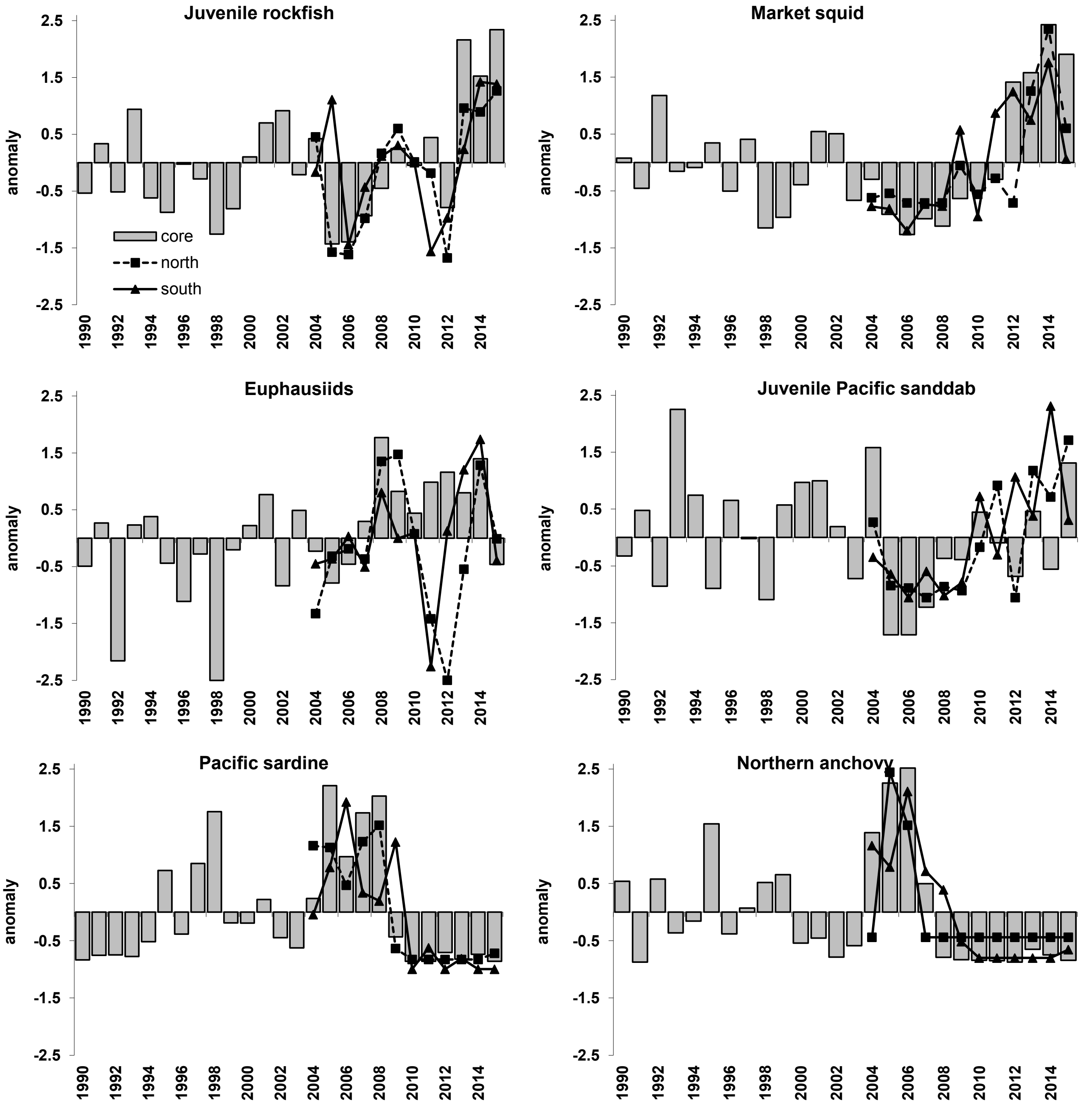

Figure 20. Long-term standardized anomalies of several of the most frequently encountered pelagic forage species from rockfish recruitment survey in the core (central California) region (1990–2015) and the southern and northern California survey areas (2004–15, excluding 2012 for the northern area).

YOY rockfish and other groundfish were at very low levels in both 2014 and 2015 (R. Brodeur, unpublished data), consistent with occasionally dramatic differences in catch rates of YOY rockfish over broader spatial scales (Ralston and Stewart 2013).

In addition to the high catches of YOY rockfish and other groundfish, catches tended to be very high for a suite of both less commonly encountered and less consistently reported (over the course of the time series) species. Although catches of scyphozoan jellyfish (primarily *Aurelia* spp. and *Chrysaora* spp.) were unusually low in 2015 (fig. 21), catches of pelagic tunicates (primarily *Salpa* spp., *Thetys vagina* and *Pyrosoma* spp.) were at extreme to record high levels. Finally, despite the high abundance (inferring high productivity and transport of subarctic water) of both YOY groundfish and of pelagic tunicates, the 2015 survey also encountered unusually high numbers of warm water species (many of which had never previously been encountered), which are typically considered to be harbingers of strong El Niño

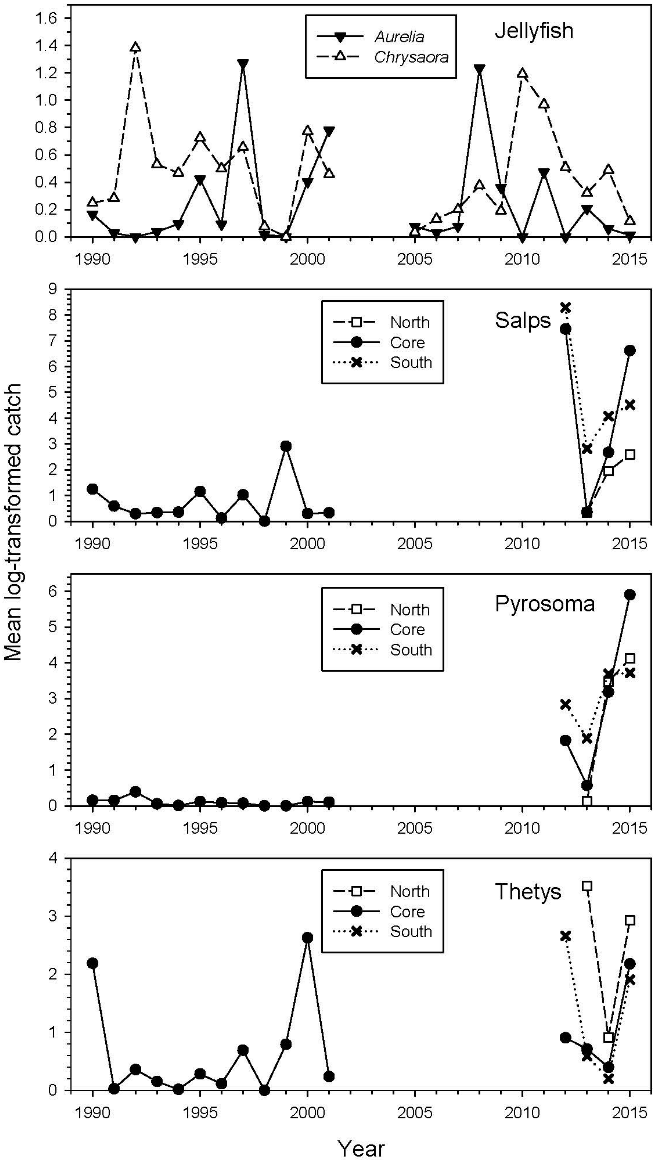

Figure 21. Standardized catches of jellyfish (*Aurelia* spp. and *Chrysaora* spp.) in the core area and pelagic tunicates in the expanded survey area.

events, northward transport of subtropical waters, and unusually low productivity. These included record-high numbers of pelagic red crabs (*Pleuroncodes planipes*), California spiny lobster (*Panulirus interruptus*) phyllosoma (pelagic larvae), and the largely subtropical krill *Nyctiphanes simplex*. Additionally, these included the first time catches (in this survey) of the greater argonaut (*Argonauta arga*), the slender snipefish (*Macroramphosus gracilis*), and the subtropical krill *Euphausia eximia*. The 2015 survey was highly unusual in that species characteristic of all three of what might very generally be considered nominal states (YOY groundfish dominated catches, pelagic tunicate dominated catches, and subtropical species dominated catches) were encountered in high abundance throughout this region.

In addition to the six species shown in fig. 20, an additional 14 species and groups were included in the analysis of the forage assemblage within the core (1990–2015) area (fig. 1; right panel, letter A) developed by Ralston et al. (2015), and are subsequently represented in the PCA of this assemblage. The additional YOY groundfish groups include Pacific hake, speckled sanddab (*C. stigmaeus*), rex sole (*Glyptocephalus zachirus*), and lingcod. The remaining species and groups in the assemblage include adult Pacific hake, octopus, sergestid shrimp, gobies, plainfin midshipman (*Porichthys notatus*), and a variety of mesopelagic species. Of those that are included, YOY groundfish, market squid, krill and several other taxa had strong positive loadings on PC1 (which explained 32% of the total variance, the first three PCs explained a total of 60% of the variance), with northern anchovy, Pacific sardine and most mesopelagic species loading negatively. This PC was not significantly related to basin-scale environmental indicators such as the PDO, MEI, and the NPGO, but rather was strongly related to both localized physical conditions (temperature, salinity, density and depth of the 26.0 sigma theta isopycnal; see also Santora et al. 2014) and indicators of large-scale transport (AVISO sea surface height anomalies), such that the YOY rockfish, market squid, and krill groups were more abundant during cool, high transport conditions. The second PC tended to load more strongly on the mesopelagic community, but related poorly to environmental indicators, while PC3 had strong loadings on a suite of taxa and was highly correlated to basin-scale climate indicators (see Ralston et al. 2015 for details). Unfortunately, the pelagic tunicates have not been consistently quantified over the time period of the survey, while the subtropical species are typically rare and therefore did not meet the minimum percentage of frequency of occurrence (10%) from the analysis. Thus, those groups are not represented in the PCA results.

The two leading PCs for the assemblage are shown in a phase plot as Figure 22, and the dramatic (and apparently ongoing) separation of the 2013 through 2015 period is noted as being on the opposite end of the PC1 scale compared to the low productivity years of 1998, 2005, and 2006. Such shifts have important implications for higher trophic level species, such as seabirds, marine mammals, salmon, and adult groundfish that forage primarily or exclusively on one or another component of this assemblage. The observed dynamics of the YOY groundfish and high turnover invertebrates is thought to largely represent shifts in productivity associated with higher survival (recruitment) of early life history stages for these species, while the trends observed for coastal pelagic and mesopelagic species (which load negatively on PC1 and positively on PC2) are thought to be related to both variability in abundance as well as shifts in their

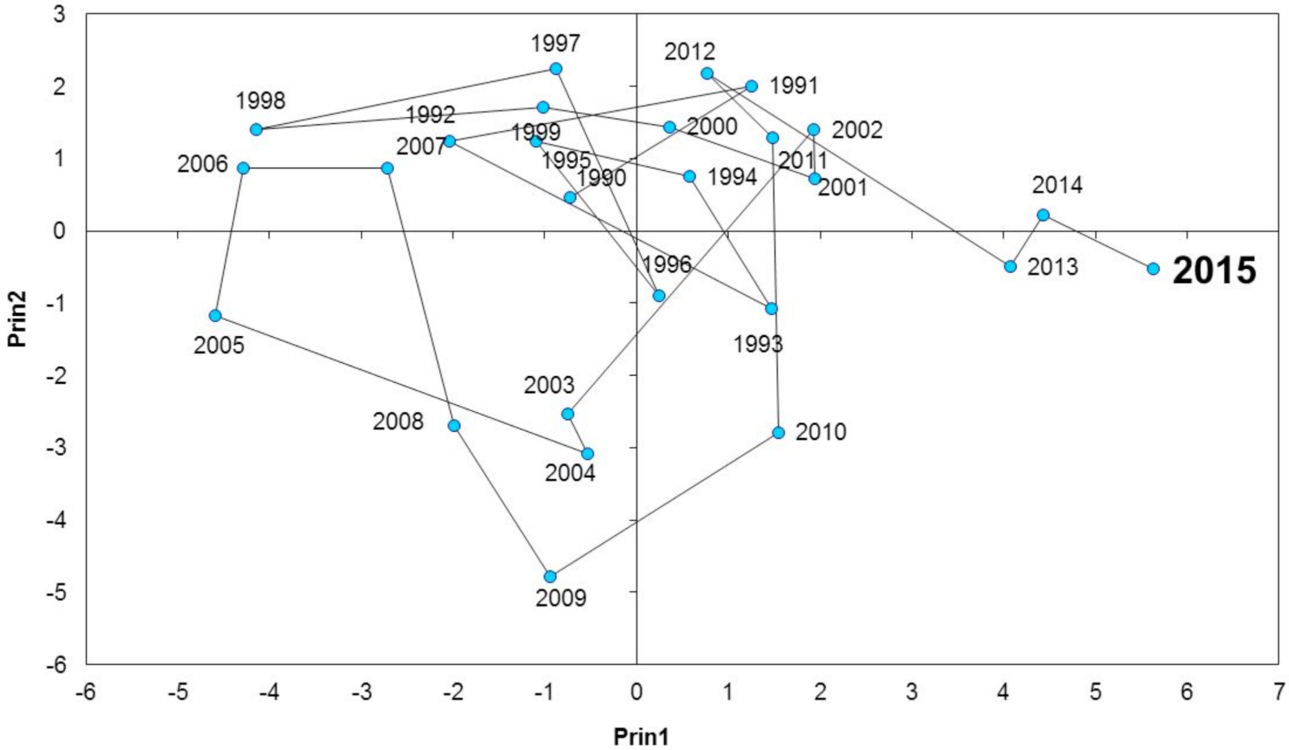

Figure 22. Principal component scores plotted in a phase graph for the twenty most frequently encountered species groups sampled in the central California core area in the 1990–2014 period.

distribution and consequent availability to the midwater trawl. Yet overall the results of the PCA clearly indicate that in the core area, and presumably in the northern and southern regions as well, the micronekton community composition is highly unusual relative to those observed throughout the history of this survey.

Ecosystem Indicators for the Southern California, CalCOFI Region

Coastal pelagic fish egg abundance has declined off central and southern California in the last 15 years (2000–15) (fig. 23). Sardine, anchovy, and jack mackerel eggs were found at very low concentrations in the spring of 2015. Although peak anchovy spawning occurs in December–February, which is earlier than the March–April spring survey, the anchovy spawning that extends into spring shows the same trend to lower egg densities as do sardine and jack mackerel. Anchovy and jack mackerel are lightly fished, and although commercial catches of sardine are higher, the observed decline in egg densities of all three species suggests that environmental factors are likely to be the major cause of the decline in spawning of these forage fishes.

Jack mackerel eggs were an order of magnitude more abundant than sardine or anchovy eggs in spring 2015 (fig. 24). Despite their relatively higher abundance, jack mackerel eggs were less abundant than during every spring in the last 15 years, except for 2010–12 (fig. 23). The distribution of jack mackerel eggs in 2015 was also more restricted than in previous years, particularly when compared to 2000–06 (fig. 24). The offshore spawning of mackerel, which is commonly regarded as being typical, occurred at very low densities in spring 2015 (figs. 23 and 24).

Conditions off central and southern California were unusually warm in spring 2015 (see elsewhere in this report). Mackerel eggs were found in water with surface temperatures of 14°–18°C. Sardine eggs are rarely found north of San Francisco in the spring, but in 2015 sardine spawned 445–556 km further north than usual (fig. 24). Sardine spawning centered near the California–Oregon border (41°–43°N) in a band about 90–110 km from shore in surface water temperatures of 12°–13°C (fig. 24). Egg densities off Oregon in spring 2015 were <1.5 eggs m^{-3}, which was extremely low compared to spring 2000–13 (fig. 24). There were also reports of sardine and anchovy spawning very close to shore off Newport, Oregon (R. Brodeur, NWFSC, personal communication), but inshore spawning was not detected by the SWFSC spring coastal pelagic fish survey.

During the summer 2014 CalCOFI cruise, dorado (*Coryphaena hippurus*) eggs were found in the continuous underway fish egg sampler (CUFES) samples in the southern part of the core area. Dorado apparently rarely spawn as far north as southern California—there

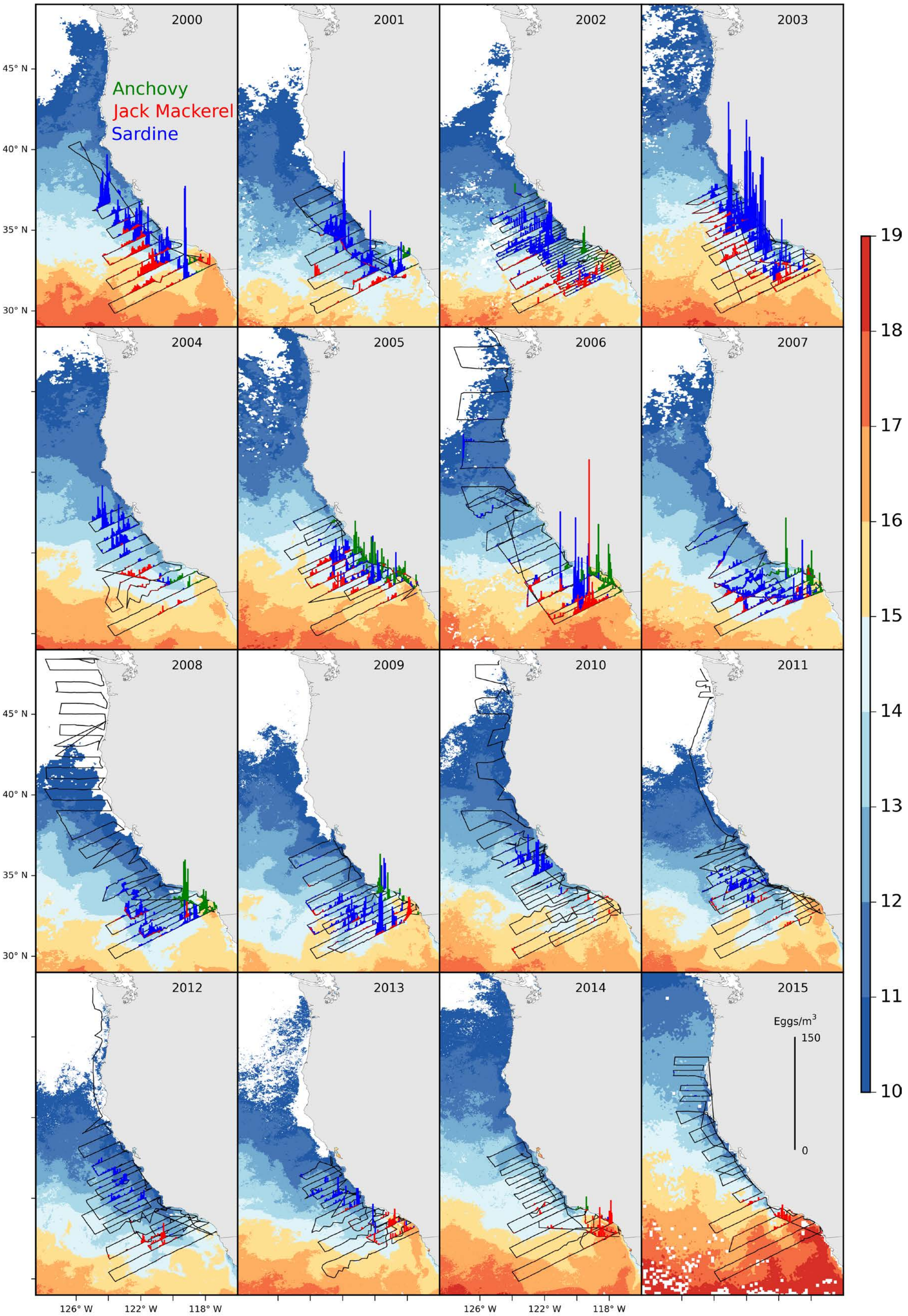

Figure 23. Density of eggs of sardine (blue), anchovy (green), and jack mackerel (red) collected with the continuous underway fish egg sampler (CUFES) overlaid on satellite sea surface temperatures (°C) derived from a monthly composite of April Pathfinder 5.5-km resolution (2000–08) or AVHRR 1.4 km resolution (2009–15) imagery. Ship track is shown by the black line.

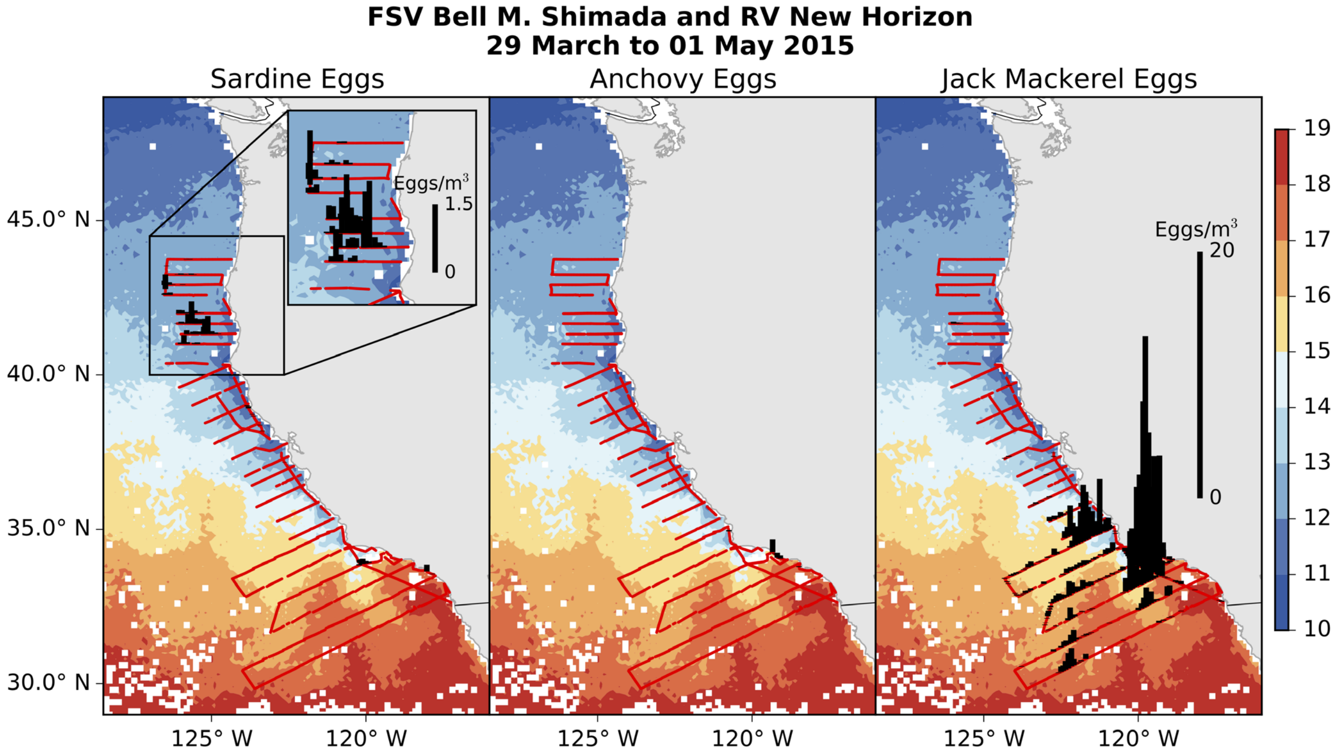

Figure 24. Density of eggs of sardine, anchovy, and jack mackerel collected with the continuous underway fish egg sampler (CUFES) during the spring 2015 CalCOFI and coastal pelagic fish cruises overlaid on satellite sea surface temperatures (°C).

are only two records north of the Mexican border since 1951 in the CalCOFI ichthyoplankton database—and spawning in the north during 2014 likely reflects the warm conditions at that time.

REGIONAL PATTERNS IN BIRDS AND MARINE MAMMALS

Common Murres at Yaquina Head, Oregon

Median hatch date for common murres at Yaquina Head in 2014 was 3 July, continuing the trend of later hatch dates beginning in 2010 (with a minor exception of 2012; fig. 25). Only 23% (+0.13 SE, 0.00–0.86 range) of the eggs laid hatched a chick (hatching success) and 17% (+0.11 SE, 0.00–0.81 range) of the eggs laid produced chicks that fledged (reproductive success; chicks > 15 days were considered fledged; fig. 25). Reproductive success in 2014 continued the trend of negative anomalies starting in 2011. Reproductive success in 2014 was the lowest recorded for this colony during 13 years of data collection, maintaining a 4 year run (2011–14) of low reproductive success that is less than half the success for the first four years of our study (2007–10, fig. 25). Only the reproductive success during the 1998 El Niño was slightly lower (Gladics et al. 2015).

Like the previous two seasons, much of the reproductive loss in 2014 was due to egg and chick preda-

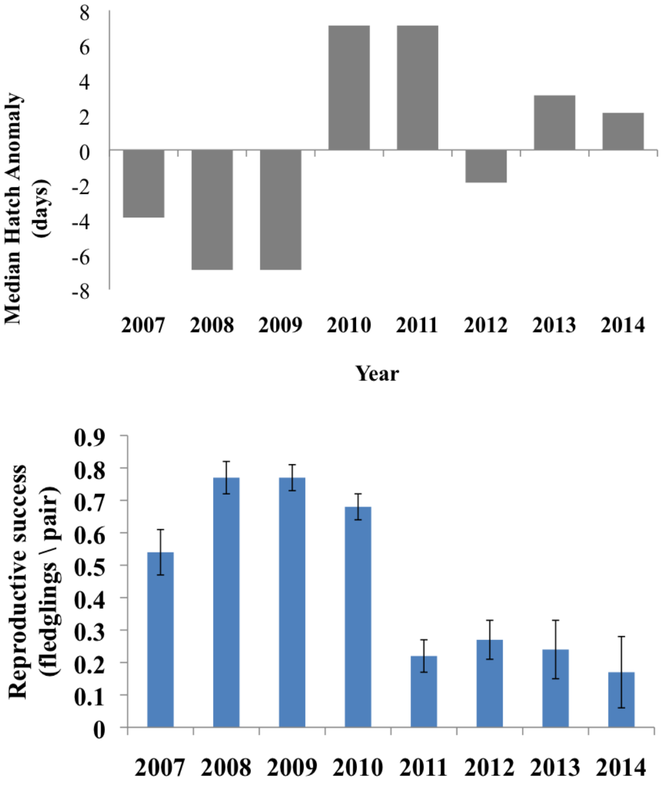

Figure 25. A) Median hatch date anomaly, and B) Reproductive success for common murres nesting at Yaquina Head, Oregon, 2007–14.

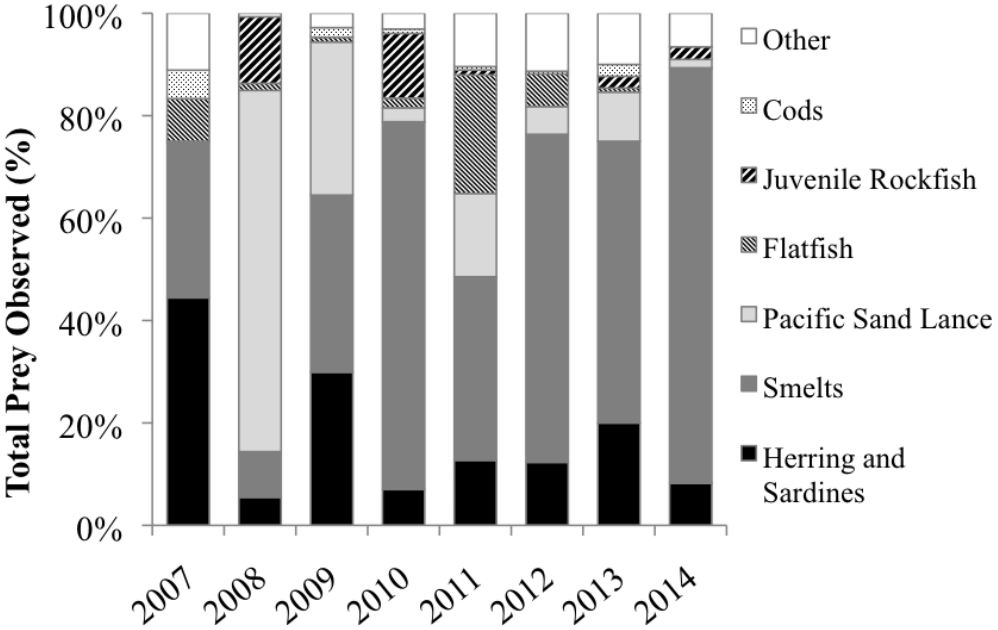

Figure 26. Prey fed to common murres chicks (% occurrence) at Yaquina Head Oregon, 2007–14.

tors. The total number of disturbances and the rate of murre egg and adult loss in 2014 was again high, similar to the previous four years. Disturbances and losses in 2010–14 were all 3–10 times higher than 2007–09. Disturbance rates first began to increase in 2010, and then greatly escalated during 2011–14 (Horton 2014). Bald eagles (*Haliaeetus leucocephalus*) were again the dominant disturbance source (49%, 36 of 75 disturbances). The frequent disturbances to a subcolony (flat top) resulted in total reproductive failure for those plots (reproductive success = 0.00 + 0.00 SE for 6 plots)—this was the first year that we observed complete failure of either subcolony. Unlike in 2012 when juvenile brown pelicans (*Pelecanus occidentalis*) resorted to eating fish regurgitated by murre chicks or eating murre chicks directly (Horton and Suryan 2012), there were no dramatic disturbances caused by pelicans in 2014, and pelicans were not observed landing on the colonies until the majority of murres had fledged.

Murre diets at Yaquina Head have varied annually. Forage fish species consumed in 2014 included primarily smelt (Osmeridae) and secondarily Pacific herring or sardine (Clupeidae; fig. 26). A notable difference in diets in recent years has been the dominance of smelt since 2010 (with minor exception of 2011). Prior to this period, annual diet composition varied annually between dominance of smelt, Pacific sand lance (*Ammodytes hexapterus*), and clupeids, or occasionally relatively equal proportions of each in a given year (fig. 26). The lack of sand lance and clupeids since 2010 continued and was especially prominent in 2014. Sand lance are generally more prominent in cold water years (Gladics et al. 2014, 2015), as highlighted by their prevalence in 2008 (fig. 26). Clupeids (primarily Pacific herring, *Clupea pallasii*), are generally associated with warmer water and positive PDO (Gladics et al. 2015).

Summary of Common Murre Reproductive Success, Phenology, and Diet at Castle Rock National Wildlife Refuge: 2007–14

Castle Rock National Wildlife Refuge (hereafter Castle Rock) is the most populous single-island seabird breeding colony in California. Located in the northern California Current system, this island is off the coast of Crescent City, just south of Point St. George. To facilitate long-term monitoring of seabirds nesting at this colony, a remotely-controlled video monitoring system was installed at this island in 2006. For purposes of assessing the state of the California Current, the reproductive performance of common murre and Brandt's cormorants is provided. For common murre, the composition of prey delivered to chicks between 2007 and 2014 is also provided.

Common murre are the most abundant surface-nesting seabird at Castle Rock and their reproductive success, nesting phenology, and chick diet have been studied since 2007. The percent of nesting pairs that successfully fledged young in 2014 was based on 81 nest-sites that were monitored every other day for the entire breeding season. During 2014, 83% of nests fledged young, which was 10% greater than the long-term average for this colony (fig. 27). Although murres do not reflect upwelling directly, the increased availability of food associated with upwelling improves the body condition of egg-laying

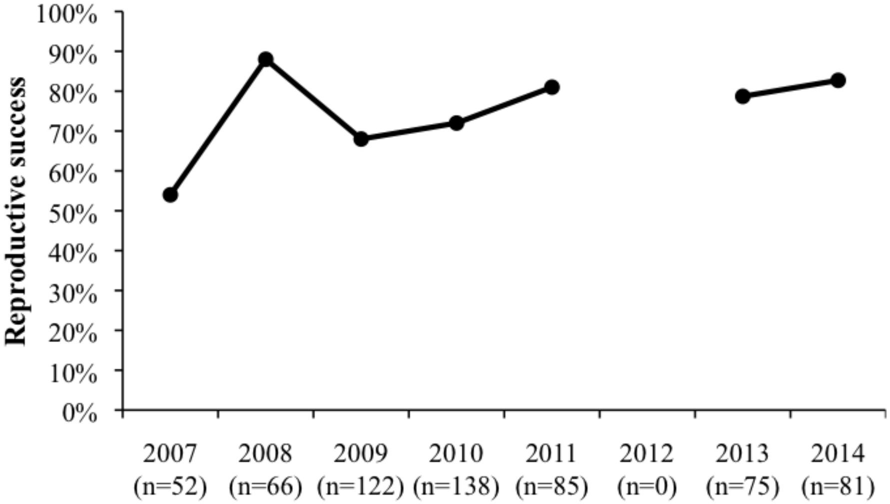

Figure 27. Percent of common murre (*Uria aalge*) nesting pairs that successfully fledged young between 2007 and 2014 at Castle Rock National Wildlife Refuge, Del Norte County, CA. The sample size (n) represents the total number of nesting pairs observed per year, and this figure does not include the success of replacement clutches. Reproductive success could not be determined in 2012 due to early failure of the video monitoring system.

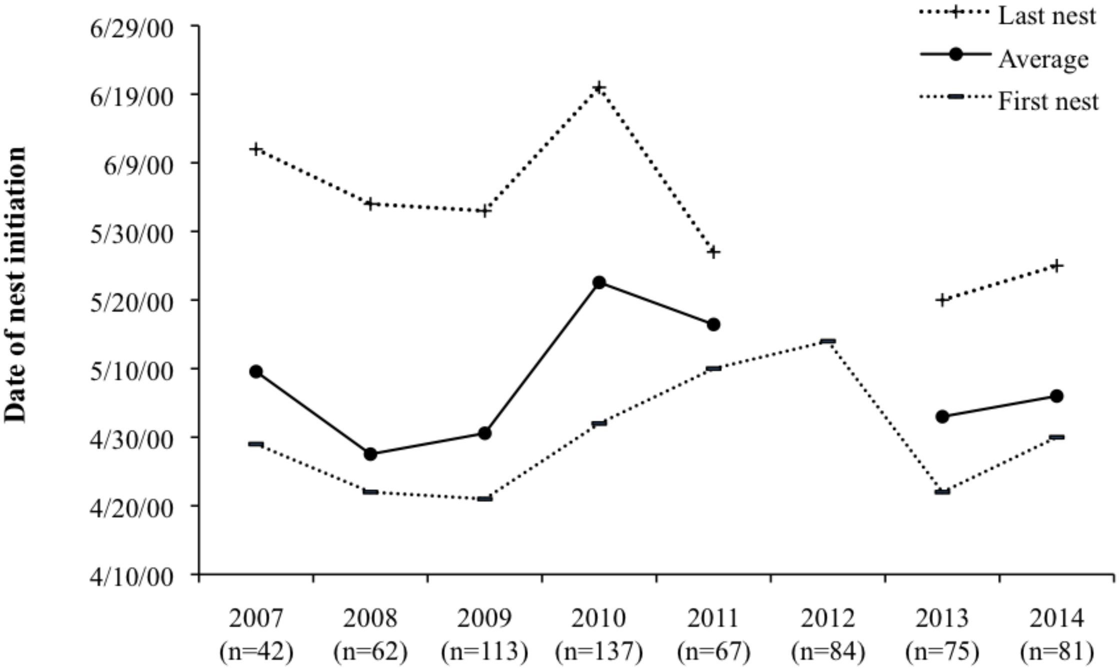

Figure 28. First, average, and last dates for nests initiated by common murres between 2007 and 2014 at Castle Rock National Wildlife Refuge, Del Norte County, CA. The date of nest initiation was the defined as the day that an egg was laid at a nest site. The sample size (n) represents the total number of nests observed each year where nest initiation dates were accurate to ±3.5 days. The average and last date of nest initiation could not be determined in 2012 due to early failure of the video monitoring system.

females and thereby influences the timing of nesting (Perrins 1970; Reed et al. 2006; Schroeder et al. 2009). In 2014, the average nest initiation date was 6 May, which is 2 days earlier than the long-term average observed at this colony (fig. 28). To determine prey composition, 2-hour diet surveys were conducted 6 days per week during the murre chick-rearing period (approximately 70 hours surveyed in 2014). In 2013, a total of 12 prey types were identified and all prey types had been observed in previous years. Prey composition was generally similar to other years, with smelt (*Osmeridae*) being the predominant prey fed to chicks and rockfish being the second most common prey fed to chicks (fig. 29). Unlike other years, California Market Squid (*Loligo opalescence*) observations were 2.2 times more frequent and was the third most common prey type fed to chicks in 2014.

Brandt's cormorant are the second-most abundant surface-nesting seabird at Castle Rock and their repro-

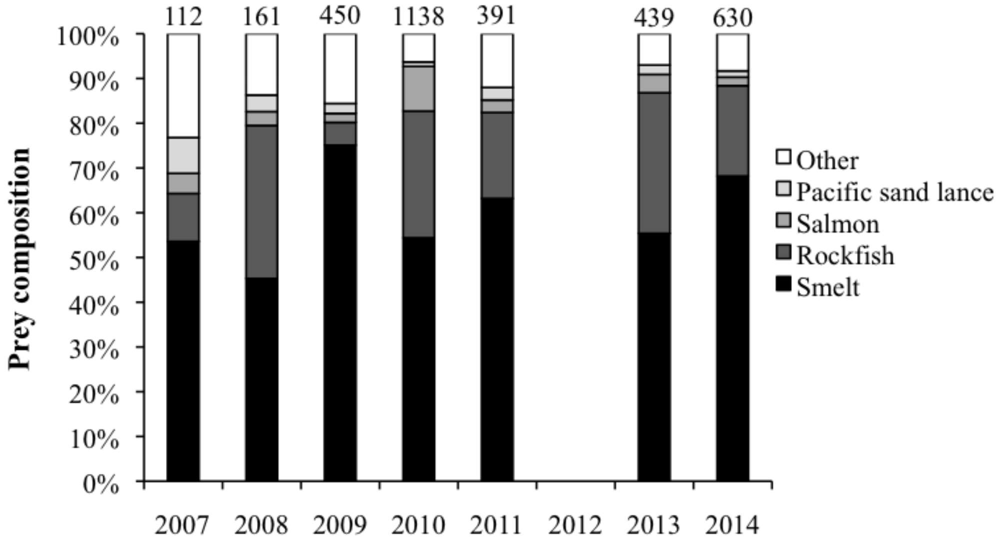

Figure 29. Composition of prey delivered to chicks by common murre between 2007 and 2014 at Castle Rock National Wildlife Refuge, Del Norte County, CA. Numbers above each bar indicate the total number of prey identified each year. Prey composition could not be determined in 2012 due to early failure of the video monitoring system.

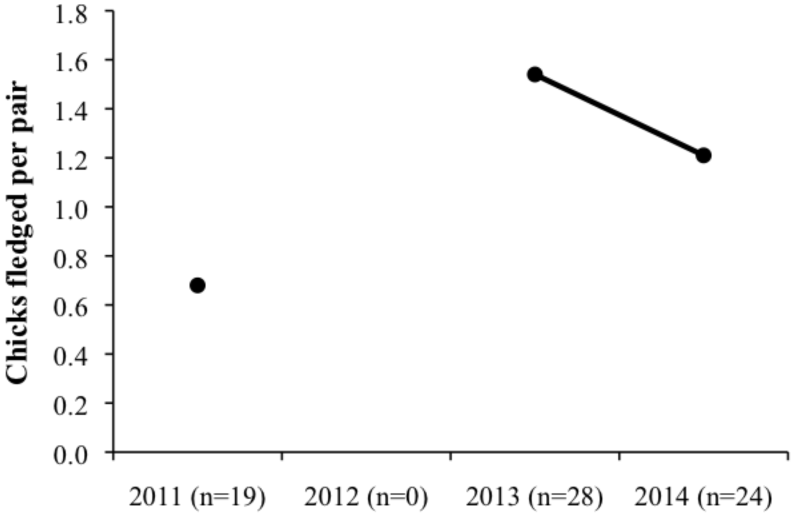

Figure 30. Chicks fledged per nesting pair of Brandt's cormorant (*Phalacrocorax penicillatus*) between 2007 and 2014 at Castle Rock National Wildlife Refuge, Del Norte County, CA. The sample size (n) represents the total number of nesting pairs observed per year, and this figure does not include the success of replacement clutches. Reproductive success could not be determined in 2012 due to early failure of the video monitoring system.

ductive success has been studied since 2011. The reproductive success of Brandt's cormorants, measured as the number of fledglings produced per pair, was determined by monitoring 24 nests every four days for the entire breeding season. In 2014, breeding pairs produced 1.21 chicks on average, which was 43% greater than the year with the poorest reproduction (2011) and 27% less than the year with the most successful reproduction (2013; fig. 30).

Breeding Success of Seabirds at Southeast Farallon Island

The 2014 seabird breeding season at Southeast Farallon Island (SEFI), California was a mixed year with higher breeding populations and increased productivity for some species while declines were observed for others (fig. 31). Reproductive success of the planktivorous Cassin's auklets (*Ptychoramphus aleuticus*), though lower than the previous four years, continued to be exceptionally high relative to the long-term mean for this colony. The fledging success for first broods was the highest observed in the time series, as Cassin's were again able to take advantage of high zooplankton production during the early part of the breeding season. However, Cassin's auklets were unable to successfully fledge any second broods for the first time since 2008, leading to the overall productivity decline observed this year. In contrast, piscivorous species including pigeon

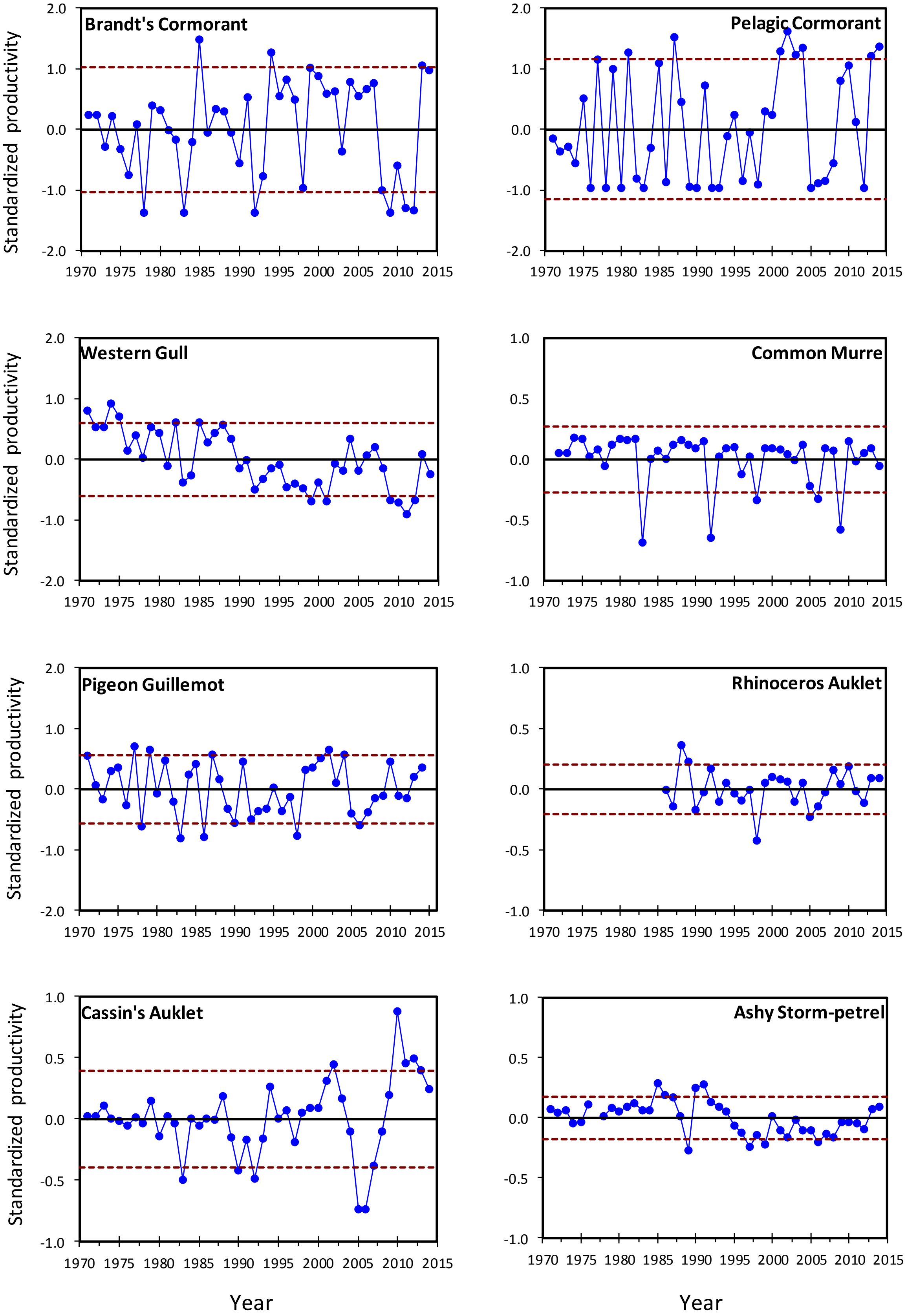

Figure 31. Standardized productivity anomalies (annual productivity—long term mean) for 8 species of seabirds on SEFI, 1971–2014. The dashed lines represent the 80% confidence interval for the long-term mean.

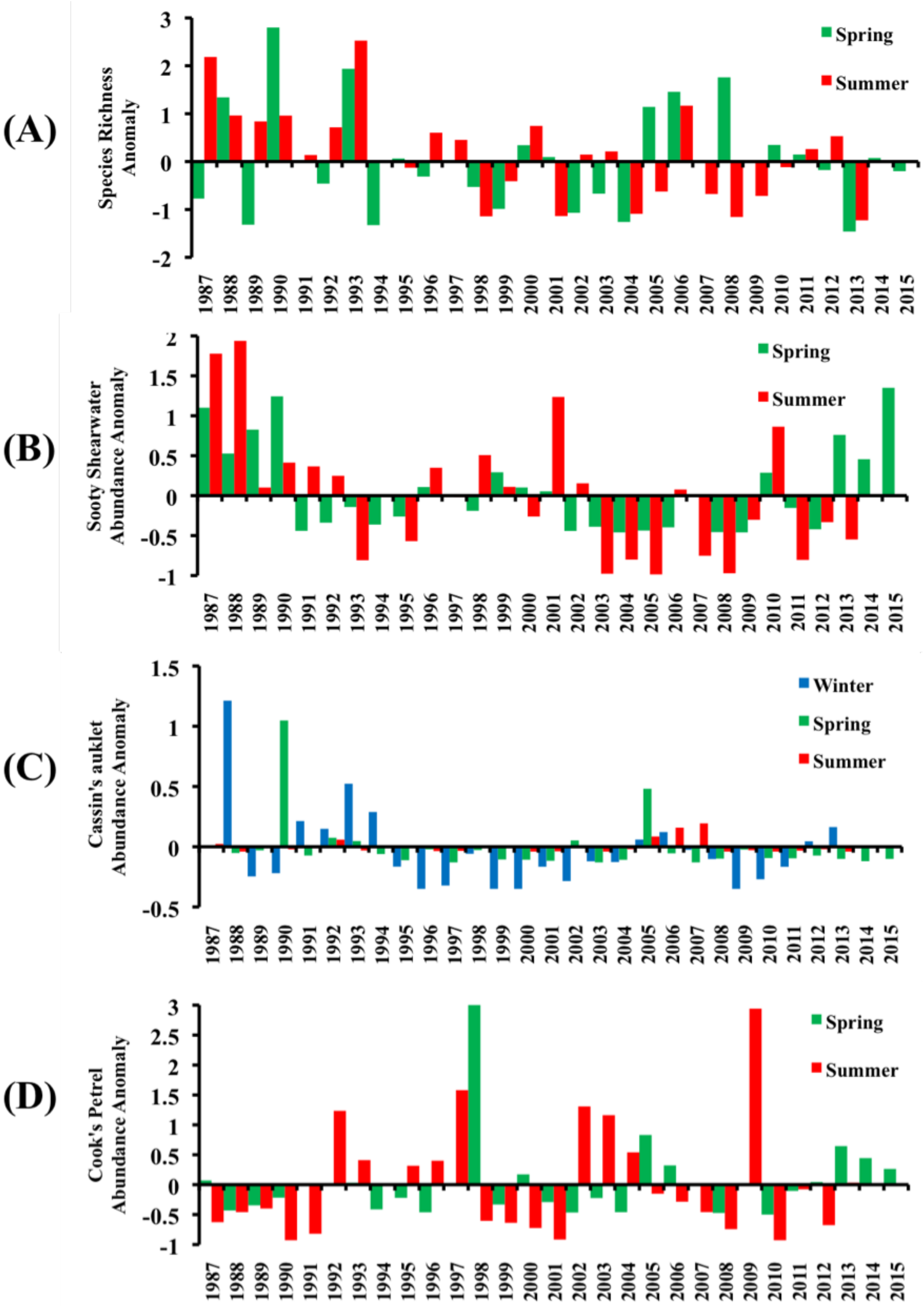

Figure 32. Patterns of change in the abundance (expressed as anomaly of log density; long-term mean subtracted) of (a) seabird species richness, (b) sooty shearwater (*Puffinus griesus*), (c) Cassin's auklet (*Ptychoramphus aleuticus*), and (d) Cook's petrel (*Pterodroma cookii*).

guillemots (*Cepphus columba*), rhinoceros auklets (*Cerorhinca monocerata*), Brandt's cormorants (*Phalacrocorax penicillatus*) and Pelagic cormorants (*Phalacrocorax peligacus*) exhibited higher reproductive success relative to last season and well above the long-term mean (fig. 31). Success for these species was likely driven by a high abundance of juvenile rockfish available throughout the early and middle parts of the season. Common murres (*Uria aalge*), though also benefiting from high rockfish abundance to achieve exceptionally high fledging success, exhibited lower than average reproductive success due to an unusually high rate of egg failure. During mid-July, ocean conditions deteriorated, with a rapid increase in sea surface temperature and a corresponding reduction in prey availability leading to poor success for later breeding individuals of all species and the failure of second broods for Cassin's auklets. Anchovies and other larger forage fishes continued to be largely absent from seabird diet, but it would appear that the birds were able to compensate this season with other prey items.

Seabirds in the CalCOFI Region

As part of CalCOFI, now supplemented by the CCE-LTER and SCCOOS programs, data on seasonal seabird distribution and abundance has been collected since spring 1987. Seabird distribution and abundance derived from CalCOFI surveys have indicated several important aspects regarding the biological conditions of the southern California Current, including: long-term declines in seabird abundance and species richness related to ocean climate and forage fish availability (Veit et al. 1996; Hyrenbach and Veit 2003; Sydeman et al. 2009, 2015; Santora and Sydeman 2015), as well as the presence and persistence of biological "hotspots" (Yen et al. 2006; Santora and Sydeman 2015). As examples of long-term variability of seabird abundance (ln anomaly density, expressed as numbers km^{-2}), we present data up to spring 2015 on seabird species richness (number of species observed per survey) as well as sooty shearwater (*Puffinus griseus*), Cassin's auklet (*Ptychoramphus aleuticus*) and Cook's petrel (*Pterodroma cookii*) abundance as "cold-water" (shearwater and auklet) and "warm-water" (petrel) indicators.

Seabird species richness (fig. 32A) has exhibited a long-term decline in the CalCOFI region, and has been negative since 2013. The decline in species richness possibly indicates that biophysical changes occurring in the southern California Current is impacting the overall at-sea avifauna. Hyrenbach and Veit (2003) suggested that species with warm-water affinities increased during warm ocean conditions, while those with cold-water affinities decreased. Sooty shearwaters (fig. 32B), a species with cold-water affinities, are southern hemisphere migrants and are most abundant in coastal waters of the California Current during the spring and summer. Shearwater density during spring has declined since surveys began in 1987, with each successive peak in abundance (i.e., 1990, 2001, and 2010) lower than the preceding one. However, shearwaters have shown strong consecutive positive anomalies since spring 2013, with spring 2015 being the highest anomaly since 1990; this is surprising given the warm-water conditions that have persisted off southern California since 2014. Further research is needed to examine why shearwaters have increased in number and what the mechanism(s) may be for their recent influx to the CalCOFI region (i.e., poor breeding leading to abandonment of colonies during 2013–14). Cassin's auklets (fig. 32C) are resident in the California Current year-round, but are most abundant in the CalCOFI region in winter. After exhibiting a positive anomaly in winter 2013, the anomaly of auklet abundance has been close to zero, suggesting that auklets have not undergone any major redistribution patterns during winter. Cook's petrels (fig. 32D) are southern hemisphere migrants and generally occur in hotspots associated with subtropical waters within the western edge of the CalCOFI grid (Santora and Sydeman 2015). Strong peaks in Cook's petrel anomalies, usually during summer surveys, are generally associated with El Niño years. Recent spring surveys indicate moderate positive anomalies of Cook's petrel and it's anticipated that given the recent warm ocean conditions off southern California, that this species should show a strong positive anomaly in summer 2015.

California Sea Lions at San Miguel Island, California

California sea lions (*Zalophus californianus*) are permanent residents of the CCS, breeding in the California Channel Islands and feeding throughout the CCS in coastal and offshore habitats. They are also sensitive to changes in the CCS on different temporal and spatial scales and so provide a good indicator species for the status of the CCS at the upper trophic level (Melin et al. 2012). Two indices are particularly sensitive measures of prey availability to California sea lions, pup production, and pup growth during the period of nutritional dependence. Pup production is a result of successful pregnancies and is an indicator of prey availability to and nutritional status of adult females from October to the following June. Pup growth from birth to 7 months of age is an index of the transfer of energy from the mother to the pup through lactation between June and the following February, which is related to prey availability to adult females during that time.

At San Miguel Island, successful pup births, as measured by counts of live pups, in 2014 were 11% higher

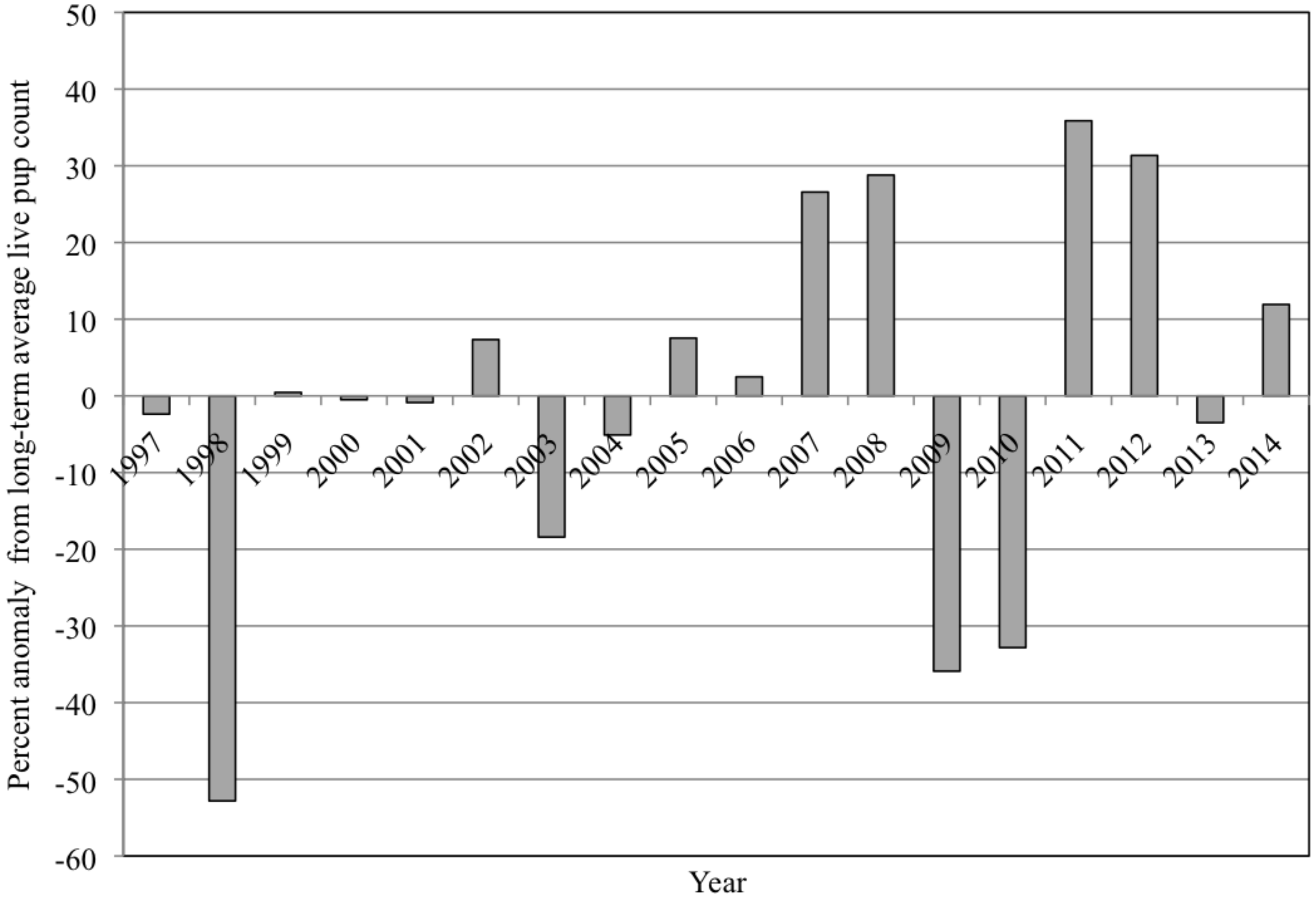

Figure 33. The percent anomaly of live California sea lion pup counts at San Miguel Island, California, based on a long-term average of live pup counts between 1997–2014 in late July when surviving pups were about 6 weeks old.

than the long-term average between 1997 and 2014 (fig. 33). However, similar to previous years, pup condition and pup growth was poor for the 2014 cohort. The average weight of three-month-old pups were 17% and 20% lower than the long-term average for female and male pups, respectively (fig. 34). Growth rates from three to seven months old were 78% below normal for both sexes and similar to the 2012 cohort (fig. 35).

For the past five of six years, the California sea lion population has experienced low pup survival, low pup births or both (Melin et al. 2010; Melin et al. 2012; Leising et al. 2014). An unusual mortality event (UME) was declared for California sea lions in southern California (http://www.nmfs.noaa.gov/pr/health/mmume/californiasealions2013.htm) in response to unprecedented numbers of young pups from the 2012 and 2014 cohorts stranding along the coast between January and April and poor condition of pups at San Miguel Island and other rookeries during the winter (Wells et al. 2013; Leising et al. 2014). The two cohorts experienced dramatically different ocean conditions. During winter 2013, ocean conditions were unusually cold and had high primary productivity (Wells et al. 2013) and should have produced good foraging conditions for nursing females. In contrast, ocean conditions during the winter 2014 were unusually warm due to the continuation of a positive signal in the Pacific Decadal Oscillation and the presence of anomalously large warm water pools along the West Coast. Fisheries surveys during the springs in both years indicated that several of the primary fish prey of California sea lions including Pacific sardine (*Sardinops sagax*), northern anchovy (*Engraulis mordax*), and Pacific hake (*Merluccius productus*) were not abundant along the central California coast in the foraging range of nursing females (Bjorkstedt et al. 2012; Wells et al. 2013; Leising et al. 2014: this volume). Analysis of scat contents of California sea lion females during these periods indicated increased consumption of rockfish (*Sebastes* spp.) and market squid (*Doryteuthis opalescens*) (Melin et al. in Review). Thus, the composition of the prey community available to nursing females was similar in 2012 and 2014 but quite different from previous years when pups were in better condition (Melin et al. 2012). Consequently, the current hypothesis for the poor condition of dependent pups and ultimately, large numbers of weaned pups stranding on the coasts is that alterations in

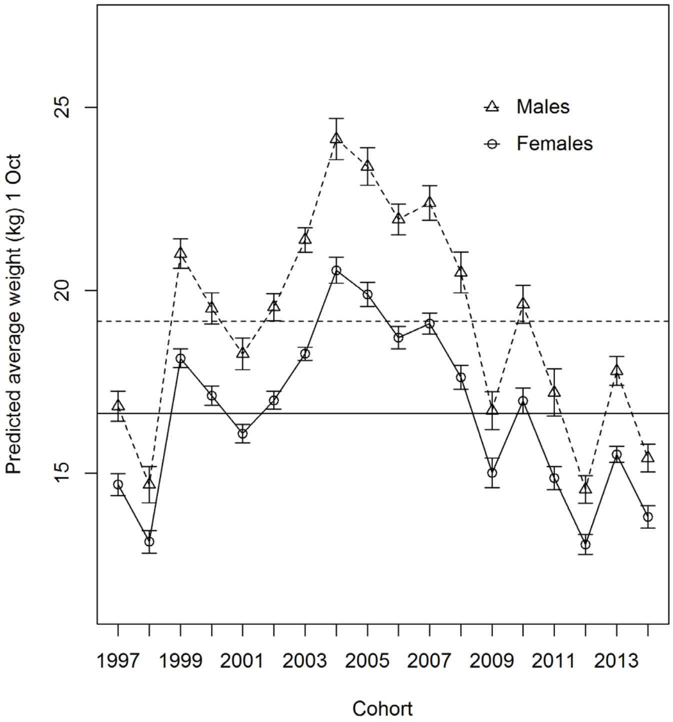

Figure 34. Predicted average weights of 3-month-old female (open circle) and male (open triangle) California sea lion pups at San Miguel Island, California, 1997–2014 and long-term average between 1975 and 2014 for females (solid line) and males (dashed line). Error bars are ± 1 standard error.

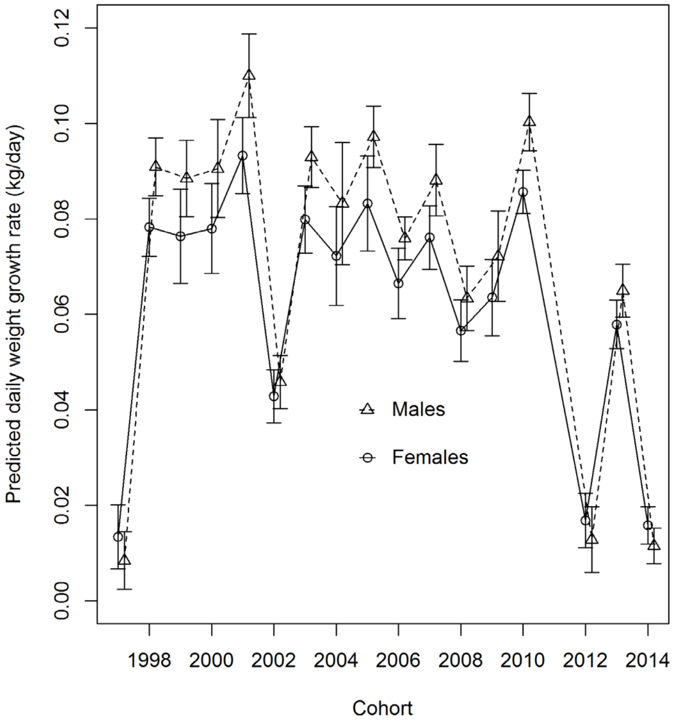

Figure 35. Predicted average daily growth rate of female (open circle) and male (open triangle) California sea lion pups between 4 and 7 months old at San Miguel Island, California, 1997–2014. Error bars are ±1 standard error.

the prey community due to oceanographic changes on local and regional scales have resulted in nursing females being unable to fully support lactation and the needs of their dependent pups. We anticipate this trend to continue until the diversity and abundance of the prey community increases and provides greater nutritional value to nursing females.

DISCUSSION

The winter of 2013–14 saw a drastic change in the conditions throughout the California Current as compared to the previous years (2013 being a record-breaking year of high cumulative upwelling; Wells et al. 2013; Leising et al. 2014). Between fall of 2013 and spring of 2014, the PDO switched sign to positive, indicating warming coastal waters, the NPGO switched sign to negative, typically indicating lower productivity in the southern CCS, and the MEI switched sign to positive, indicating the possible development of an El Niño. During 2014, these trends continued, along with increasingly warm waters throughout the CCS. During spring 2015, there was some moderate cooling along the central and northern coast within the CCS, due to upwelling. Meanwhile, surface waters along the eastern equatorial Pacific continued to warm during mid-2015, leading to high values of the MEI, suggesting potentially the strongest El Niño since 1997–98, with impacts likely reaching the CCS during winter 2015–16. Preceding the development of the El Niño, the fall of 2013 in the NE Pacific saw a rise of sea surface temperatures, likely due to a shift in wind patterns, a lack of winter storms, and an increase in sea level pressure (Bond et al. 2015); this large area of high SST anomaly was labeled the blob by Bond. There was also a rise in sea surface temperatures both coastally and offshore of southern California (distinct from the main portion of the blob in the NE Pacific) in mid-2014, also most likely related to changes in wind patterns (detailed below). Typical atmospheric patterns over the NE Pacific were replaced by a resilient ridge of high pressure, which greatly altered the ocean surface structure, and continues to do so as of the writing of this report. The result has been a continued warming of surface waters in the NE Pacific, at times in excess of 4°C above the climatological mean.

Warming in the Southern CCS

The Southern California Warm Anomaly (SCWA; as distinct geographically from the blob in the NE Pacific) was first evident in the spring of 2014 as a band of warm surface water along the shelf break (fig. 36). It is unlikely that this feature advected into the region from the north since the CC was located at this time in the offshore areas of the domain (west of Station 80). During the summer this feature intensified, but its spatial footprint

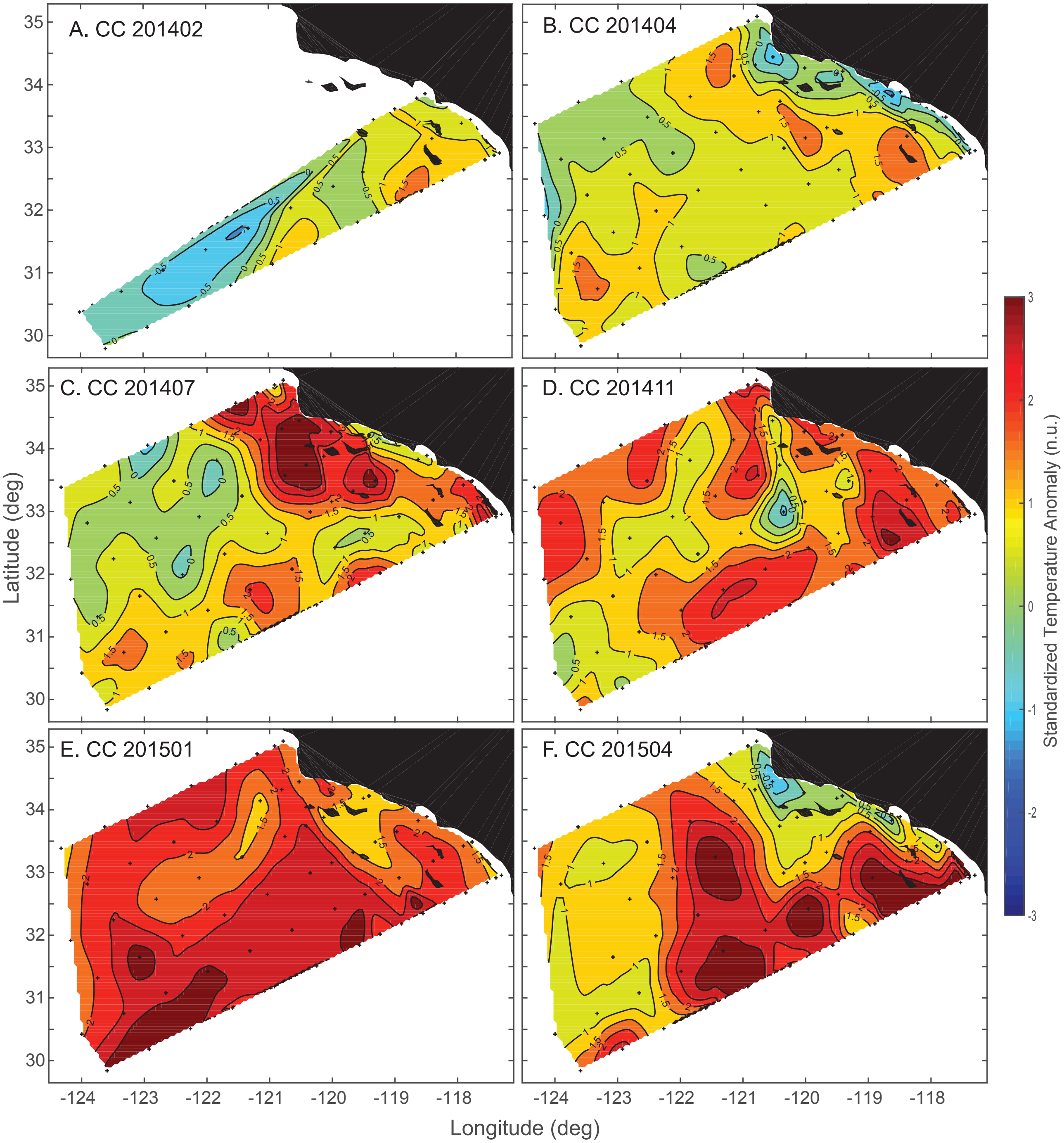

Figure 36. Temperature anomalies at a depth of 10 m standardized by the standard deviation of temperature for the CalCOFI 66 station standard grid for the last six CalCOFI cruises that covered the 2014–15 warm anomaly, i.e., the winter (A), spring (B), summer (C), and fall (D) of 2014 and the winter (E) and spring (F) of 2015. The 2014 winter cruise was not completed due to ship failure.

did not. Warm surface layer anomalies off Pt. Conception during the summer of 2014 were partly driven by extremely low rates of coastal upwelling (fig. 2); i.e., no cold water was brought into the surface layer as usually happens during this time of the year. During the fall of 2014 and winter of 2015 these 10 m anomalies intensified, covering the complete CalCOFI domain (fig. 36).

One way to place these events in context is to examine long-term data in the region to look for comparisons. Subsurface temperature data have been collected along line 90 of the CalCOFI grid since 1950. Annual temperature anomalies at a depth of 10 m along this line for the time period 1984 to 2015 (fig. 37A) are highly correlated with the temperature anomalies of the

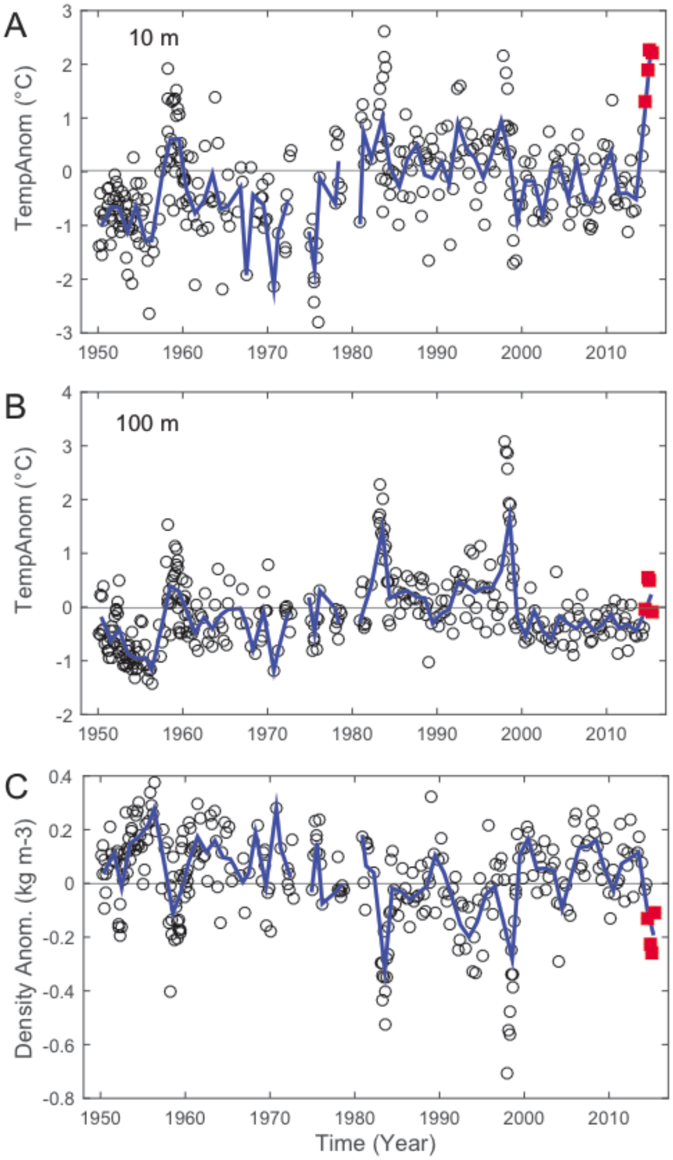

Figure 37. Cruise averages of property anomalies for CalCOFI Line 90, stations 30 to 90 for the time period 1950 to 2015. A) temperature anomaly at 10 m, B) temperature anomaly at 100 m, and C) density anomaly at 100 m. Data are derived and plotted as described for Figure 11.

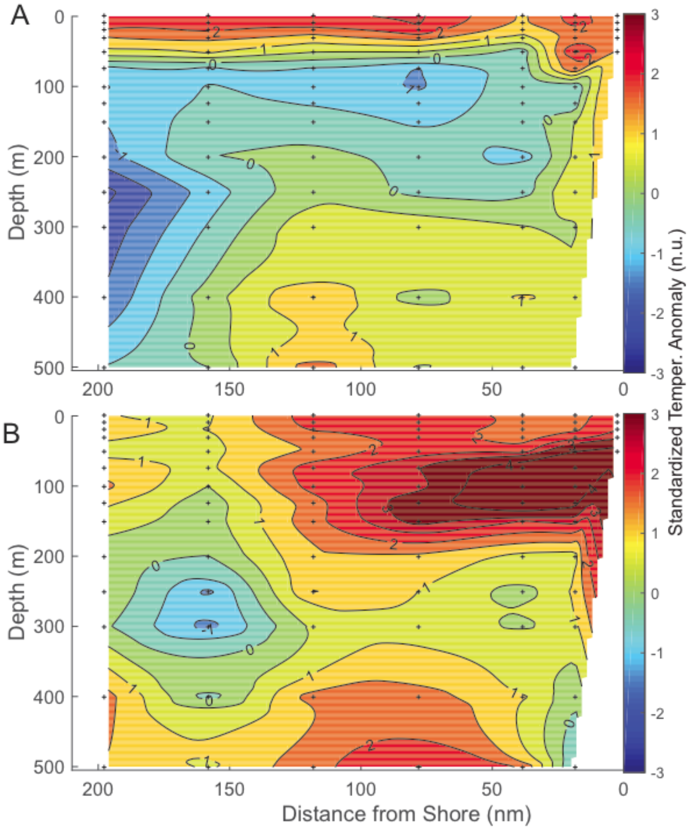

Figure 38. Standardized temperature anomalies, these have no units (n.u.), along CalCOFI line 80 plotted against depth and distance from shore for periods corresponding to the height of the 2014–15 warm anomaly (A: CC201501) and the 1998 El Niño (B: CC199802). Plotted data are deviations from expected values in terms of standard deviations in order to illustrate the strength of the relative changes at different depths.

entire CalCOFI domain (rho = 0.92, $p < 0.001$). These data show that the recent anomalies at a depth of 10 m were as large as those observed during the strong El Niños of 1957–58, 1982–83, and 1997–98 (fig. 37A). Temperature anomalies at a depth of 100 m observed during the El Niños and the SCWA differ dramatically: whereas relative anomalies during the El Niños were stronger at 100 m compared to the surface layer, anomalies at a depth of 100 m during the SCWA were slightly elevated only during the fall of 2014 and the winter of 2015. Consistent with these differences, dramatically different distributions of temperature with depth and distance from shore were observed throughout the CalCOFI domain during the winters of 1998 and 2015 (e.g., Line 80, fig. 38). The strongly positive relative temperature anomalies of 2015 extended to the far offshore but were confined to the surface layer (upper ~50 m). In contrast, the relative anomalies of 1998 were strongest at depth of 50 to 150 m and did not extend offshore (fig. 38). These patterns suggest that the coastal subsurface advective component that drives water column properties during El Niños was not active during the SCWA. Increasing transport, temperature, and salinity of the California Undercurrent (CU) are important drivers of changing water mass characteristics during El Niños (Lynn and Bograd 2002). Such changes in water mass characteristics are clearly evident in the core of the CU (CalCOFI station 90.30, depth 200 to 300 m) during the strong El Niños of 1982–83 and 97–98; (e.g., spiciness, fig. 39). Interestingly, strongly positive spiciness anomalies were only observed during the summer of 2014 and not during any other time period corresponding to the SCWA.

Properties at the σ_t 26.4 isopycnal (fig. S6), which is found at a depth of about 200 m in the CalCOFI

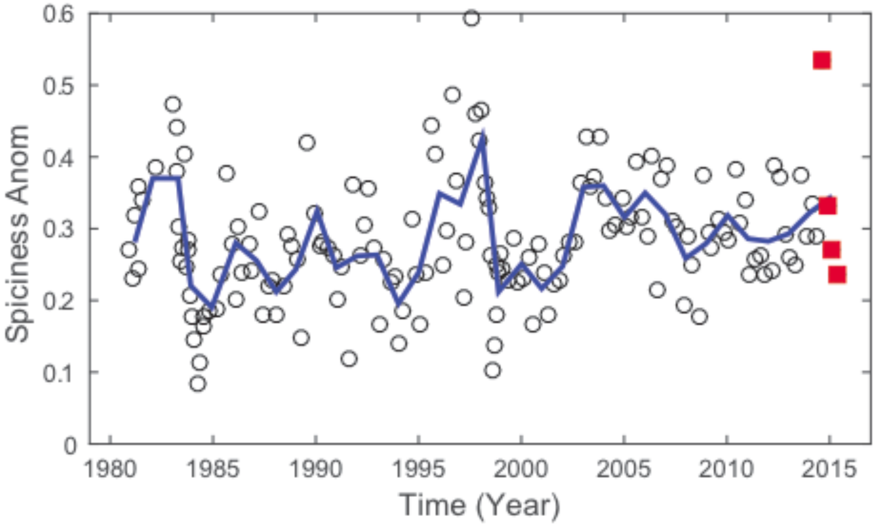

Figure 39. Cruise averages of spiciness at a depth of 200 to 300 m at Station 90.30 for the time period 1981 to 2015. The core of the California Undercurrent is usually found in this location. Data are derived and plotted as described for Figure 11.

domain, also did not change in synchrony with the SCWA. The depth of this isopycnal increased by about 20 m during this time (fig. S6A), with values slightly less than those observed during the 1997–98 El Niño. Properties on this isopycnal have been used in the past as indicators of long-term changes of southern California Current deep waters (e.g., Bjorkstedt et al. 2011, 2012; Bograd et al. 2014). The decline of oxygen concentrations between the years 2000 and 2012, and the concomitant increase of NO_3 (fig. S6), was assumed to be driven by basin-wide drivers (Bjorkstedt et al. 2012). The dramatic reversal of the oxygen and nitrate trends over the last 3 years forces us to rethink this assumption. The drivers of these recent changes are unclear at the present.

The potential drivers of the SCWA are local warming of the surface layer due to atmospheric anomalies, the advection of anomalously warm surface waters into the region from the North Pacific blob, and Kelvin waves travelling up the coast driven by equatorial anomalies. The above analysis of the waters of the California Undercurrent suggests that waters of equatorial origin may have been present in the region during the summer of 2014 but not during other periods of time. The absence of positive temperature anomalies close to the coast at depths of 50 to 150 m during the SCWA supports the conclusion that equatorial forcing of the region was weak or negligible during this time. Further supporting this conclusion are the observations from the IMECOCAL, Baja, California region. As noted above, although surface waters when averaged across the IMECOCAL survey were warm and salty as compared to the long-term mean, these anomalies were confined to the surface, and there was no northward flow north of Punta Eugenia, as has occurred in the past during warm events such as El Niño (Durazo 2015). The strongly positive surface layer anomalies observed during the summer of 2014 within the CalCOFI region were in part driven by weak coastal winds, i.e., weak coastal upwelling not injecting cold subsurface water into the mixed layer and weak wind-induced mixing, resulting in shallow and extremely warm mixed layers. Exact identification of the drivers of the SCWA off southern California is limited by the low temporal resolution of the CalCOFI time series. An analysis of high-resolution sampling via gliders may offer a way to more explicitly address this, but is beyond the scope of this report.

Warming Throughout the CCS

Examining the timing of warming along the entire current, and comparing with the evolution of the strong El Niño of 1997–98 may help with interpreting which forces dominated within the different segments of the CCS. As noted in Bond et al. (2015), the anomalous warm blob began offshore in the Gulf of Alaska in late 2013, but began to be seen in the coastal region as early as May of 2014 off of British Columbia. The exact timing of the onset of warming throughout the CCS can be seen by examining the anomaly of remotely sensed SST data (fig. 40, left-hand panels) in the offshore region, and buoy SST temperatures from the nearshore region (fig. 40, right-hand panels). For the more-offshore locations (by approximately 1°–2° compared to the nearby buoys) examined using remotely sensed data, warming during mid-2014 to mid-2015 was very similar in magnitude to that seen during 1997–98 (between 2°–4°C positive anomaly depending on location). However, the warming that occurred during this period was not due directly to El Niño, which had only begun to warm

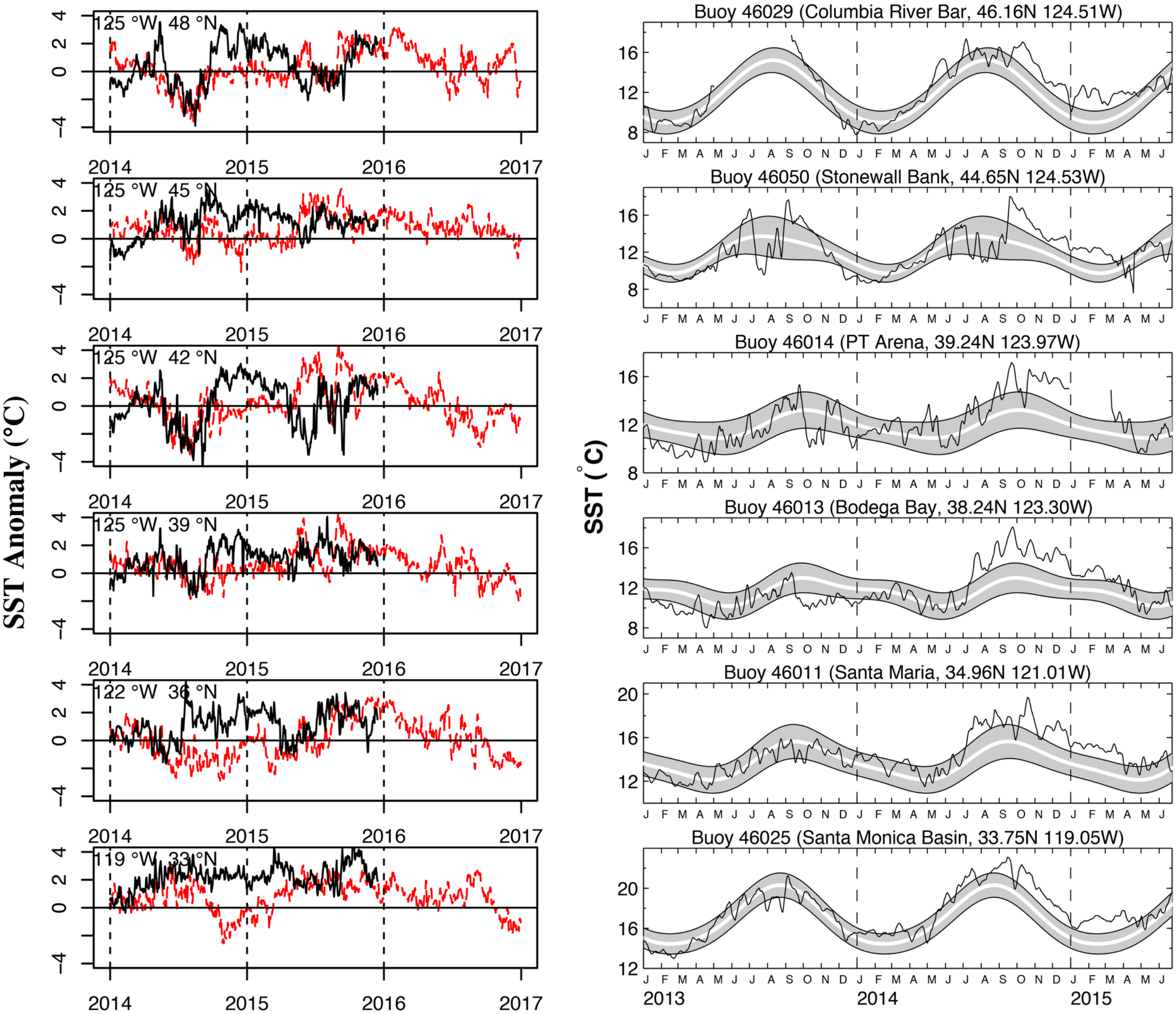

Figure 40. Daily sea surface temperature (SST) anomalies (left-hand panels) for selected locations along the US West Coast (locations same as those calculated for upwelling indices in Figure 3; data from the Daily Optimum Interpolation AVHRR data set, see http://coastwatch.pfeg.noaa.gov/erddap/griddap/ncdcOisst2Agg.html) with black line indicating 2014–15, and red line indicating 1996–98, and (right-hand panels) SST from selected buoys along the US West Coast, with grey region indicating the range of climatological values, white line the climatological mean, and black line the current (2013–15) values.

the equatorial Niño 3.4 region during mid-2014, leaving insufficient time for propagating Kelvin waves to reach even the southern portions of the CCS. Off British Columbia, anomalous warming occurred as early as May 2014, but then the water cooled, most likely due to increased upwelling, as suggested by the upwelling index for this time and location (fig. 40, top left, and fig. 2). Warmer conditions then returned very rapidly after the cessation of upwelling in September. Except for the most southerly Southern California Bight location (fig. 40, lower left panel, 33˚N), the other more-offshore locations examined followed a similar pattern during 2014 as that described above; gradual warming during spring, followed by cooling as summertime upwelling occurred, followed by very rapid warming between August and September. This rapid warming in the fall was due to an advection of the blob waters into the coastal region, which is particularly apparent in the buoy data for locations between 34˚N and 45˚N (fig. 40, right-hand panels). For those stations, the increase in temperatures from slightly above the climatological mean to greater than 2 standard deviations above the mean occurred in as little as a week, or even within 1 day, as was observed off Stonewall Bank. Although this is a typical process whereby upwelling shuts down and warm waters advect onshore, the difference in 2014 was that the waters moving onshore were several degrees above the typical temperatures seen within the coastal CCS upon the cessation of upwelling. Although the blob was located more towards the northern CCS and centered near the Gulf of Alaska, warming in the nearshore regions sampled by the buoys actually began progressively earlier in the southern stations, particularly as compared to Stonewall Bank. The most likely reason for this is that upwelling was still active in the northern areas through mid-September, whereas upwelling in the south had decreased dramatically (negative anomaly) as early as July (fig. 2).

Summarizing, warming in the surface waters proceeded as follows: 1) waters within the Gulf of Alaska warmed during the fall of 2013 due to changes in atmospheric forcing, 2) waters offshore of Oregon, California, and within the Southern California Bight warmed gradually during spring 2014, also likely due to changes in atmospheric forcing, 3) coastal warming decreased during summer 2014, due to low, but still effective, coastal upwelling, 4) with the cessation of upwelling in the fall of 2014 (Aug–Sept) waters in the nearshore saw dramatic advective-related warming as the offshore anomalies moved into the coast, starting in the south first, and 5) waters in both offshore and nearshore remained anomalously warm through the winter of 2014–early spring 2015, until upwelling began in April–May of 2015. After the cessation of upwelling in summer/fall 2015, most stations then show a pattern of warming very similar to that seen during the fall of 1997 (fig. 40), suggesting that the CCS may finally be responding to the impacts of El Niño.

Ecosystem Response Overview

The productivity of the system during 2014, as observed by the standing stock of chlorophyll *a* (a proxy for system productivity), was reduced compared to 2013. The low productivity was a result of weak upwelling during the summer of 2014 and extremely low mixed layer concentrations of nitrate, or a nutrient co-varying with it, as seen throughout the CalCOFI domain. Low nutrient concentrations within the mixed layer, in turn, were a consequence of deep nitraclines (fig. 12). 2015 saw an increase in upwelling within the northern regions of the CCS relative to 2014, resulting in more phytoplankton standing stock than the previous year, however, it was spatially and temporally patchy.

Every contribution to this report that included samples for species abundance and composition during 2015 saw drastic changes from previous sampling. Off Washington and Oregon, high abundances of anchovy and sardine larvae were found, along with fish that had very rarely if ever been identified within those trawls. Similarly, off Oregon, the copepod assemblage was augmented by rare or previously unrecorded species, thought to consist mainly of warm-water offshore species (B. Peterson, pers com), along with both "northern" and high abundances of "southern" affiliated copepods, leading to high species richness. The appearance of these rare, presumably warm-water offshore species is critical, as it further supports the hypothesis that source waters were from far offshore, likely due to advection of blob waters. High abundances of jellies were also found off coastal Oregon (particularly *Aequorea* spp.), whereas high abundances of tunicates were found off the more central region of the coastal CCS. Although juvenile rockfish abundances remained high along the central coast, the abundance of euphausiids, squid, and sanddab decreased throughout much of the central CCS. Very few, if any sardine or anchovy were found off southern California, although significant numbers of dorado eggs were found (something that has rarely occurred, except during extreme warm water events). The two community analyses that were conducted both showed 2015 as an extreme outlier compared to all other years, including the 1997–98 El Niño, although in the central CCS trawls, species were found which are typically associated with strong El Niños. These same samples also contained relatively high abundances of coastal upwelling-related species, along with warm-water offshore affiliated species. The presence of these three different groups that come from different water masses within the same samples suggests 2015 may have had one of the sharpest gradients in onshore to offshore temperatures (and thus also water masses) as possibly any other recorded time, given the offshore temperatures reaching up to 4°C above the climatological mean, while at the same time, significant coastal upwelling occurred along the central and northern coast.

Unlike fish and invertebrates, seabirds and marine mammals had mixed responses during 2014 (2015 data for some of these species is yet to be processed), presumably depending on their abilities to compensate for changes in their normal prey, and depending on their location relative to the patchiness in upwelling and productivity. Murres off Yaquina Head, Oregon had decreased success during 2014 as compared to 2013, whereas the murres and Brandt's cormorants at Castle Rock, CA, showed average or increased productivity. Similarly, the seabirds on southeast Farallon Island showed both species with higher and lower breeding success during 2014. Seabirds within the CalCOFI domain had average species richness during 2014–15, and an increase in the presence of sooty shearwaters and Cook's petrel during the spring-time cruises in both 2014 and 2015. For sea lions, 2014 saw decreased weights and growth rates for the pups, and 2015 is expected to be an extremely poor year for them due to changes in their feeding environment.

Summary

The common theme for the California Current system during 2014–15 is the dramatic change from the previous year, in both physical and biological properties. The intrusion of the offshore anomalously warm waters (e.g., the blob) brought both "new" warm-water offshore species, and also typically El Niño-related species into or within near proximity of the nearshore coastal regions. Unlike the lead-in to past strong El Niño's, 2015 still saw considerable amounts of effective upwelling in the central and northern regions, thus coastal, upwelling-related species (such as rockfish juveniles) were still found in relatively high abundances. The result is a system with overall moderate productivity (depending on location), extremely high species diversity, and overall changes in ecosystem structure. Although not documented in the sampling presented here, during 2015 there was also an unprecedented harmful algal bloom, primarily of the genus *Pseudo-nitzchia* sp., which produces the toxin domoic acid. This bloom ranged form Alaska to southern California by July, and resulted in the closure of many fisheries along the US West Coast (for further details, see: http://www.nwfsc.noaa.gov/news/features/west_coast_algal_bloom/index.cfm). The question now remains as to how long these conditions will persist; has the CCS transitioned to yet a new state or phase in a cycle that is different from previously observed cycles, or are we seeing merely a transitional period? Given what is known of past El Niños and atmospheric teleconnections (Schwing et al. 2008), one possible scenario is that as the El Niño begins to more heavily influence the region, it will alter the atmospheric patterns that created the blob and thus return the system to a more typical warm-phase PDO condition, with the overlaid El Niño forcing (N. Mantua pers com). Whether the ecosystem will also return to a relatively similar "known" state, will remain to be observed.

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LITERATURE CITED

Auth, T. D. 2011. Analysis of the spring–fall epipelagic ichthyoplankton community in the northern California Current in 2004–09 and its relation to environmental factors. Calif. Coop. Oceanic. Fish. Invest. Rep. 52:148–167.

Bakun, A. 1973. Coastal upwelling indices, west coast of North America, 1946–71. U.S. Dep. Commer., NOAA Tech. Rep., NMFS SSRF-671, 103 p.

Bjorkstedt, E., R. Goericke, S. McClatchie, E. Weber, W. Watson, N. Lo, B. Peterson, B. Emmett, R. Brodeur, J. Peterson, M. Litz, J. Gomez-Valdez, G. Gaxiola-Castro, B. Lavaniegos, F. Chavez, C. A. Collins, J. Field, K. Sakuma, P. Warzybok, R. Bradley, J. Jahncke, S. Bograd, F. Schwing, G. S. Campbell, J. Hildebrand, W. Sydeman, S. Thompson, J. Largier, C. Halle, S. Y. Kim, and J. Abell. 2012. State of the California Current 2010–11: Regional Variable Responses to a Strong (But Fleeting?) La Niña. California Cooperative Oceanic Fisheries Investigations Report 52:36–68.

Bograd, S. J., I. Schroeder, N. Sarkar, X. M. Qiu, W. J. Sydeman, and F. B. Schwing. 2009. Phenology of coastal upwelling in the California Current. Geophysical Research Letters 36:doi 10.1029/2008gl035933.

Bograd, S. J., M. P. Buil, E. Di Lorenzo, C. G. Castro, I. D. Schroeder, R. Goericke, C. R. Anderson, C. Benitez-Nelson, F. A. Whitney. Changes in source waters to the Southern California Bight, Deep Sea Research Part II: Topical Studies in Oceanography, Volume 112, February 2015, Pages 42–52, ISSN 0967–0645, http://dx.doi.org/10.1016/j.dsr2.2014.04.009.

Bond, N. A., M. F. Cronin, H. Freeland, and N. Mantua. 2015. Causes and impacts of the 2014 warm anomaly in the NE Pacific. Geophys. Res. Lett., 42, 3414–3420. doi: 10.1002/2015GL063306.

Brodeur, R. D., J. P. Fisher, R. L. Emmett, C. A. Morgan, and E. Casillas. 2005. Species composition and community structure of pelagic nekton off Oregon and Washington under variable oceanographic conditions. Mar. Ecol. Prog. Ser. 298: 41–57.

Daly, E. A., T. D. Auth, R. D. Brodeur, and W. T. Peterson. 2013. Winter ichthyoplankton biomass as a predictor of early summer prey fields and survival of juvenile salmon. Mar. Ecol. Prog. Ser. doi:10.3359/meps10320.

Di Lorenzo, E., N. Schneider, K. M. Cobb, P. J. S. Franks, K. Chhak, A. J. Miller, J. C. McWilliams, S. J. Bograd, H. Arango, E. Curchitser, T. M. Powell, and P. Riviere. 2008. North Pacific Gyre Oscillation links ocean climate and ecosystem change. Geophysical Research Letters 35:doi 10.1029/2007gl032838.

Durazo, R., and T. Baumgartner. 2002. Evolution of oceanographic conditions off Baja California: 1997–99. *Progr. Oceanogr.*, 54, 7–31.

Durazo, R. 2015. Seasonality of the transitional region of the California Current System off Baja California. *Journal of Geophysical Research-Oceans,* 120, 1173–1196, doi:10.1002/2014JC010405.

Gladics, A. J., R. M. Suryan, R. D. Brodeur, L. M. Segui, and L. Z. Filliger. 2014. Constancy and change in marine predator diets across a shift in oceanographic conditions in the Northern California Current. Marine Biology 161:837–851.

Gladics, A. J., R. M. Suryan, J. K. Parrish, C. A. Horton, E. A. Daly, and W. T. Peterson. 2015. Environmental drivers and reproductive consequences of variation in the diet of a marine predator. Journal of Marine Systems 146:72–81.

Hayward, T. L. 2000. El Niño 1997–98 in the coastal waters of Southern California: A timeline of events. CalCOFI Reports 41, 98–116.

Hoton, C. A. 2014. Top-down influences of Bald Eagles on Common Murre populations in Oregon. MS thesis, Oregon State University.

Horton, C. A., and R. M. Suryan. 2012. Brown Pelicans: A new disturbance source to breeding Common Murres in Oregon? Oregon Birds 38:84–88.

Hu, S., A. V. Fedorov, M. Lengaigne, and E. Guilyardi. 2014. The impact of westerly wind bursts on the diversity and predictability of El Niño events: An ocean energetics perspective, Geophys. Res. Lett.,41, 4654–4663, doi:10.1002/2014GL059573.

Hyrenbach, K. D., and R. R. Veit. 2003. Ocean warming and seabird communities of the Southern California Current System (1987–98): response at multiple temporal scales. Deep-Sea Research Part II 50:2537–2565.

Kruskal, J. B. 1964. Nonmetric multidimensional scaling: a numerical method. Psychometrika 29: 115–130.

Leising, A. W., et al. 2014. State of the California Current 2013–14: El Niño looming. California Cooperative Ocean and Fisheries Investigations Reports 55:31–87.

Ljung, L. System Identification: Theory for the User, Upper Saddle River, NJ, Prentice-Hal PTR, 1999.

Ludescher, J., A. Gozolchiani, M. I. Bogachev, A. Bunde, S. Havlin, and H. J. Schellnhuber. 2014. Very early warning of next El Niño. Proceedings of the National Academy of Sciences 111:2064–2066.

Lynn, R. J., and S. J. Bograd. 2002. Dynamic Evolution of the 1997–99 El Niño-La Niña cycle in the southern California Current system. Prog. Oceanogr. 54.

Lynn, R. J., and J. J. Simpson. 1987. The California Current system: The seasonal variability of its physical characteristics. *J. Geophys. Res.*, 92, 12,947–12,966.

Mantua, N. J., S. R. Hare, Y. Zhang, J. M. Wallace, and R. C. Francis. 1997. A Pacific Interdecadal Climate Oscillation with Impacts on Salmon Production. Bulletin of the American Meteorological Society 78:1069–1079.

Melin, S. R., A. J. Orr, J. D. Harris, J. L. Laake, R. L. DeLong, F. M. D. Gulland, and S. Stoudt. 2010. Unprecedented mortality of California sea lion pups associated with anomalous oceanographic conditions along the central California coast in 2009. California Cooperative Ocean and Fisheries Investigations Reports 51: 182–194.

Melin, S. R., A. J. Orr, J. D. Harris, J. L. Laake, and R. L. DeLong. 2012. California sea lions: An indicator for integrated ecosystem assessment of the California Current System. California Cooperative Ocean and Fisheries Investigations Reports 53:140–152.

Ohman, M., and E. Venrick. 2003. CalCOFI in a changing ocean. Oceanography 16, 76–85.

Perrins, C. M. 1970. The timing of birds' breeding seasons. Ibis 112: 242–255.

Ralston, S., and I. J. Stewart. 2013. Anomalous distributions of pelagic juvenile rockfish on the U.S. west coast in 2005 and 2006. CalCOFI Reports 54:155–166.

Ralston, S., K. M. Sakuma, and J. C. Field. 2013. Interannual variation in pelagic juvenile rockfish (*Sebastes* spp.) abundance—going with the flow. Fisheries Oceanography 22:4: 288–308.

Ralston, S., J. C. Field, and K. M. Sakuma. 2015. Longterm variation in a central California pelagic forage assemblage. Journal of Marine Systems (in press). http://dx.doi.org/10.1016/j.jmarsys.2014.06.013.

Reed, T. E., S. Waneless, M. P. Harris, M. Frederiksen, L. E. B. Kruuk, and E. J. A. Cunningham. 2006. Responding to environmental change: plastic responses vary little in a synchronous breeder. Proceedings of the Royal Society of London B 273:2713–2719.

Santora, J. A., I. D. Schroeder, J. C. Field, B. K. Wells, and W. J. Sydeman. 2014. Spatio-temporal dynamics of ocean conditions and forage taxa reveals regional structuring of seabird-prey relationships. Ecological Applications Ecological Applications 24:7:1730–1747.

Santora, J. A., and W. J. Sydeman. 2015. Persistence of hotspots and variability of seabird species richness and abundance in the southern California Current. Ecosphere, *in press*.

Schroeder, I. D., W. J. Sydeman, N. Sarkar, S. A. Thompson, S. J. Bograd, and F. B. Schwing. 2009. Winter pre-conditioning of seabird phenology in the California Current.

Schwing, F. B., M. O'Farrell, J. M. Steger, and K. Baltz. 1996. Coastal upwelling indices, West Coast of North America, 1946–1995, NOAA Tech. Memo., NOAA-TMNMFS-SWFSC-231, 144 pp.

Schwing, F. B., R. Mendelssohn, S. J. Bograd, J. E. Overland, M. Wang, S. Ito. Climate change, teleconnection patterns, and regional processes forcing marine populations in the Pacific, Journal of Marine Systems, Volume 79, Issues 3–4, 10 February 2010, Pages 245–257, ISSN 0924-7963, http://dx.doi.org/10.1016/j.jmarsys.2008.11.027.

Suchman, C. L., R. D. Brodeur, E. A. Daly, and R. L. Emmett. 2012. Large medusae in surface waters of the Northern California Current: variability in relation to environmental conditions. *Hydrobiologia*. 690:113–125.

Sydeman, W. J., K. L. Mills, J. A. Santora, S. A. Thompson, D. F. Bertram, K. H. Morgan, B. K. Wells, J. M. Hipfner, and S. G. Wolf. 2009. Seabirds and climate in the California Current—A synthesis of change. CalCOFI Report 50:82–104.

Sydeman, W. J., S. A. Thompson, J. A. Santora, J. A. Koslow, R., Goericke, and M. D. Ohman. 2015. Climate-ecosystem change off southern California: time-dependent seabird predator-prey numerical responses. Deep-Sea Research Part II:158–170.

Veit, R. R., P. Pyle, and J. A. McGowan. 1996. Ocean warming and long-term change in pelagic bird abundance within the California Current system. Marine Ecology Progress Series 139:11–18.

Wells, B. K., and 47 other authors. 2013. State of the California Current 2012–13: No such thing as an "average" year. CalCOFI Reports 54: 37–71.

Wolter, K. and M. S. Timlin. 1998. Measuring the strength of ENSO events—how does 1997/98 rank? Weather 53:315–324.

Yen, P. P. W., W. J. Sydeman, S. J. Bograd, and K. D. Hyrenbach. 2006. Springtime distributions of migratory marine birds in the southern California Current: oceanic eddy associations and coastal habitat hotspots over 17 years. Deep-Sea Research II 53: 399–418.

Part II

SYMPOSIUM OF THE 2014 CALCOFI CONFERENCE: PREDICTING THE CALIFORNIA CURRENT SYSTEM

PREDICTING THE CALIFORNIA CURRENT SYSTEM: SYMPOSIUM OF THE 2014 CALCOFI CONFERENCE

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The California Current system (CCS) extends from British Columbia to Baja California. The southern end of the CCS has been observed by CalCOFI[1] for more than 66 years. What will the CCS be like in the coming decades and beyond? How well can the CCS, or parts of it, be forecast on the scale of days to seasons and predicted on the scale of climate change? How will warming, stratification, acidification, and deoxygenation affect the CCS? Our ability to inform management and policy decisions depends on answers to such questions. The Symposium of the 2014 CalCOFI Conference was planned to address these issues. Presentations included hindcasting and prediction of the California Current using statistical and dynamical models, ranging from physics to fishers, and including the atmosphere and ocean. Model types included general circulation models, regional models, Atlantis-type models, and hybrid models including fish and humans.

Dunne et al. used the GFDL's Earth System Model[2] (ESM). A key question was how to bridge scales, from global, which is coarse in resolution but inclusive in processes, to regional, which has the desired resolution but excludes interactions with other regions and the earth. Both have inherent biases with regard to Eastern Boundary Currents. Dunne et al. presented results for a 0.1° (~10 km) ocean and 50 km atmosphere ESM that includes lower trophic levels. This spatial resolution is necessary to resolve currents in the EBCs, whose lateral dimensions scale with the Rossby radius. Comparsion of EBC temperature and chlorophyll with observations improved markedly from the 1° to 0.1° models, though challenges remain. The value of ESMs in predicting EBC dynamics was demonstrated by the unexpected result of the predicted influence of distant processes in the NW Pacific on the nitrate concentration of water upwelled in the California Current under a future climate (Rykaczewski and Dunne 2010).

Curchitser et al. addressed this scale issue by combining model types. A multi-scale ocean was incorporated as part of the NCAR CESM[3]. Scales ranged from a 7 km ocean model in the 1° CESM (ocean, atmosphere) and from months to 150 years. Not only was the fidelity of the model to observations enhanced in the multiscale model but feedbacks between regional and global models, particularly large-scale perturbations by regional upwelling, were discovered.

Rose et al. focused on End-to-End modeling—from physics to fishers in the California Current and with anchovy and sardine. The Regional Ocean Modeling System (ROMS) was used with ~10 km and daily resolution and ~1000 km and 50 y domain. A distinguishing feature of this effort is the inclusion of an "individual-based, full life cycle anchovy and sardine submodel" and characterizations of predators, including fishing fleets (Rose et al. in press). This model recreates the decadal-scale variation in anchovy and sardine dynamics, giving hope to our ability to predict such dynamics under a future, changed climate.

Edwards et al. hindcast and nowcast the state of the California Current system using the UCSC ROMS 4D-Var model[4]. A key element of this work is the use of data assimilation, i.e., the continuous incorporation of observational data into the model. Resolution is ~10 km and 8d/cycle and domain being waters off California, Oregon, and Washington and 31 years. This model has enabled the evaluation of fundamental physical processes, such as wind-induced upwelling and stratification, to characterize the habitat of rockfish.

Seo et al. focused on the effects of mesoscale SST and surface currents on eddy kinetic energy (EKE) and Ekman pumping. A 7 km regional coupled model showed a 25%–30% dissipation of EKE due to primarily to eddy-wind interactions, showing the need to include high-resolution air-sea coupling in both directions.

Siedlecki et al. focused on seasonal forecasts of ocean conditions that are "testable and relevant to annual management decisions" in the CCS using J-SCOPE[5].

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[1] CalCOFI (California Cooperative Oceanic Fisheries Investigations) http://www.calcofi.org/

[2] GFDL ESM (Geophysical Fluid Dynamics Laboratory's Earth System Model) http://www.gfdl.noaa.gov/earth-system-model

[3] UCAR CESM (University Corporation for Atmospheric Research Community Earth System Model) http://www.cesm.ucar.edu/models/ccsm4.0/

[4] UCSC Ocean Modeling and Data Assimilation http://oceanmodeling.ucsc.edu/

[5] J-SCOPE (JISAO Seasonal Coastal Ocean Prediction of the Ecosystem) http://www.nanoos.org/products/j-scope/

Seasonal forecasts are needed for management decisions yet have been largely neglected due to their being between short-term forecasts and long-term predictions. J-SCOPE combines a ROMS model with the NOAA Climate Forecast System (3-dimensional with data assimilation) and a detailed model of dissolved oxygen to hindcast and forecast SST, O_2, and pH locally and regionally. Forecast skill is good to several months. This model is of particular value to inform management decisions in a region with significant climate-related changes in biogeochemistry and ecology, including fisheries and aquaculture.

Kaplan describes the use of the Atlantis[6] End-to-End model in the California Current system. Atlantis is a ROMS-based model with differential equations defining interactions between physical, chemical, and biological, including human, components of a system. It is a highly parameterized model that can be tuned with observations. Resolution is 12-h time steps and domain is the coastal waters of California, Oregon, and Washington.

Ye et al. describe how nonlinear systems do not lend themselves to analysis and prediction using linear models. They show that nonlinear properties of systems, derived from the analysis of time series of system variables, can be used for short-term forecasting, hence management, using equation-free models.

Themes derived from the combined presentations in the Symposium include:

- Scale is important. As Levin (1992) wrote, we perceive "only a low-dimensional slice through a high-dimensional cake" (p. 1945). In general, populations (e.g., of fish) affected by management decisions are at a scale currently resolved poorly in global-scale models. Yet the latter are useful, if not necessary, to inform higher-resolution models, e.g., with boundary conditions. Increasing computing power and new modeling schemes give promise here.
- Two-way coupling is often important.
- Trade-offs and limits exist. Resolution and domain vary inversely. Forecasting and prediction of nonlinear systems may be inherently limited by their chaotic behavior.
- Long-term, continuous observing programs, such as CalCOFI, are necessary to support all modeling efforts to understand and forecast the CCS. Observations are needed to create models and evaluate their predictive skill. Environmental intelligence requires environmental knowledge.
- Communication and collaboration are important, within both the modeling community writ large and between it, those who observe and those who rely on models, particularly to make decisions in management and policy.

Highest priority should be given to enhancing collaboration among governmental agencies and academic institutions. CalCOFI's success is due in large part to the federal (National Oceanic and Atmospheric Administration[7]), state (California Department of Fish and Wildlife[8]) and university (University of California, San Diego's Scripps Institution of Oceanography[9]) partnership of 66 years. The Symposium papers demonstrate the strengths of individual NOAA and academic entities in state-of-the-art prediction of the California Current system. An investment in an enhanced partnership among NOAA line offices, centers and labs and cooperative institutes working on the California Current system would have a high return in regard to informing decisions on management and policy. Such entities include Geophysical Fluid Dynamics Laboratory[10], the Northwest and Southwest Fisheries Science Centers[11,12], the Pacific Marine Environmental Laboratory[13], the Joint Institute for the Study of the Atmosphere and Ocean[14], the Cooperative Institute for Marine Resources Studies[15], and the Cooperative Institute for Marine Ecosystems and Climate[16].

LITERATURE CITED

Levin, S. A. 1992. The problem of pattern and scale in ecology. Ecology 73(6):1943–67.

Rose, K. A., J. Fiechter, E. N. Curchitser, K. Hedstrom, M. Bernal, S. Creekmore, A. Haynie, S.-I. Ito, S. Lluch-Cota, B. A. Megrey, C. A. Edwards, D. Checkley, T. Koslow, S. McClatchie, F. Werner, A. MacCall, and V. Agostini. 2015. Demonstration of a fully-coupled end-to-end model for small pelagic fish using sardine and anchovy in the California Current. Progress in Oceanography, doi: 10.1016/j.pocean.2015.01.012.

Rykaczewski, R. R., and J. P. Dunne. 2010. Enhanced nutrient supply to the California Current Ecosystem with global warming and increased stratification in an earth system model. Geophysical Research Letters 37, L21606, doi:10.1029/2010GL045019.

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[6] Atlantis Ecosystem Model http://www.nwfsc.noaa.gov/research/divisions/cb/documents/atlantis_ecosystem_model.pdf

[7] NOAA http://www.noaa.gov/

[8] CDFW https://www.wildlife.ca.gov/

[9] UCSD/SIO https://scripps.ucsd.edu/

[10] GFDL http://www.gfdl.noaa.gov/

[11] NWFSC http://www.nwfsc.noaa.gov/

[12] SWFSC https://swfsc.noaa.gov/

[13] PMEL http://www.pmel.noaa.gov/

[14] JISAO http://www.jisao.washington.edu/

[15] CIMRS http://hmsc.oregonstate.edu/cimrs

[16] CIMEC https://scripps.ucsd.edu/cimec

REPRESENTATION OF EASTERN BOUNDARY CURRENTS IN GFDL'S EARTH SYSTEM MODELS

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ABSTRACT

The world's major Eastern Boundary Currents (EBC) are critically important areas for global fisheries. Computational limitations have divided past EBC modeling into two types: high-resolution regional approaches that resolve the strong mesoscale structures involved; and coarse global approaches that represent the large-scale context for EBCs but crudely resolve only the largest scales of their local manifestation. These latter global studies have illustrated the complex mechanisms involved in the climate change and acidification response in these regions, with the EBC response dominated not by local adjustments but large-scale reorganization of ocean circulation through remote forcing of water mass supply pathways. While qualitatively illustrating the limitations of regional high-resolution studies in long-term projections, these studies lack the ability to robustly quantify change because of the inability of these models to represent the baseline mesoscale structures of EBCs. In the present work, we compare current generation coarse resolution (1°) and a prototype next generation high-resolution (1/10°) Earth System Models (ESMs) from NOAA's Geophysical Fluid Dynamics Laboratory in representing the four major EBCs. We review the long-known temperature biases that the coarse models suffer in being unable to represent the timing and intensity of upwelling-favorable winds. In promising contrast, we show that the high-resolution prototype is capable of representing not only the overall mesoscale structure in physical and biogeochemical fields, but also the appropriate offshore extent of temperature anomalies and other EBC characteristics. In terms of representation of large-scale circulation, results were mixed, with the high-resolution prototype addressing some, but not all, of the biases in the coarse-resolution ESM. The ability to simulate EBCs in the global context at high resolution in global ESMs represents a fundamental milestone towards both seasonal to interannual ecological forecasting and long-term projection of climate, ecosystem, and acidification baselines and sensitivity.

INTRODUCTION

Past work on the sensitivity of the California Current system has shown the potential for large changes in ecosystem state under climate variability and change (Rykaczewski and Dunne 2010) that agree qualitatively with long-term observations from CalCOFI (Bograd et al. 2008). Specifically, GFDL's coarse resolution ESMs projected increased nitrate (NO_3) in the California Current. While temperature and NO_3 are negatively correlated seasonally and interannually, they are positively correlated under climate change. The mechanisms underlying these changes were found to be a combination of poleward migration of the source-water formation region leading to increase in light limitation and preformed nutrient supply combined with an increase in residence time of source waters before upwelling that led to additional accumulation of nutrients before upwelling. This dominance of remote forcing of local California Current changes demonstrated the potentially complex interplay of changes in atmospheric winds and heat fluxes, stratification, ventilation, and water mass pathways modulating the biogeochemical response. Even excluding global climate change driven components of variation, EBCs are exposed to a suite of forcing modes, including: the seasonal cycle driving pressure gradients and winds; remote interannual forcing like El Niño Southern Oscillation, Pacific Decadal Oscillation, and North Pacific Gyre Oscillation; mesoscale eddies (100–150 days, 30–50 km); squirts, fronts, and jets (e.g., topographic forcing); weather (days to weeks); and the diurnal sea breeze (diurnal, few km scale). Perhaps most challenging, the observed pattern of natural upwelling and intensification of coastal chlorophyll, remineralized nutrients, hypoxia, and associated acidification is coherent all along the EBC, but restricted to 10–100 km from the coast (e.g., Feely et al. 2008). This broad combination of challenges has motivated further work in global-scale Earth System Modeling to retain the inclusion of basin-scale climate change mechanisms while addressing limited resolution of coastal dynamics within coarse-resolution global ESMs.

The nature of this challenge is daunting. While ocean observations indicate a strong role for mesoscale (10–100 km scale) variability, Earth System modelers do not have access to computers powerful enough to develop models to resolve these scales in global imple-

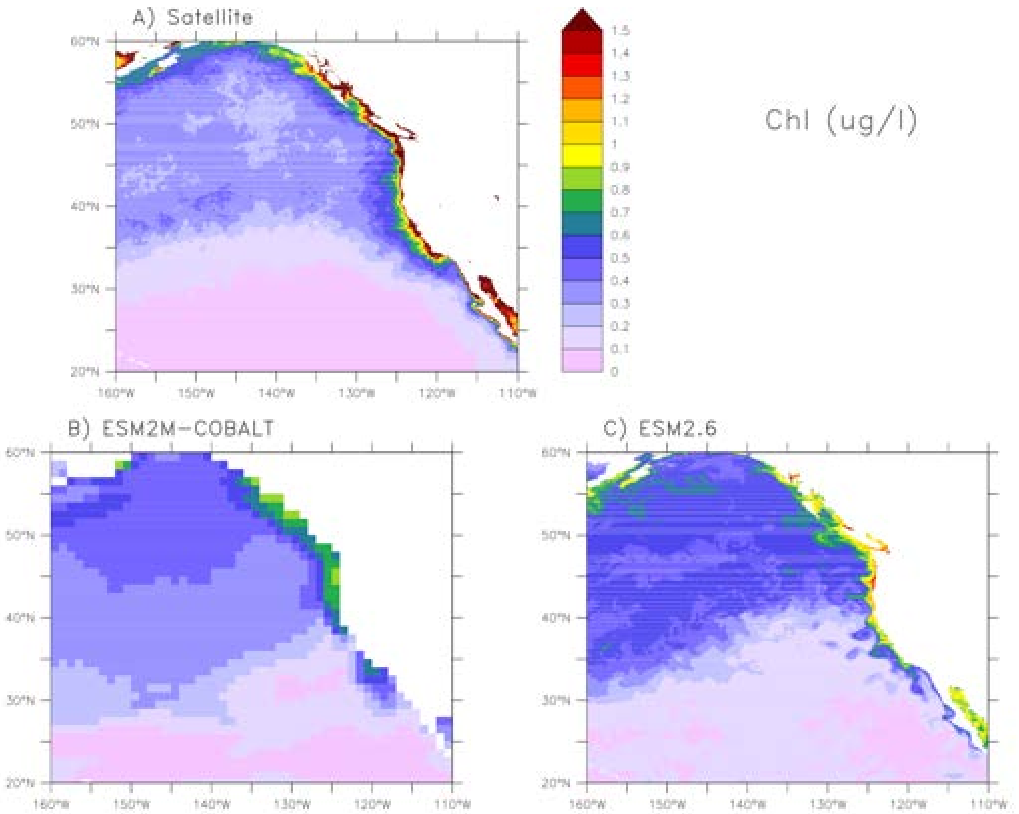

Figure 1. Comparison of surface chlorophyll from SeaWiFS satellite observations (top; http://oceandata.sci.gsfc.nasa.gov/SeaWiFS/Mapped/Monthly/9km/) with coarse, 1° resolution COBALT in ESM2M (bottom left; Stock et al. 2014) and 1/10° resolution COBALT in ESM2.6 (bottom right; present study).

mentations; the current generation ~1° ESMs have considerable regional process-level and fidelity biases. This implies that they commonly misrepresent phenomena such as the position and variability of the major current structures, the scales of either coastal and curl-driven upwelling, topographic and land-sea atmospheric interactions, and mechanistic ecological interactions. At least 1/10° resolution is necessary to resolve the Rossby radius of mesoscale eddies in the mid to high latitudes where these phenomena modulate the connection between the ocean surface and interior. Finally, adding biogeochemical tracers is computationally expensive, about 10%–20% per tracer over that of temperature and salinity alone. Overall, while the 1° ESM takes about 1.6 hours to run a year on 432 cores, the full 1/10° takes about 60 hours to run a year on 15,744 cores—an increase of over a thousand-fold in cost. Such simulations are extremely difficult to configure and run and their results more indicative of prototypes than of exhaustively developed and vetted products.

METHODS

To address the challenge of our computational inability to run long simulations of comprehensive biogeochemical and ecological models at high global resolution, we considered a suite of models assessing sensitivity across three dimensions of potential efficiency: biogeochemical comprehensiveness, spatial resolution, and simulation time. We compared a hierarchy of biogeochemical comprehensiveness including: CMIP5 GFDL Earth System Models which used Tracers of Ocean Phytoplankton with Allometric Zooplankton version 2 (TOPAZv2); the next generation Carbon Ocean Biogeochemistry and Lower Trophics (COBALT); the simplified Biogeochemistry with Light, Nutrients and Gas (BLING; Galbraith et al. 2012); and even further reduced mini-BLING with only dissolved inorganic carbon, phosphate, and oxygen. In the spatial resolution dimension, we compare mini-BLING and COBALT at 1° (ESM2M; Dunne et al. 2013) and 1/10° (Delworth et al. 2013; Griffies et al. 2015) ocean resolution for baseline simulation characteristics and fidelity. In the simulation time dimension, we compared ESM2M TOPAZ long spin-up with short spin-up to assess the role of equilibration, and compared historical/future simulation (240 years) with the shorter, idealized 1%CO2/yr to doubling perturbation (80 years) to assess the role of perturbation timescale to biogeochemical response. The analysis described herein focuses on the baseline simulation characteristics of the short simulation combining the comprehensive COBALT ecosystem model with the highest spatial resolution climate simulation (~1/10 degree ocean, 50 km atmosphere). We refer to this model as ESM2.6.

GFDL's current ESM2M and ESM2G are publicly available as part of CMIP5. They use Tracers of Ocean Phytoplankton with Allometric Zooplankton version 2 (TOPAZv2) to simulate a coupled suite of multi-elemental mechanisms controlling the ocean carbon cycle. This, in turn, is done through their interacting cycles that incorporate allometric, optimal allocation, and ballast theory through global process-level calibration and distributional biogeochemical validation. Taking TOPAZ as it's starting point, GFDL's next generation biogeochemistry enhances representation of ecosystem structure towards improvement of resolution of energy flows through the planktonic food web and more robust applications, meeting NOAA's stewardship mandate for Living Marine Resources. This model, Carbon Ocean Biogeochemistry and Lower Trophics (COBALT; Stock and Dunne 2010; Stock et al. 2013), increases the number of zooplankton types from 1 to 3 and adds explicit bacteria with a considerable augmentation of theoretical and observational justification for structural and parameter decision making.

RESULTS

The sensitivity to resolution at higher comprehensiveness is illustrated for the California Current EBC in Figure 1. Comparison of 1° and 1/10° resolutions in the most comprehensive COBALT model demonstrates vast improvement in the ability to represent the ecological response to mesoscale dynamics. Most striking is the improved ability to represent high chlorophyll associated with mesoscale upwelling and transport along the northern portion of the California Current upwelling region. In addition, there are improvements in the representation of the transition between mesotrophy in the offshore subpolar gyre and oligotrophy in the offshore subtropical gyre (blue to purple in fig. 1). Furthermore, the high-resolution model captures modes of mesoscale variance within the subpolar gyre that the coarse model is incapable of generating.

The relative ability of these models to represent the patterns of depressed temperature and elevated chlorophyll associated with EBC upwelling is shown more quantitatively in Figure 2. While the 1° resolution model (red) struggles to capture the signature of upwelling at all latitudes, ESM2.6 captures both the quantitative depression of temperature at the coast and the spatial scale of return to open ocean conditions offshore (top panel of fig. 2). However, those offshore temperatures tend to be too warm in both models to a similar extent. In terms of chlorophyll, ESM2.6 exhibits both similarly vast improvement in the qualitative structure nearshore and marked improvement offshore, but the highest values of chlorophyll in ESM2.6 (about 1.2 µg/l; <0.1 after the log transform in fig. 2) remain an order of magnitude lower than satellite observations, which exceed 10 µg/l (>1 after the log transform in fig. 2).

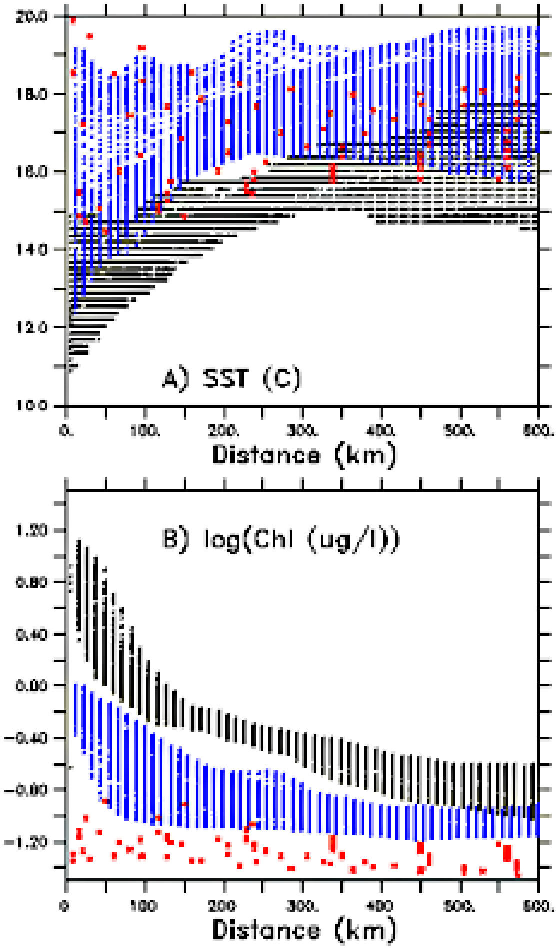

Figure 2. Comparison of Satellite Observations (Black), with coarse, 1° resolution COBALT in ESM2M (red; Stock et al. 2014) and 1/10° resolution COBALT in ESM2.6 (red; present study) for sea surfaces temperature (C; top; http://www.nodc.noaa.gov/SatelliteData/pathfinder4km/) and log(chlorophyll µg/l) (bottom; http://oceandata.sci.gsfc.nasa.gov/SeaWiFS/Mapped/Monthly/9km/). The number of points in each case reflects the pixel resolution in each case—similar for ESM2.6 and the satellite observations, but considerably lower in the 1° resolution model.

Overall, we consider these extremely exciting results and are highly confident that future high-resolution models will be vastly more applicable to living marine resource applications when computational capacities allow full implementation. While these models are revolutionary in representing various aspects of mesoscale dynamics as they may impact ecosystems on the global scale, many challenges remain. One of these challenges is that the high-resolution model retains much of the large-scale biases seen in the coarse-resolution model. A second challenge is that while higher resolution improved representation of areas with peak chlorophyll values about 1.2 μg/l, satellite and field observations commonly exceed 10 μg/l chlorophyll in blooms. Whether this lack of ecological dynamism captured in ESM2.6 is related to a lack of physical dynamics of fronts and other submesoscale phenomena, to lack of pelagic ecological biodiversity—particularly with respect to coastal diatoms, or related to a lack of representation of coastal and benthic interactions—is a focus of current and future work.

LITERATURE CITED

Bograd, S. J., C. G. Castro, E. Di Lorenzo, D. M. Palacios, H. Bailey, W. Gilly, and F. P. Chavez. 2008. Oxygen declines and the shoaling of the hypoxic boundary in the California Current. Geophysical Research Letters, 35(12).

Delworth, T. L., A. Rosati, W. G. Anderson, A. Adcroft, V. Balaji, R. Benson, K. W. Dixon, S. M. Griffies, H.-C. Lee, R. C. Pacanowski, G. A. Vecchi, A. T. Wittenberg, F. Zeng, and R. Zhang. 2012. Simulated climate and climate change in the GFDL CM2.5 high-resolution coupled climate model. Journal of Climate, 25(8), DOI:10.1175/JCLI-D-11-00316.1.

Dunne, J. P., J. John, A. Adcroft, S. M. Griffies, R. W. Hallberg, E. Shevliakova, R. J. Stouffer, W. F. Cooke, K. A. Dunne, M. J. Harrison, J. P. Krasting, S. Malyshev, P. C. D. Milly, P. Phillipps, L.T. Sentman, B. L. Samuels, M. J. Spelman, M. Winton, A. T. Wittenberg, and N. Zadeh. 2012. GFDL's ESM2 global coupled climate-carbon Earth System Models Part I: Physical formulation and baseline simulation characteristics. Journal of Climate, 25(19), DOI:10.1175/JCLI-D-11-00560.1.

Dunne, J. P., J. John, E. Shevliakova, R. J. Stouffer, J. P. Krasting, S. Malyshev, P. C. D. Milly, L. T. Sentman, A. Adcroft, W. F. Cooke, K. A. Dunne, S. M. Griffies, R. W. Hallberg, M. J. Harrison, H. Levy II, A. T. Wittenberg, P. Phillipps, and N. Zadeh. 2013. GFDL's ESM2 global coupled climate-carbon Earth System Models Part II: Carbon system formulation and baseline simulation characteristics. Journal of Climate, 26(7), DOI:10.1175/JCLI-D-12-00150.1.

Feely, R. A., C. L. Sabine, J. M. Hernandez-Ayon, D. Ianson, and B. Hales. 2008. Evidence for upwelling of corrosive "acidified" water onto the continental shelf. science, 320(5882), 1490–1492.

Galbraith, E. D., A. Gnanadesikan, J. P. Dunne, and M. R. Hiscock. 2010. Regional impacts of iron-light colimitation in a global biogeochemical model. Biogeosciences, 7(3), DOI:10.5194/bg-7-1043-2010.

Griffies, S. M., M. Winton, W. G. Anderson, R. Benson, T. L. Delworth, C. O. Dufour, J. P. Dunne, P .Goddard, A. K. Morrison, A. T. Wittenberg, J. Yin, and R. Zhang, 2015: Impacts on ocean heat from transient mesoscale eddies in a hierarchy of climate models. Journal of Climate, 28(3), DOI:10.1175/JCLI-D-14-00353.1.

Rykaczewski, R., and J. P. Dunne. 2010. Enhanced nutrient supply to the California Current Ecosystem with global warming and increased stratification in an earth system model. Geophysical Research Letters, 37, L21606, DOI:10.1029/2010GL045019.

Stock, C. A., and J. P. Dunne. 2010. Controls on the ratio of mesozooplankton production to primary production in marine ecosystems. Deep-Sea Research, Part I, 57(1), DOI:10.1016/j.dsr.2009.10.006.

Stock, C. A., J. P. Dunne, and J. John. 2014. Global-scale carbon and energy flows through the marine food web: an analysis with a coupled physical-biological mode. Progress in Oceanography, 120, DOI:10.1016/j.pocean.2013.07.001.

REGIONAL CLIMATE MODELING IN THE CALIFORNIA CURRENT SYSTEM

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BACKGROUND

Though global climate models can represent many identifiable features of the climate system, they also suffer from significant localized biases. Climate model biases are not uniform over the globe. For example, in the ocean, modeled sea surface temperature (SST) errors are often largest along the continental margins. Many coupled climate models generate very large SST biases in the coastal upwelling regions of the California Current system (CCS), the Humboldt Current System (HCS), and the Benguela Current System (BCS), where simulated mean SSTs are much warmer than observed. The NCAR-CCSM3 (spectral atmosphere) used in IPCC-AR4 was no exception, with biases in excess of 3°C in all three regions. Furthermore, these SST biases have significant remote effects on surface and subsurface temperature and salinity, and on precipitation and hence atmospheric heating and circulation (Collins et al. 2006). Large and Danabasoglu (2006) showed, in particular, with observed SSTs imposed along the BCS coast in an otherwise freely-evolving CCSM3 simulation there are significant improvements in precipitation in the western Indian Ocean, over the African continent, and across the Equatorial Atlantic. Imposed SSTs along the HCS coast reduce precipitation in the so-called double Intertropical Convergence Zone (ITCZ) region of the south tropical Pacific.

These errors often coincide with regions of importance to oceanic ecosystems and nearby human populations. In the Intergovernmental Panel on Climate Change Fourth (IPCC-AR4) Working Group 1 Assessment Report, where the reliability of the models used to make projections of future climate change is assessed, Randall et al. (2007) discuss the many improvements and the strengths of the current generation of coupled models of the physical climate system, but they also highlight a number of remaining significant model errors. Furthermore, they state, "The ultimate source of most such errors is that many important small-scale processes cannot be represented explicitly in models, and so must be included in approximate form as they interact with larger-scale features." Some of the reasons given for the deficiencies are limited computer power, data availability, and scientific understanding. Conversely, regional models have shown significant skill in modeling coastal processes (e.g., Curchitser et al. 2005; Powell et al. 2007; Combes et al. 2009; Veneziani et al. 2009a,b). This creates the opportunity to develop multi-scale numerical solution schemes that adapt the resolution in specific areas of interest, such as the California Current system.

Coastal winds in the latest CCSM4 with a 2° resolution (finite volume) atmosphere produce even larger SST biases than were apparent in CCSM3, despite many improvements to the physical model components. Improving the coastal winds by increasing the atmospheric resolution to 1° however, significantly reduces the coastal SST biases. The implication is that the further reductions in the SSTs required to eliminate the coastal biases under present day conditions will likely also need to come from improvements to the ocean physics and the upwelling of cold water in particular. These improvements must be realized before the regional biogeochemistry and ecosystem models can be expected to behave accurately because of the sensitivity to temperature and the critical importance of upwelled nutrients for biological processes.

In order to address the above issues we developed a new multi-scale ocean as part of the U.S. National Center for Atmospheric Research Community Earth System Model (NCAR-CESM). The new composite ocean consists of the global Parallel Ocean Program (POP) and the Regional Ocean Modeling System (ROMS). The new composite ocean is connected to the rest of the CESM climate model through a modified flux coupler.

RESULTS FROM THE MULTI-SCALE COUPLED MODEL

In order to test and demonstrate the capabilities of the multi-scale climate model, we have been carrying out a series of simulations where the northeast Pacific upwelling region is solved using a high-resolution (7 km) ocean within a global (1°) model and a 1° atmosphere. Sea ice is solved on the ocean grid and the land surface model on the atmospheric grid. The CESM is initialized from a spun-up climatology and time-stepped

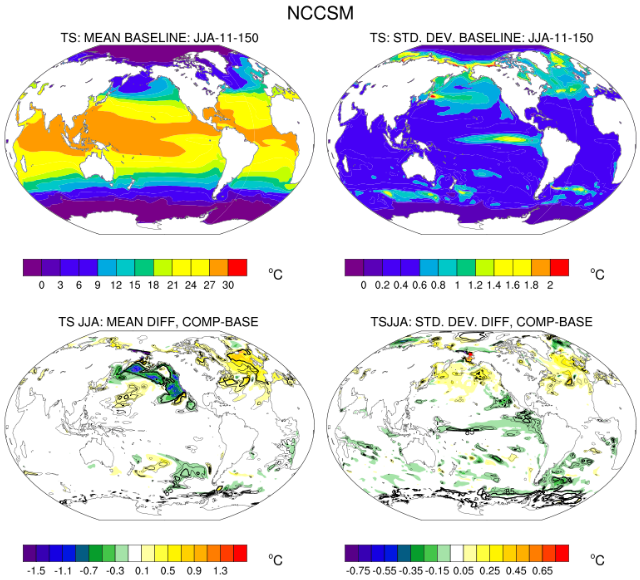

Figure 1. Mean and standard deviation for the summer months of both the control and composite simulations. Thick black lines indicate 95% confidence level using the T- and F-test for the mean and deviation, respectively. Note both the local and remote effects caused by the perturbation that results from resolving the upwelling signal in the northeast Pacific region.

for 150 years. This simulation is then compared to a control run without the high-resolution ocean. The new multi-scale ocean is able to resolve the upwelling that is mostly missing from the global simulations, and this has a significant effect on the regional wind patterns.

Figure 1 shows the surface sea temperature and standard deviation for summer months (June–August) of the control simulation and the corresponding anomalies with the composite model for the last 140 years of simulation. The thick black lines outline regions of 95% confidence based on T- and F-tests for the mean and standard deviations, respectively. The temperature anomaly plot shows the local cooling effect that results from resolving the upwelling in the northeast Pacific and also remote effects in the Atlantic ocean. Significant, and robust, effects are also seen in other variables such as tropical precipitation and sea level pressure.

SUMMARY

A new multi-scale capability was developed by merging a global ocean and a regional ocean model within a global climate model. The goal was to address some of the biases exhibited by low-resolution global models in regions with implications for marine ecosystems. Long integrations show that this configuration is able to address some of these regional biases. Furthermore, by preserving the feedbacks between the regional and global climate models we are able to study upscaling effects that arise from the regionally introduced perturbations. In the case presented here we see effect as far afield as the North Atlantic Ocean. Further studies are proceeding by studying the effects of resolving other major upwelling regions as well a new study in a western boundary current region where global models also show sea surface temperature biases. Future plans include adding a biogeochemistry model to this configuration in order to study the role of upwelling regions in the global CO_2 cycles.

LITERATURE CITED

Collins, W. D., C. M. Bitz, M. L. Blackmon, G. B. Bonan, C. S. Bretherton, et al. 2006. The Community Climate System Model version 3 (CCSM3). *J. Climate* 19: 2122–43.

Combes, V., E. Di Lorenzo, and E. Curchister. 2009. Interannual and decadal variations in cross-shore mixing in the Gulf of Alaska. *J. Phys. Oce.*, 39(4): 1050–1059.

Curchitser, E. N., D. B. Haidvogel, A. J. Hermann, E. Dobbins, T. M. Powell, and A. Kaplan. 2005. Multi-scale modeling of the North Pacific Ocean: Assessment of simulated basin-scale Variability (1996–2003). *J. Gophys. Res.*, 110, C11021, doi:101029/2005JC002902.

Ito, S.-I., K. A. Rose, A. J. Miller, K. Drinkwater, K. M. Brander, J. E. Overland, S. Sundby, E. N. Curchitser, J. W. Hurell, and Y. Yamanaka. 2009. Ocean ecosystem responses to future global change scenarios: A way forward. In press.

Kalnay, E., M. Kanamitsu, R. Kistler, W. Collins, D. Deaven, L. Gandin, M. Iredell, S. Saha, G. White, J. Woollen, Y. Zhu, M. Chelliah, W. Ebisuzaki, W. Higgins, J. Janowiak, K. C. Mo, C. Ropelewski, J. Wang, A. Leetma, R. Reynolds, R. Jenne, and D. Joseph. 1996. The NCEP/NCAR 40-year reanalysis project, *Bull. Am. Meteor.* Soc., 77, 437–471.

Large, W. G., and G. Danabasoglu. 2006. Attribution and impacts of upper-ocean biases in CCSM3. *J. Climate,* 19, 2325–2346.

Randall, D., and co-authors. 2007. Climate Models and Their Evaluation. *In*: Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change [Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor and H. L. Miller (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Veneziani, M., C. A. Edwards, and J. D. Doyle. 2009a. A Central California coastal ocean modeling study. Part I: The forward model and the influence of realistic versus climatological forcing, J. Geophys. Res., 114, C04015, doi:10.1029/2008JC004774.

Veneziani, M., C. A. Edwards, and A. M. Moore. 2009b. A Central California coastal ocean modeling study. Part II: Adjoint sensitivities to local and remote driving mechanisms, J. Geophys. Res., 114, C04020, doi:10.1029/2008JC004775.

END-TO-END MODELING OF SARDINE AND ANCHOVY IN THE CALIFORNIA CURRENT SYSTEM

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End-to-end models are receiving increasing attention as a quantitative tool for investigating marine ecosystem responses to climate variation and fisheries management. End-to-end models typically combine submodels of physics (hydrodynamics), lower trophic levels (nutrient-phytoplankton-zooplankton, NPZ), and upper trophic levels (fish, birds, fishers) into a single modeling framework (Plagányi 2007). Such models are attractive because they can simulate a wide variety of effects, including ecosystem responses to interannual environmental variation, changes in fishing, and episodic and long-term trends in climate conditions. Our focus in this paper is on the development of an end-to-end model (climate to fish to fishers), using the sardine-anchovy system of the California Current (CC). The sardine-anchovy low-frequency population cycles have been studied for decades (Lluch-Belda et al. 1989). We focus here on how interannual variation in environmental conditions affected the decadal cycles in sardine and anchovy populations.

Our end-to-end model is 3-dimensional, time-varying, and multispecies, and consists of four coupled submodels: hydrodynamics, Eulerian nitrogen-phytoplankton-zooplankton (NEMURO NP_2Z_3), an individual-based full life cycle anchovy and sardine submodel, and an agent-based fishing fleet submodel (Rose et al. 2015). All submodels were coded within the ROMS community software package, and used the same resolution spatial grid and were all solved simultaneously to allow for possible feedbacks among the submodels. A historical simulation of 1959-2008 was performed (fig. 1) that showed a switch from anchovy dominance to sardine dominance in the mid-1990s. A more in-depth analysis of the causes for the population cycles in the historical simulation is reported in Fiechter et al. (2015). Results illustrate how slightly different temperature and diet preferences between sardine and anchovy can lead to their different responses to environmental variability. Simulated adult population fluctuations were associated with age-1 growth (via age-2 egg production) and prey availability for anchovy, while they depended primarily on age-0 survival and temperature for sardine.

Our analysis demonstrates that the technology is available for developing and using 3-dimensional fully-coupled multispecies end-to-end models. We conclude with a discussion about the prospects for using such end-

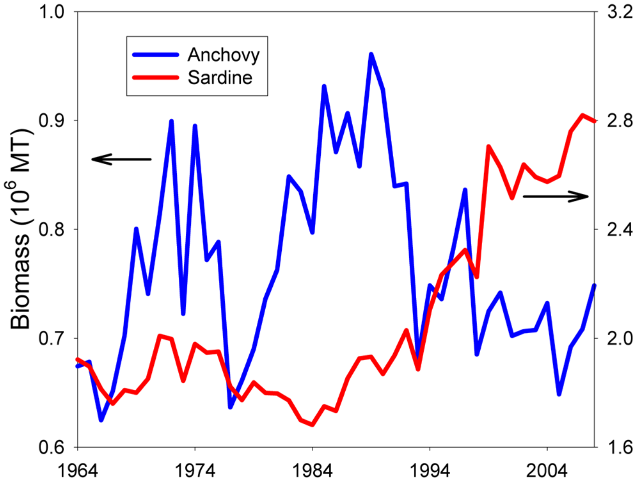

Figure 1. Annual values on January 1 of age-1 and older simulated biomasses of anchovy and sardine in the historical simulation.

to-end models for strategic and tactical predictions. The time is now for development and testing of these end-to-end models so we are ready with models of sufficient and documented confidence for wide-spread usage within the next decade.

LITERATURE CITED

Fiechter, J., K. A. Rose, E. N. Curchitser, and K. S. Hedstrom. 2015. The role of environmental controls in determining sardine and anchovy population cycles in the California Current: Analysis of an end-to-end model. *Progress in Oceanography*.

Lluch-Belda, D, R. J. M. Crawford, T. Kawasaki, A. D. MacCall, R. H. Parrish, R. A. Schwartzlose, and P. E. Smith. 1989. World-wide fluctuations of sardine and anchovy stocks: The regime problem. *South African Journal of Marine Science*. 8: 195–205.

Plagányi, É. E. 2007. Models for an ecosystem approach to fisheries. FAO Fisheries Technical Paper No. 477. Food and Agriculture Organization of the United Nations, Rome.

Rose, K. A., J. Fiechter, E. N. Curchitser, K. Hedstrom, M. Bernal, S. Creekmore, A. Haynie, S. Ito, S. Lluch-Cota, B. A. Megrey, C. Edwards, D. Checkley, T. Koslow, S. McClatchie, F. Werner, and V. Agostini. 2015. Demonstration of a fully-coupled end-to-end model for small pelagic fish using sardine and anchovy in the California Current. *Progress in Oceanography.*

HINDCASTING AND NOWCASTING THE PHYSICAL AND BIOLOGICAL STATE OF THE CALIFORNIA CURRENT SYSTEM

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Assessing the past or present state of the ocean and predicting its future state are challenging enterprises. Observing activities are expensive, and as a result the ocean is woefully undersampled relative to important scales of variability spanning several orders of magnitude (from meters to hundreds of kilometers) in space and hours to decades in time. Numerical ocean models offer a relatively inexpensive alternative to observational sampling, and provide fully 4-dimensional representation of ocean fields and governing processes to better understand field distributions and changes. Yet numerical ocean models offer imperfect representations of nature for many unavoidable reasons, including errors in model initial conditions, forcing fields, model parameterizations, and discretization of the model on a finite grid. In ocean state estimation modelers use methods of data assimilation to rigorously adjust control variables (e.g., model initial conditions or forcing fields) to reduce discrepancies between model fields and observations (Edwards et al. 2015).

The widely-used Regional Ocean Modeling System (ROMS; Shchepetkin and McWilliams 2005) includes an advanced 4-dimensional variational data assimilation capability (Moore et al. 2011a) that has been applied in various California Current system configurations. The UC Santa Cruz Ocean Modeling Group implementation consists of a domain extending from 30°N to 48°N (Baja California, Mexico, to near Puget Sound, Washington) and offshore to 134°W, resolved at 1/10 degree, with 42 terrain-following levels spanning the water column (Broquet et al. 2010, Moore et al. 2011b, 2013). Experience assimilating a variety of physical data types has shown that the system produces ocean state estimates with reduced root-mean-square error of both assimilated and unassimilated observations relative to unconstrained model output (Broquet et al. 2009). Forecast-like calculations in which the final state of one assimilation cycle is used as an initial state for an unconstrained forecast indicate that model skill is sustained beyond the period of assimilation alone.

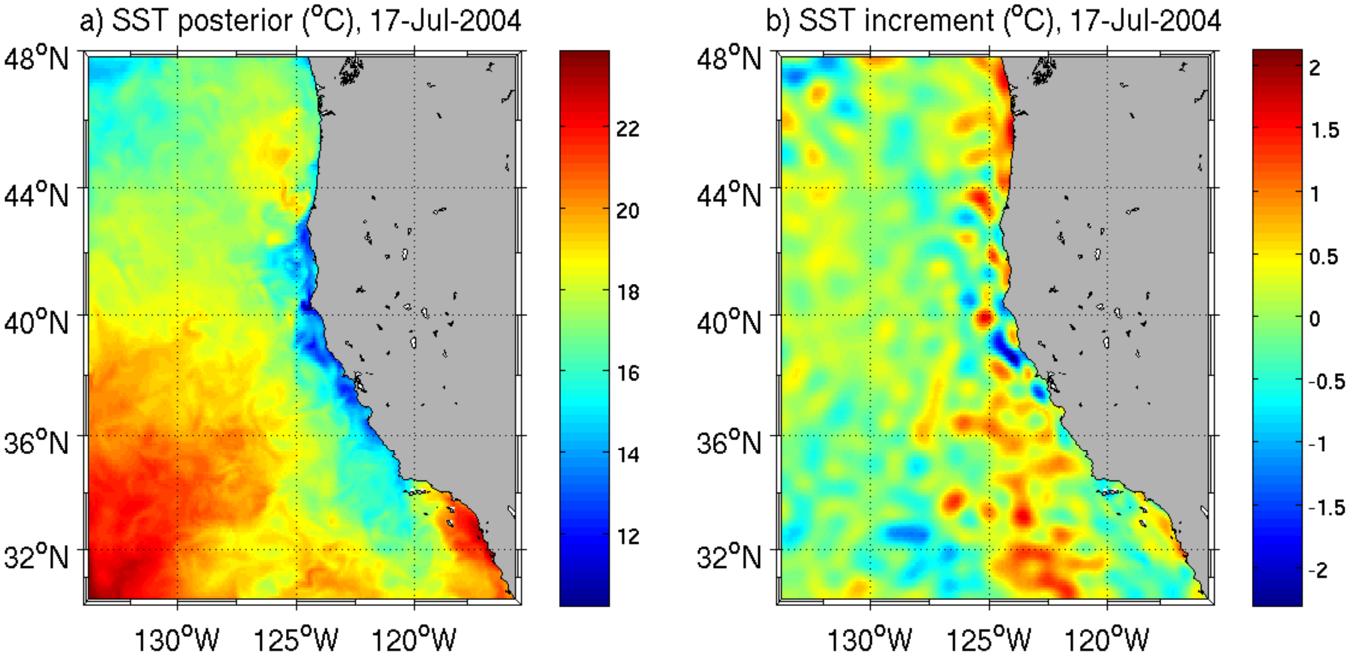

Figure 1. (a) Reanalysis sea surface temperature (SST) on July 17, 2004. (b) Corrections to the prior estimate of SST that were calculated through data assimilation and resulted in the field shown in (a).

A set of data assimilative reanalyses using the UCSC ROMS 4D-Var configuration has been calculated for the CCS (Neveu et al. 2015; Crawford et al. 2015). This product assimilated sea surface temperature (SST) from multiple satellite platforms, satellite-derived sea surface height, and in situ hydrography from various sources in a series of 8-day cycles extending from 1980 to 2010. Lateral boundary conditions were derived from the SODA global ocean state estimate (Carton and Giese 2008). Surface forcing was provided by a combination of CCMP winds (Atlas et al. 2011) and other atmospheric fields from the ERA40 (Källberg et al. 2004) and ERA-Interim (Dee et al. 2011) products. This model output represents a best estimate 31-year, hindcast of the physical state of the California Current, and is served by the UC Ocean Modeling Group for analysis (http://oceanmodeling.ucsc.edu).

Example output from a reanalysis assimilation cycle is shown in Figure 1. SST on this date exhibits cold upwelled water along the central California coast, with warm water bathing the Southern California Bight. Largely mesoscale corrections to a prior estimate, ranging up to about 2 degrees, result in this posterior state estimate.

This set of reanalyses has several applications that may be of interest to the CalCOFI community. It can be used for evaluation of fundamental physical processes. For example, upwelling within the CCS is challenging to observe directly, and in the absence of other information, a coastal upwelling index based on Ekman theory is often used as a proxy (Bakun 1973). The reanalyses reveal that modeled upwelling transport is reasonably approximated by the upwelling index north of about 39°N, but is poorly represented south of this latitude (fig. 2; Jacox et al. 2014). Actual upwelling transport differs from Ekman transport in regions where cross-shore geostrophic transport encounters the coastal boundary (Marchesiello and Estrade 2010). Reduction of the reanalyses into empirical orthogonal functions reveals anomalous nearshore upwelling transport whose principal component relates to large-scale climate indices such as the NPGO and PDO (Jacox et al. 2014).

Ocean state estimates can also be used to provide context for fisheries studies. Schroeder et al. (2014) evaluated the reanalyses against data collected from the NMFS Rockfish Recruitment and Ecosystem Assessment Surveys. That study identified correlations between biological stocks (juvenile rockfish and krill) and physical variables from the reanalyses such as the depth of the 26.0 kg/m^3 isopycnal surface.

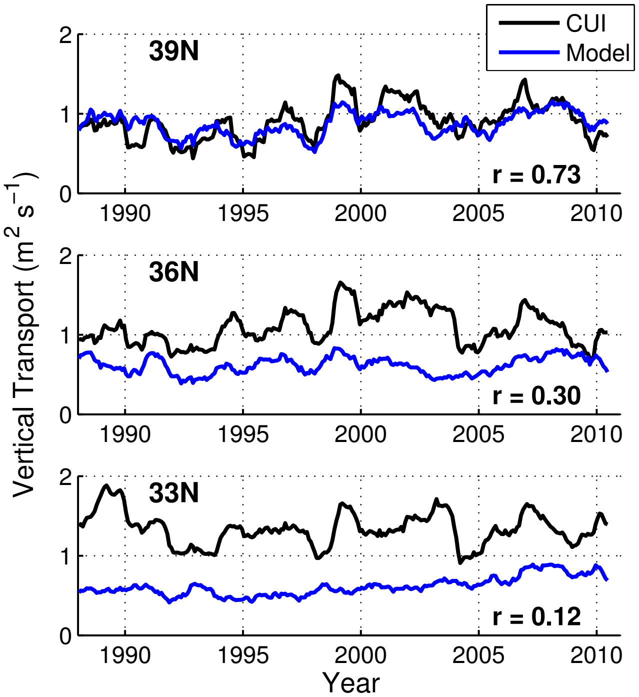

Figure 2. 12-month running means of upwelling estimates from the NOAA Coastal Upwelling Index (CUI, black) and the ROMS-CCS model (blue) of Moore et al. (2013). Model transports are integrated from the coast to 200 km offshore, averaged over 3° of latitude for consistency with the CUI, and calculated as transport across a depth level of 40 m. Adapted from Jacox et al. (2014).

Ocean data assimilation is increasingly becoming a routine activity in global and many regional ocean environments. To date, however, most research has focused on physical data assimilation in which ocean currents, temperature, salinity, and sea surface height are constrained by observations. Exciting developments are underway to extend this capability to biogeochemical variables. The UC Santa Cruz Ocean Modeling Group has implemented a form of 4D-Var that accounts for the differing statistics of ecosystem variables relative to physical variables. Chlorophyll in the ocean has been shown to be better represented by lognormal statistics than by Gaussian distributions (Campbell 1995). The coupled physical-biogeochemical assimilation system incorporates surface chlorophyll, and offers considerable promise for hindcasting and nowcasting the combined physical and lower trophic level biological ocean state (Song et al. in prep.).

LITERATURE CITED

Atlas, R., R. N. Hoffman, J. Ardizzone, S. M. Leidner, J. C. Jusem, D. K. Smith, and D. Gombos. 2011. A cross-calibrated, multiplatform ocean surface wind velocity product for meteorological and oceanographic applications. Bull. Amer. Meteor. Soc., 92, 157–174. doi: 10.1175/2010BAMS2946.1.

Bakun, A. 1973. Coastal upwelling indices, west coast of North America, 1946–71, NOAA Tech. Rep., NMFS SSRF-671, 103 pp., U.S. Dep. of Commer.

Broquet, G., A. M. Moore, H. G. Arango, and C. A. Edwards. 2010. Corrections to ocean surface forcing in the California Current System using 4D variational data assimilation, Ocean Mod. 36, doi:10.1016/j.ocemod.2010.10.005.

Broquet G., A. M. Moore, H. G. Arango, C. A. Edwards, and B. S. Powell. 2009. Ocean state and surface forcing correction using the ROMS-IS4DVAR data assimilation system, Mercator Ocean Quarterly Newsletter, Mercator Ocean Quarterly Newsletter, 34, pp. 5–13.

Broquet G., C. A. Edwards, A. M. Moore, B. S. Powell, M. Veneziani, and J. D. Doyle. 2009. Application of 4D-Variational data assimilation to the California Current System, Dyn. Atmos. Oceans, doi:10.1016/j.dynatmoce.2009.03.001.

Carton, J. A., and B. S. Giese. 2008. A reanalysis of ocean climate using simple ocean data assimilation (SODA). Mon. Weather Rev., 136, 2999–3017.

Campbell, J.W. 1995. The lognormal distribution as a model for bio-optical variability in the sea. J. Geophys. Res. 100 (C7), 13237–13254.

Crawford, W., A. M. Moore, M. G. Jacox, E. Neveu, J. Fiechter, and C. A. Edwards. 2015. An historical analysis of the California Current using ROMS 4D-Var. Part II: Climate variability. Ocean Modelling, submitted.

Dee, D. P., S. M. Uppala, A. J. Simmons, P. Berrisford, P. Poli, S. Kobayashi, U. Andrae, M. A. Balmaseda, G. Balsamo, P. Bauer, P. Bechtold, A. C. M. Beljaars, L. van de Berg, J. Bidlot, N. Bormann, C. Delsol, R. Dragani, M. Fuentes, A. J. Geer, L. Haimberger, S. B. Healy, H. Hersbach, E. V. Hólm, L. Isaksen, P. Källberg, M. Köhler, M. Matricardi, A. P. McNally, B. M. Monge-Sanz, J.-J. Morcrette, B.-K. Park, C. Peubey, P. de Rosnay, C. Tavolato, J.-N. Thépaut and F. Vitart. 2011. The ERA-Interim reanalysis: configuration and performance of the data assimilation system, Q. J. R. Meteorol. Soc., 137, 553-597, doi: 10.1002/qj.828.

Edwards, C.A., A. M. Moore, I. Hoteit and B. D. Cornuelle. 2015. Regional ocean data assimilation. Annu. Rev. Mar. Sci., 7, 6.1–6.22, doi: 10.1146/annurev-marine-010814-015821.

Jacox, M. G., A. M. Moore, C. A. Edwards, and J. Fiechter. 2014. Spatially resolved upwelling in the California Current System and its connections to climate variability, Geophys. Res. Lett., 41, 3189–3196, doi:10.1002/2014GL059589.

Källberg, P., A. Simmons, S. Uppala, and M. Fuentest. 2004. The ERA-40 Archive. ERA-40, Project Report Series No. 17.

Marchesiello, P., and P. Estrad. 2010. Upwelling limitation by onshore geostrophic flow, J. Mar. Res., 68, 37–62, doi:10.1357/002224010793079004.

Moore, A.M., C. A. Edwards, J. Fiechter, P. Drake, H. G. Arango, E. Neveu, S. Gurol, and A.T. Weaver. 2013. A 4D-Var Analysis System for the California Current: A Prototype for an Operational Regional Ocean Data Assimilation System. *In* "Data Assimilation for Atmospheric, Oceanic and Hydrological Applications, Vol. II," Liang Xu and Seon Park, Eds. Springer, Chapter 14, 345–366.

Moore, A. M., H. G. Arango, G. Broquet, B. S. Powell, A. T. Weaver, and J. Zavala-Garay. 2011a. The Regional Ocean Modeling System (ROMS) 4-dimensional variational data assimilation systems: Part I—System overview and formulation, Prog. Oceanogr., 91, 34–49.

Moore, A. M., H. G. Arango, G. Broquet, C. Edwards, M. Veneziani, B. Powell, D. Foley, J. D. Doyle, D. Costa, and P. Robinson. 2011b. The Regional Ocean Modeling System (ROMS) 4-dimensional variational data assimilation systems: Part II—Performance and application to the California Current System, Prog. Oceanogr., 91, 50–73.

Neveu, E., A. M. Moore, C. A. Edwards, J. Fiechter, P. T. Drake, M. G. Jacox, and E. Nuss. 2015. An historical analysis of the California Current using ROMS 4D-Var. Part I: System configuration and diagnostics. Ocean Modelling, submitted.

Schroeder, I. D., J. A. Santora, A. M. Moore, C. A. Edwards, J. Fiechter, E. L. Hazen, S. J. Bograd, J. C. Field, and B. K. Wells. 2014. Application of a data-assimilative regional ocean modeling system for assessing California Current System ocean conditions, krill, and juvenile rockfish interannual variability, Geophys. Res. Lett., 41, 5942–5950, doi:10.1002/ 2014GL061045.

Shchepetkin, A. F., and J. C. McWilliams. 2005. The regional oceanic modeling system (ROMS): A split-explicit, free-surface, topography-following-coordinate oceanic model, Ocean Modell., 9, 347–404.

Song, H., C. A. Edwards, A. M. Moore, J. Fiechter. In prep. Incremental, lognormal 4D-Var data assimilation into a coupled physical-ecosystem model of the California Current System: Part 3, Realistic assimilation of physical and biological data.

EFFECT OF EDDY-WIND INTERACTION ON EKMAN PUMPING AND EDDY KINETIC ENERGY: A REGIONAL COUPLED MODELING STUDY FOR THE CALIFORNIA CURRENT SYSTEM

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The California Current system (CCS) is characterized by the energetic summertime mesoscale and filamentary eddies with typical anomalies in sea surface temperature (SST) and surface current exceeding 2˚C and 0.5 cms^{-1}, respectively. Recent satellite observations show that both SST and surface current at oceanic mesoscales significantly influence the Ekman pumping velocity, suggestive of a subsequent dynamical feedback effect on the eddy energetics. The extent to which this mesoscale coupling is important for the Ekman pumping and the eddy kinetic energy (EKE) budget in the CCS is the focus of this study.

A series of the 7 km SCOAR regional coupled model simulations is carried out, in which the effects of mesoscale SST and mesoscale surface current are selectively removed in the formulation of surface wind stress. This is achieved by invoking an interactive spatial smoother, which removes oceanic structures with scales smaller than 300 km from the wind stress calculation. The total summertime Ekman pumping velocity is explained largely by two terms having comparable magnitudes: the linear Ekman pumping resulting from the curl of wind stress and the nonlinear Ekman pumping due to the gradient of surface vorticity by mesoscale current. The Ekman pumping due to the mesoscale SST through the linear relationship between the wind stress curl and the crosswind SST gradient is comparatively small. The simulated summertime EKE level in the CCS is reduced by ~30% (fig. 1) when the mesoscale eddies are allowed to influence the wind stress, and this reduction is almost entirely due to the effect of mesoscale current.

Examination of the upper ocean EKE budget terms shows that the dissipation of the EKE results mainly from the increased surface drags associated with a stronger correlation between the eddy-induced current and the wind stress. The change in SST climatology in the CCS is a resulting response from the offshore temperature advection by the mean and eddy currents of the upwelled water over the shelf. The magnitude of the mean SST change is greater with the mesoscale current than the mesoscale SST. Overall, the demonstrated importance of the eddy-wind interactions via mesoscale surface current suggests that the high-resolution ocean and coupled modeling studies over the energetic (sub) mesoscale variability and transient mixed layer fronts need to evaluate the dynamics and impact of small-scale air-sea coupling via surface current.

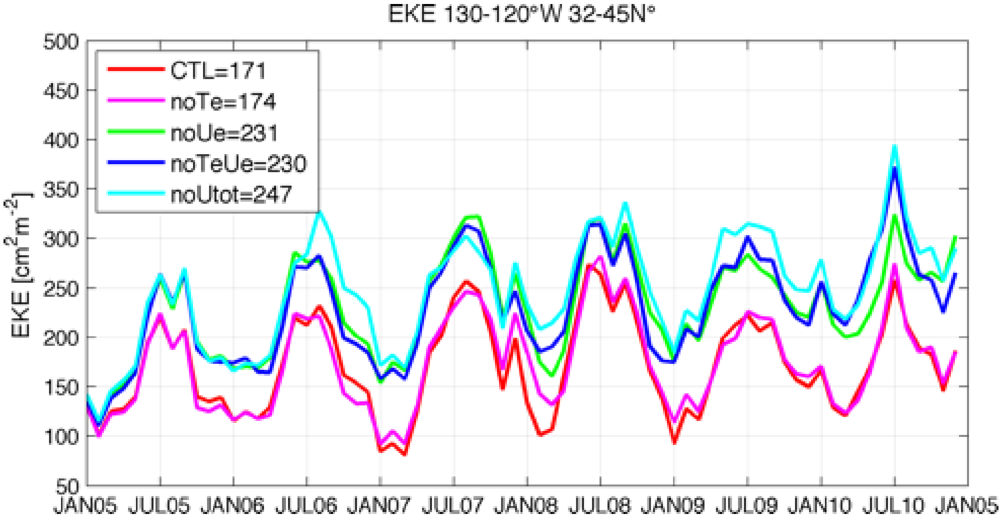

Figure 1. Eddy kinetic energy (EKE) for simulated surface currents in the five model cases averaged over each month of the year from 2005–10. Red is for full coupling. Purple is for no mesoscale SST coupling in wind stress. Green is for no mesoscale current coupling in wind stress. Dark blue is for no mesoscale SST or current coupling in wind stress. Light blue is for no ocean (mesoscale and large-scale) current coupling in wind stress. Allowing mesoscale eddies to affect the wind stress coupling reduces EKE by 25%–30%, while mesoscale SST coupling has very small effects on EKE.

PREDICTING HYPOXIA AND OCEAN ACIDIFICATION OF THE COASTAL WATERS OF THE CCS: WHAT DO WE KNOW AND WHAT CAN WE EXPECT?

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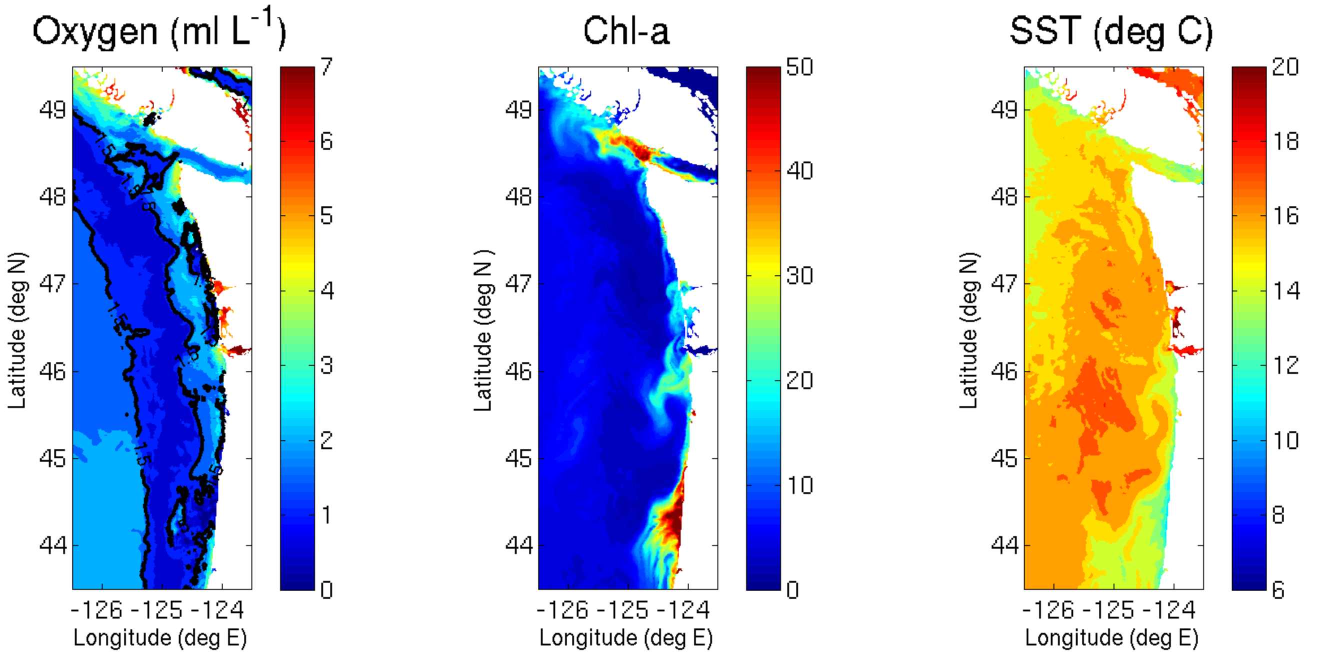

Figure 1. Study region for the J-SCOPE forecast system model. Maps of bottom oxygen (left), chlorophyll (middle, µg/l), and SST from the April 2013 forecasts of August, 2013.

Predictions of ocean acidification and hypoxia were incorporated into the IPCC report (2013) for the first time last year, and forecasts on shorter time scales have now been developed in the California Current system. High-resolution, regional, hindcast models capable of simulating hypoxia and ocean acidification events exist and provide the foundation for forecasting efforts. To build a forecast system, the necessary ingredients include a real-time observational network, a validated down-scaled hindcast simulation for the region complete with biogeochemistry, a region with predictive skill in both winds and SST, and an identified group of stakeholders with products designed in mind for them. Here, we use ROMS as the link from short-term, large-scale, climate forecasts to ecological processes relevant to the California Current Integrated Ecosystem Assessment. Our overarching goal is to provide short-term (six to nine month) forecasts of ocean conditions that are testable and relevant to annual management decisions for biological components in the California Current Integrated Ecosystem Assessment (CCIEA) (Levin and Schwing 2011). Regional hindcast models have been developed to understand the dynamics on the shelf with success, such that biogeochemical models can be designed and linked to them as well (Liu et al. 2009; MacCready et al. 2009; Banas et al. 2009; Sutherland et al. 2011; Giddings et al. 2014; Davis et al. 2014; Siedlecki et al. 2015). Ocean models have advanced in their ability to simulate, or hindcast, spatial structures, seasonal variability, and interannual variability when the forcing is known. JISAO's Seasonal Coastal Ocean Prediction of the Ecosystem (J-SCOPE) is a combination of the Regional Ocean Modeling System (ROMS; Haidvogel et al. 2008) with a detailed oxygen model (Siedlecki et al. 2015) and large-scale predictions from NOAA's Climate Forecast System (CFS) (Saha et al. 2006, 2010; Wen et al. 2012). CFS provides skillful predictions for the region in terms of winds and SST. The CFS is currently being run operationally by NOAA/NCEP/CPC for seasonal weather prediction. In the case of J-SCOPE, NANOOS, the Pacific Northwest regional component of US IOOS, provides the access point to the J-SCOPE seasonal forecasts (http://www.nanoos.org/products/j-scope/), as well as a portal for real-time regional observations. Additionally NANOOS brings linkage to and feedback from resource managers and other stakeholders with interest in the J-SCOPE forecast information. Finally, the CCIEA has partnered with us to advise on the developing product. Through comparisons of model hindcasts and re-forecasts for 2009 and 2013 with local observations, predictive capabilities have been examined for SST, oxygen, and pH. Challenges in forecasting seasonally in the coastal environment include prediction of the fall transition, radiation biases, and the ability of the large-scale model to predict the frequency of relaxations events. Results for the years tested suggest J-SCOPE forecasts had skill on the timescales of a few months.

LITERATURE CITED

Banas N. S., E. Lessard, R. Kudela, P. MacCready, T. Peterson, B. M. Hickey, and E. Frame. 2009. Planktonic growth and grazing in the Columbia River plume region: A biophysical model study, J. Geophys. Res., 114, C00B06, doi:10.1029/2008JC004993.

Davis, K. A., N. S. Banas, S. N. Giddings, S. A. Siedlecki, P. MacCready, E. J. Lessard, R. M. Kudela, and B. M. Hickey. 2014. Estuary-enhanced upwelling of marine nutrients fuels coastal productivity in the U.S. Pacific Northwest, J. Geophys. Res. Oceans, 119, doi:10.1002/2014JC010248

Giddings, S., P. MacCready, B. Hickey, N. Banas, K. Davis, S. Siedlecki, V. Trainer, R. Kudela, N. Pelland, and T. Connolly. 2014. Hindcasts of harmful algal bloom transport on the Pacific Northwest coast, J. Geophys. Res., 119: 2439–2461, doi:10.1002/2013JC009622.

Haidvogel, D. B., H. Arango, W. P. Budgell, B. D. Cornuelle, E. Curchitser, E. Di Lorenzo, K. Fennel, W. R. Geyer, A. J. Hermann, L. Lanerolle, J. Levin, J. C. McWilliams, A. J. Miller, A. M. Moore, T. M. Powell, A. F. Shchepetkin, C. R. Sherwood, R. P. Signell, J. C. Warner, J. Wilkin. 2008. Ocean forecasting in terrain-following coordinates: Formulation and skill assessment of the Regional Ocean Modeling System. Journal of Computational Physics, 227 (7): 3595–3624.

IPCC. 2013. Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change, edited by T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P. Midgley, p. 1535, Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Levin, P. S., and F. Schwing. 2011. Technical background for an IEA of the California Current: Ecosystem Health, Salmon, Groundfish, and Green Sturgeon. NOAA Technical Memorandum NMFS-NWSC-109.

Liu, Y., P. MacCready, B. M. Hickey, E. P. Dever, P. M. Kosro, and N. S. Banas. 2009. Evaluation of a coastal ocean circulation model for the Columbia River plume in summer 2004, J. Geophys. Res., 114, C00B04, doi:10.1029/2008JC004929.

MacCready, P., N. S. Banas, B. M. Hickey, E. P. Dever, and Y. Liu. 2009. A model study of tide- and wind-induced mixing in the Columbia River Estuary and plume, Cont. Shelf Res., 29(1), 278–291, doi:10.1016/j.csr.2008.03.015.

Saha, S., et al. 2010. The NCEP Climate Forecast System Reanalysis. Bull. Amer. Meteor. Soc., 91, 1015.1057. doi: 10.1175/2010BAMS3001.1

Siedlecki, S. A., N. S. Banas, K. A. Davis, S. Giddings, B. M. Hickey, P. MacCready, T. Connolly, and S. Geier. 2015. Seasonal and interannual oxygen variability on the Washington and Oregon continental shelves, J. Geophys. Res. Oceans, 120, doi:10.1002/ 2014JC010254.

Sutherland, D. A., P. MacCready, N. S. Banas, and L. F. Smedstad. 2011. A Model Study of the Salish Sea Estuarine Circulation*, J. Phys. Oceanogr., 41(6), 1125–1143, doi: 10.1175/2011JPO4540.1.

Wen, C., Y. Xue, and A. Kumar. 2012. Seasonal Prediction of North Pacific SSTs and PDO in the NCEP CFS Hindcasts. J. Climate, 25, 5689–5710.

END-TO-END MODELING TO PREDICT GLOBAL CHANGE EFFECTS IN THE CALIFORNIA CURRENT ECOSYSTEM

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End-to-end models of marine ecosystems couple climate, oceanography, food webs, and fisheries (Travers et al. 2007). These kinds of large-scale approaches are necessary to understand the cumulative and synergistic impacts of global change and the implications of marine management. End-to-end models of the California Current, such as Atlantis (Kaplan et al. 2013) and the NEMURO plankton-sardine model (Fiechter et al. 2014) simulate mechanisms of ecological interactions and are mainly of use for decadal time scales, and in these ways differ from some other marine forecasting techniques presented in this CalCOFI symposium and elsewhere. The oceanographic features of end-to-end models are often directly driven by simulations of ocean physics (Curchitser et al. 2005) and increasingly by projections of the ocean and atmosphere under climate change (Dunne et al. 2012).

End-to-end models can play a predictive role, ranking management options and investigating scenarios and hypotheses regarding how global change will unfold. Approximately five years ago, Rose and colleagues (2010) urged "restraint in using end-to-end models in a true forecasting mode." Five years later, end-to-end models have advanced substantially, as evidenced by both basic research and fisheries management applications. End-to-end models can now meet higher standards for model review, fitting, and consideration of uncertainty. One example was a recent multiday review of the California Current Atlantis model, conducted by external reviewers and members of the Pacific Fishery Management Council's Scientific and Statistical Committee[1]. The review included consideration of model calibration, fits to history, uncertainty, and parameter sensitivity.

End-to-end models have already provided some simple predictions of climate change impacts in the California Current (Kaplan et al. 2010; Ainsworth et al. 2011). Additionally, they have been used to predict food web impacts of fisheries, fishery management actions, and harvest of forage stocks (Kaplan et al. 2012, 2013). These efforts using the California Current Atlantis model are now being refined to provide improved spatial and taxonomic resolution of the biology, and more detailed projections of oceanography under climate change. Finally, California Current Atlantis model results have been applied to strategic management questions in the context of an Environmental Impact Statement for groundfish fisheries (Pacific Fishery Management Council and National Marine Fisheries Service 2014).

In conclusion, end-to-end models such as the California Current Atlantis model can be used to predict food web impacts of fisheries; these efforts depend on collaboration with field-based programs such as CalCOFI. Predictions of global change are possible and are improving and depend on collaboration with oceanographic research groups. End-to-end models are not tactical tools, and are not intended for short-term predictions (e.g., annual decision cycles). However, strategic management advice from end-to-end models is appropriate for a variety of ecosystem-based management needs, for instance within fishery management plans, fishery ecosystem plans, and cumulative impacts assessments.

LITERATURE CITED

Ainsworth, C. H., J. F. Samhouri, D. S. Busch, W. W. L. Cheung, J. Dunne, and T. A. Okey. 2011. Potential impacts of climate change on Northeast Pacific marine foodwebs and fisheries. ICES Journal of Marine Science 68:1217–1229.

Curchitser, E. N., D. B. Haidvogel, A. J. Hermann, E. L. Dobbins, T. M. Powell, and A. Kaplan. 2005. Multi-scale modeling of the North Pacific Ocean: Assessment and analysis of simulated basin-scale variability (1996–2003). Journal of Geophysical Research: Oceans (1978–2012) 110.

Dunne, J. P., J. G. John, A. J. Adcroft, S. M. Griffies, R. W. Hallberg, E. Shevliakova, R. J. Stouffer, W. Cooke, K. A. Dunne, and M. J. Harrison. 2012. GFDL's ESM2 Global Coupled Climate-Carbon Earth System Models. Part I: Physical Formulation and Baseline Simulation Characteristics. Journal of Climate 25:6646–6665.

Fiechter, J., K. A. Rose, E. N. Curchitser, and K. S. Hedstrom. 2014. The role of environmental controls in determining sardine and anchovy population cycles in the California Current: Analysis of an end-to-end model. Progress in Oceanography.

Kaplan, I. C., C. J. Brown, E. A. Fulton, I. A. Gray, J. C. Field, and A. D. M. Smith. 2013. Impacts of depleting forage species in the California Current. Environmental Conservation 40:380–393.

Kaplan, I. C., P. J. Horne, and P. S. Levin. 2012. Screening California Current Fishery Management Scenarios using the Atlantis End-to-End Ecosystem Model. Progress In Oceanography 102:5–18.

Kaplan, I. C., P. S. Levin, M. Burden, and E. A. Fulton. 2010. Fishing catch shares in the face of global change: a framework for integrating cumulative impacts and single species management. Canadian Journal of Fisheries and Aquatic Sciences 67:1968–1982.

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[1] http://www.nwfsc.noaa.gov/research/divisions/cb/ecosystem/marineecology/aem.cfm

Pacific Fishery Management Council, and National Marine Fisheries Service. 2014. Draft Environmental Impact Statement (DEIS) for proposed Harvest Specifications and Management Measures for the Pacific Coast Groundfish Fishery and Amendment 24 to The Pacific Coast Groundfish Fishery Management Plan. Page 1074. PFMC and NMFS, http://www.westcoast.fisheries.noaa.gov/publications/nepa/groundfish/1516spexdeis.pdf.

Rose, K., J. I. Allen, Y. Artioli, M. Barange, J. Blackford, F. Carlotti, R. Cropp, U. Daewel, K. Edwards, K. Flynn, S. Hill, R. HilleRisLambers, G. Huse, S. Mackinson, B. Megrey, A. Moll, R. Rivkin, B. Salihoglu, C. Schrum, L. Shannon, Y.-J. Shin, S. L. Smith, C. Smith, C. Solidoro, M. St. John, and M. Zhou. 2010. End-To-End Models for the Analysis of Marine Ecosystems: Challenges, Issues, and Next Steps. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 2:115–130.

Travers, M., Y. J. Shin, S. Jennings, and P. Cury. 2007. Towards end-to-end models for investigating the effects of climate and fishing in marine ecosystems. Progress in Oceanography 75:751–770.

PREDICTING THE FUTURE IN A NONLINEAR WORLD

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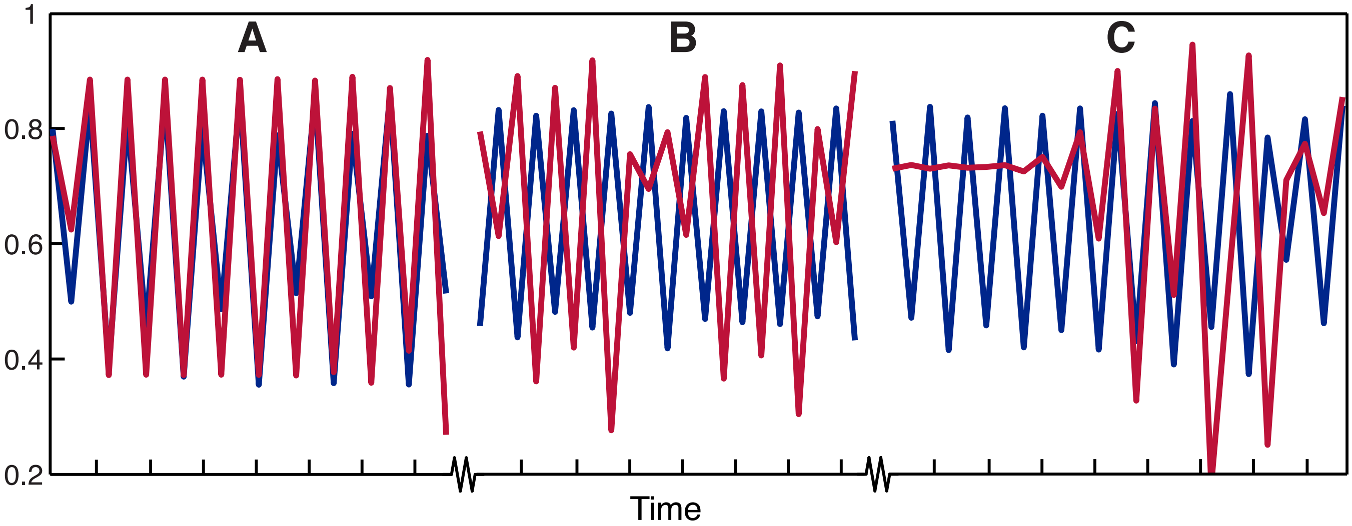

Figure 1. (From Sugihara et al. 2012). Correlations between variables (red and blue) can be ephemeral in nonlinear systems. In panel A, the two variables appear correlated, but in panel b, the variables appear anti-correlated. In panel c, and over longer time periods, there is no correlation, even though the system is dynamically coupled. See Sugihara et al. 2012 for model details and parameters.

Complex nonlinear dynamics are a general characteristic of ecosystems and a challenge for scientists who seek to understand, model, and manage them. These complex dynamics can result from the interaction between endogenous feedbacks, external forcing, and noise (i.e., stochasticity) and can lead to gradual shifts, switching between alternative stable states, deterministic chaos, mirage correlations, and critical transitions. Although the presence of nonlinear, state-dependent behavior means that it may not be possible able to predict the exact state of ecosystems 10–50 years from now, there remains a need for analytical tools that can address the nonlinear behaviors of real ecosystems. Such tools are important to produce accurate forecasts in the short-term, to understand key ecological mechanisms, and to enable adaptive management strategies that remain robust in response to such phenomena as climate change and invasive species.

A fundamental problem with traditional modeling approaches is that they are based on parametric equations, which represent very specific hypotheses about system behavior that can be difficult to justify (Wood and Thomas 1999). Moreover, these models often make simplifying assumptions (e.g., that systems are at equilibrium, different interactions are linearly separable) that do not line up with the known nonlinear reality. Consequently, these models can lack the flexibility to predict future behavior even when they are able to fit the observed data. For example, in nonlinear systems, correlations between variables may not be detectable even if they are dynamically coupled (fig. 1). Thus, variables can appear correlated for the duration of a research study, but this correlation may vanish even though the dynamics have not changed.

One alternative to conventional parametric models is the framework of Empirical Dynamic Modeling (EDM), which does not assume any particular set of equations for the relationships between variables, but instead reconstructs behavior directly from time series data. EDM is based on Takens' Theorem (Takens 1981) and the method of time delay embedding (Packard et al. 1980), which enables it to describe dynamical relationships that are too complex or subtle to capture in a simple set of equations. A brief description of the methods can be found in this short animation: http://simplex.ucsd.edu/EDM_101_RMM.mov.

In addition to the basic methodology of EDM, different techniques have been developed that extend the approach for specific applications: testing for the influence of exogenous factors (Dixon et al. 1999; Deyle et al. 2013), identifying causal interactions (Sugihara et al. 2012; Clark et al. 2015), and even leveraging data from ecological or spatial replicates (Hsieh et al. 2008; Clark et al. 2015). Here, we describe the usage of EDM in two real-world examples of ecological forecasting: (1) identification of a causal linkage between sea surface temperature and Pacific sardine populations in the California Current system and (2) an investigation into the influence of environmental variability on Fraser River sockeye salmon recruitment.

Sea Surface Temperature and Pacific Sardine in the California Current Ecosystem

There has been a long-standing question about whether fluctuations in forage fish abundance are environmentally driven. A well-known example is found in the case of Pacific sardine (*Sardinops sagax*) in the California Current Ecosystem. In California, the Pacific sardine fishery was a rare example of management that explicitly considers environmental conditions. The rationale for this policy was based on work by Jacobson and MacCall (1995), which reported a significant relationship between sea surface temperatures (SST) and recruitment. However, several more recent studies that reanalyze the relationship using newer data have brought the correlation between SST and recruitment into question. The conclusions depend on both the temperature measures examined and the fitting methodology employed (McClatchie et al. 2010; Lindegren and Checkley 2013; Jacobson and McClatchie 2013).

This conundrum can be resolved by using EDM. From a nonlinear perspective, the lack of a significant correlation does not necessarily indicate a lack of causality. Indeed, an analysis of this system using the method of convergent cross mapping (CCM) revealed that information about sea surface temperature (SST) was encoded in sardine time series, suggesting an effect of SST on sardine populations (Sugihara et al. 2012). However, a bottom-line test of whether temperature should be considered for management purposes is if temperature measurements can actually improve forecasts of sardine abundance.

Using EDM models with different environmental measures included as additional coordinates, we found that several temperature variables (SIO pier temperature and the Pacific Decadal Oscillation) did significantly improve forecasts (Deyle et al. 2013). These results provide confirmation that environmental factors do contain information (beyond that of the biological time series) useful for prediction, but to different degrees depending on the variable. Thus, for management purposes, it makes sense to include as robust a measure as possible of the relevant ecosystem affecting Pacific sardines. Indeed, the latest revision to management, by the Pacific Fishery Management Council, establishes harvest control guidelines that respond to a temperature index derived from CalCOFI data, thought to be a better indicator of whether conditions are beneficial or detrimental for recruitment.

Environmental Influences on Fraser River Sockeye Salmon

A similar question of environmental drivers involves sockeye salmon from the Fraser River system in British Columbia, Canada. Early work on this system found that the productivity of these salmon was related to ocean regimes (Beamish et al. 1997) and recent studies suggested that anomalous oceanic conditions experienced by juvenile salmon were responsible for extreme recruitment in 2009 and 2010 (Thomson et al. 2012). However, explicit incorporation of environmental factors into extensions of the standard Ricker model have, to date, produced no significant improvement in actual forecasts (MacDonald and Grant 2012).

Using time series of salmon abundance and the same environmental variables tested in official forecast models, we applied the equation-free framework of EDM, and found that forecasts were significantly improved by the inclusion of environmental factors for the 9 historically most abundant stocks (Ye et al. 2015). In conjunction with the lack of improvement in conventional fisheries models, these results suggest that the interaction between environment and Fraser River sockeye salmon is state-dependent, and therefore not readily encapsulated in simple mechanistic equations (i.e., the extended Ricker stock-recruitment model).

More generally, we note that, although simple parametric models may work over short time periods, such models need to be constantly refit (e.g., an analysis by Beamish et al. 2004 showing better fits of the simple Ricker model when data are partitioned by climate and ocean regimes, a Kalman-filter based approach from Peterman et al. 2000 wherein the Ricker model parameters undergo random drift). Consequently, when the system enters a new state where relationships change, the models will lack predictive power. Moreover, such models are unsatisfactory from a scientific perspective, because they do not explain actual ecological mechanisms—instead the models track the nonlinear behavior of the system phenomenologically as if it were random and therefore do not predict.

CONCLUSIONS

These examples demonstrate the utility of EDM as a data-driven approach for understanding and predicting the future in a nonlinear world. As a general framework, current methods (e.g., CCM, simplex projection) only address certain basic applications, but further developments will continue to bridge the gap between theory and practical usage. As a result, there is a huge potential for increasing use of the EDM framework in situations where parametric models are currently the norm. In addition to the situations described above, where the advantages of EDM for understanding nonlinear behavior are clear, we also note that the ability of EDM models to evolve with new data means that it is inherently more flexible than fixed model structures. Consequently, it is an ideal tool for adaptive prediction in systems changing due to climate change, human impacts, or other unknown factors.

LITERATURE CITED

Beamish, R. J., C.-E. M. Neville, and A. J. Cass. Production of Fraser River sockeye salmon (*Oncorhynchus nerka*) in relation to decadal-scale changes in the climate and the ocean. Canadian Journal of Fisheries and Aquatic Sciences, 54(3):543–554, 1997.

Beamish, R. J., J. T. Schnute, A. J. Cass, C. M. Neville, and R. M. Sweeting. The influence of climate on the stock and recruitment of pink and sockeye salmon from the Fraser River, British Columbia, Canada. Transactions of the American Fisheries Society, 133(6):1395–1412, 2004.

Clark, A. T., H. Ye, F. Isbell, E. R. Deyle, J. Cowles, D. Tilman, and G. Sugihara. Spatial 'convergent cross mapping' to detect causal relationships from short time-series. Ecology, 96(5):1174-1181, 2015.

Deyle, E. R., M. Fogarty, C.-H. Hsieh, L. Kaufman, A. D. MacCall, S. B. Munch, C. T. Perretti, H. Ye, and G. Sugihara. Predicting climate effects on Pacific sardine. Proceedings of the National Academy of Sciences, 110(16):6430–6435, 2013.

Dixon, P. A., M. Milicich, and G. Sugihara. Episodic fluctuations in larval supply. Science, 283:1528–1530, 1999.

Hsieh, C.-H., C. Anderson, and G. Sugihara. Extending nonlinear analysis to short ecological time series. The American Naturalist, 171(1):71–80, Jan 2008.

Jacobson, L. D., and A. D. MacCall. Stock-recruitment models for Pacific sardine (*Sardinops sagax*). Canadian Journal of Fisheries and Aquatic Sciences, 52(3):566–577, 1995.

Jacobson, L. D., and S. McClatchie. Comment on temperature-dependent stock-recruit modeling for Pacific sardine (*Sardinops sagax*) in Jacobson and MacCall (1995), McClatchie et al. (2010), and Lindegren and Checkley (2013). Canadian Journal of Fisheries and Aquatic Sciences, 70:1566–1569, 2013.

Lindegren, M., and D. M. Checkley Jr. Temperature dependence of Pacific sardine (*Sardinops sagax*) recruitment in the california current ecosystem revisited and revised. Canadian Journal of Fisheries and Aquatic Sciences, 70:245–252, 2013.

MacDonald, B. L., and S. C. H. Grant. Pre-season run size forecasts for Fraser River sockeye salmon (*Oncorhynchus nerka*) in 2012. DFO Can. Sci. Advis. Sec. Res. Doc. 2012/011, Fisheries and Oceans Canada, 2012.

McClatchie, S., R. Goericke, G. Auad, and K. Hill. Re-assessment of the stock-recruit and temperature-recruit relationships for Pacific sardine (*Sardinops sagax*). Canadian Journal of Fisheries and Aquatic Sciences, 67:1782–1790, 2010.

Packard, N. H., J. P. Crutchfield, J. D. Farmer, and R. S. Shaw. Geometry from a time series. Physical Review Letters, 45:712–716, 1980.

Peterman, R. M., B. J. Pyper, and J. A. Grout. Comparison of parameter estimation methods for detecting climate-induced changes in productivity of Pacific salmon (*Oncorhynchus* spp.). Canadian Journal of Fisheries and Aquatic Sciences, 57:181–191, 2000.

Sugihara, G., R. May, H. Ye, C.-H. Hsieh, E. Deyle, M. Fogarty, and S. Munch. Detecting causality in complex ecosystems. Science, 338:496–500, 2012.

Takens, F. Detecting strange attractors in turbulence. Dynamical Systems and Turbulence, Lecture Notes in Mathematics, 898:366–381, 1981.

Thomson, R. E., R. J. Beamish, T. D. Beacham, M. Trudel, P. H. Whitfield, and R. A. S. Hourston. Anomalous ocean conditions may explain the recent extreme variability in Fraser River sockeye salmon production. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science, 4:415–437, 2012.

Wood, S. N., and M. B. Thomas. Super-sensitivity to structure in biological models. Proceedings of the Royal Society of London B, 266:565–570, 1999.

Ye, H., R. J. Beamish, S. M. Glaser, S. C. Grant, C.-H. Hsieh, L. J. Richards, J. T. Schnute, and G. Sugihara. Equation-free mechanistic ecosystem forecasting using empirical dynamic modeling. Proceedings of the National Academy of Sciences, 112(13):E1569-E1576, 2015.

Part III

SCIENTIFIC CONTRIBUTIONS

AMERICAN SHAD SOUTHWARD MOVEMENT TO BAJA CALIFORNIA, MÉXICO: EVIDENCE OF LA NIÑA 2012

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ABSTRACT

The American shad (Clupeidae) is an anadromous fish native to the Atlantic coast of North America, and introduced to the West Coast in 1871. The catch of an individual of American shad (*Alosa sapidissima*) at Bahía de Todos Santos, Baja California, México, possibly is indicative of fish movements from northern areas to south temperate waters during particular oceanographic conditions. Their presence could be influenced by the La Niña event during 2012 that prevailed in the region. These conditions in the bay and south sites also led to the record of individuals of the white and green sturgeons (*Acipenser transmontanus* and *A. medirostris*). In this study, the southern limit distribution for the American shad at Bahía de Todos Santos is confirmed; this bay is located at 100 km south from the border of California (USA) and Baja California (México).

INTRODUCTION

The American shad, *Alosa sapidissima* (Wilson 1811), is the largest member of the Clupeidae and are native to the Atlantic Ocean, but introduced to the Pacific in the Sacramento River between 1871 to 1873, and later to the Columbia, Snake, and Willamette Rivers (Love 2011; Schroeter and Moyle 2006). On the Pacific Coast, the American shad is distributed as far north as Cook Inlet, Gulf of Alaska, with a population that has established itself in Kamchatka Peninsula (Russia), and south to Bahía de Todos Santos, Baja California, México (Miller and Lea 1972; Moyle 2002), most commonly from Washington State to San Francisco Bay (Love 2011). On the Atlantic coast, their distribution is from Labrador (Canada) to St. Johns River, Florida, USA (Moyle 2002).

This species is a migratory and anadromous fish that as an adult lives primarily in seawater but passes through estuaries on spawning migrations to freshwater (Allen and Pondella 2006). During summer and fall, American shad can be found in coastal waters; in the winter months they generally inhabit deeper ocean waters away from the coast at depths up to 375 m, and toward the end of winter they travel into rivers to spawn (Eddy 1957). In the next fall or early winter, juveniles make their way from rivers into the ocean, and in 2 to 5 years, adult shad return to their natal rivers to spawn (Glebe 1981).

The first documented occurrence of the American shad in the area of Bahía de Todos Santos, Ensenada, Baja California, México, was reported on July 16, 1958 (Claussen 1959); the specimen, an adult female (386 mm standard length, weight 757 g) was given by officials of the cannery Pesquera del Pacífico, in El Sauzal, a town located 8 km north of Ensenada, B.C., within the bay; according to information, a number of shad were landed with the regular sardine catch on July, 1958 (Claussen 1959). However, the collection site of this individual is unknown, because the reported geographical position (32°50'N, 116°50'W) is located on land in the continental United States. Also in those years, the sardine fishery area was located from the California border to San Quintín, B.C. (100 km north and 200 km south from Bahía de Todos Santos, respectively), and canneries were the reception facilities for sardines, only. Now, El Sauzal is a fishing port (lat. 31°53'40"N, long. 116°42'15"W) and home to a fleet of coastal fishing pangas and a medium size fishing fleet.

Based on the record by Claussen (1959), many references cite Bahía de Todos Santos as the southern limit for the American shad distribution (Allen and Pondella 2006; Hammann and Rosales-Casián 1990; Hendricks and Tryninewski 2011; Love 2011; Miller and Lea 1972; Moyle 2002). Another American shad individual was mentioned in Hammann and Rosales-Casián (1990) but without date or specific collection site, after that, no new shad records were reported. The aim of this work is to document this southward movement during La Niña conditions, and the presence of the American shad in the temperate environment of Bahía de Todos Santos, Baja California, México.

The Bahía de Todos Santos is located 100 km south of the California (USA)–Baja California (México) border (fig. 1). This bay is home to the city of Ensenada, Baja California, México, and the Punta Banda estuary. Fish studies of the bay and estuary began in 1982 (Beltrán-Felix et al. 1986; Diaz-Diaz and Hammann 1987), and after these studies, many other studies in both places and

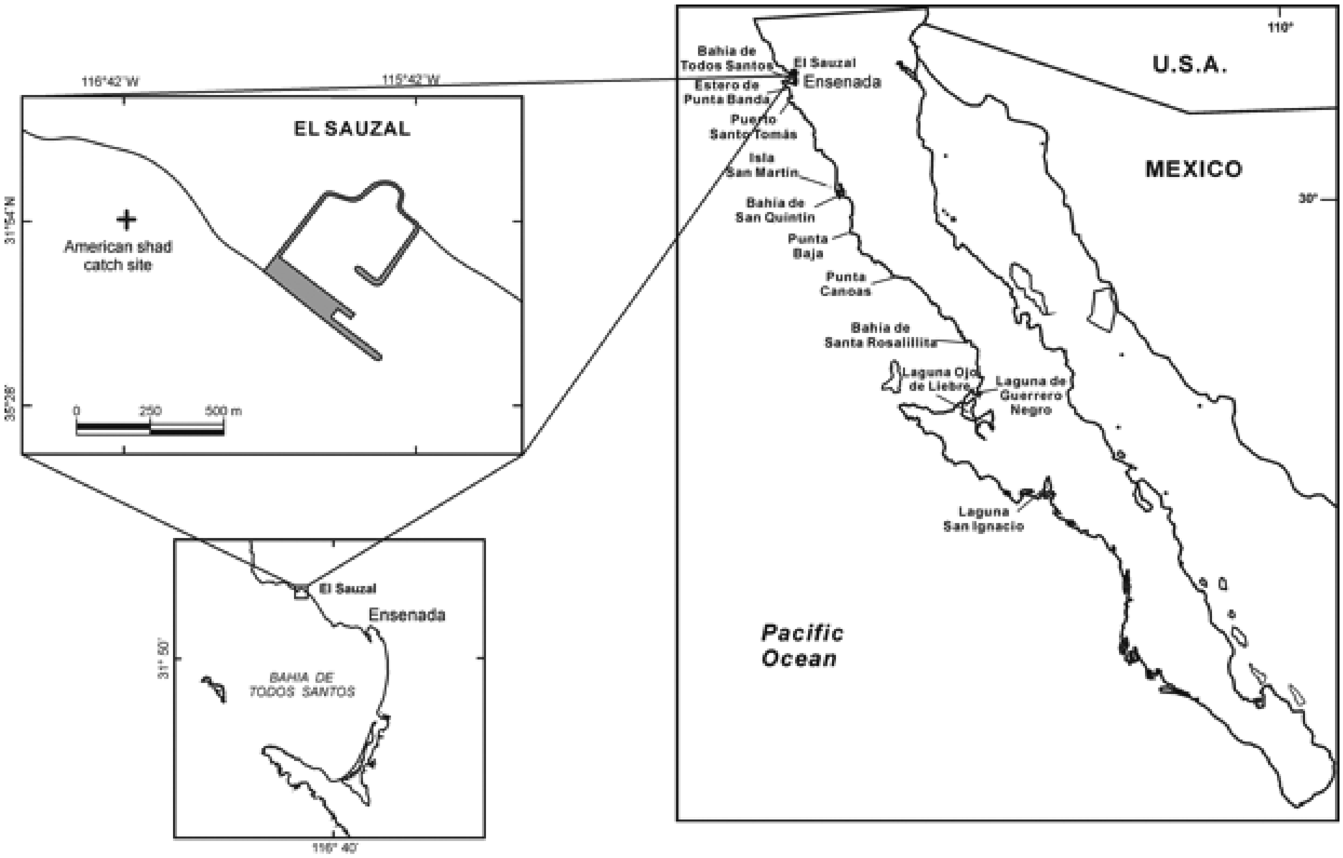

Figure 1. Catch site of American shad, *Alosa sapidissima*, at nearshore waters of Bahía de Todos Santos, Baja California, México.

further south were conducted (Rosales-Casián 2013). In the city of Ensenada is located the Ensenada Seafood Market that has 42 stalls, as well as docks and boat ramp to download fish captured from the bay and around. This place of sale receives fish caught from the Pacific of Baja California and from the Gulf of California, and is a major source for biological data.

From 2000 to 2004 and from 2008 to 2014, I have made monthly fish identifications and counts in the Ensenada Seafood Market; the fish species of the temperate zone were identified using the keys of Miller and Lea (1972). The measurements of total and standard lengths (TL, SL; mm), and also the weights (g) of some fish species, were recorded.

On June 28, 2012, and during the monthly sampling of the fish stands at the Ensenada Seafood Market, a fisherman arrived with his catch, and within the fishes, an uncommon individual was present that later was identified as the American shad (*Alosa sapidissima*). The shad was captured by the fisherman with a gill net on a commercial panga, and in the nearshore area of El Sauzal port, within the Bahía de Todos Santos (fig. 1); the fishing depth was 10–15 m, and according to information the catch site was localized close to the side west jetty, with an approximate localization of latitude 31°53'42.24"N, 116°42'41.31"W (fig. 1). Together with shad, also captured were the shortfin corbina (*Cynoscion parvipinnis*), California halibut (*Paralichtys californicus*), spotfin croaker (*Roncador stearnsii*), barred sand bass (*Paralabrax nebulifer*), white croaker (*Genyonemus lineatus*), and the queenfish (*Seriphus politus*). In June 28, 2012, the surface seawater temperature at Bahia de Todos Santos was 15.7°C, and the temperatures at 10 and 15 m depth were 12.2 y 11.3°C, respectively.

The individual of American shad measured 363 mm TL, 294 mm SL, and weighed 550 g (fig. 2). This species was identified by the combination of the following characteristics: body coloration was bluish on back and white on belly; compressed body; midlateral scales: 59; dorsal fin: 16 rays; anal fin: 21 rays; sharp sawlike scales or "scutes" along its belly: 21 anterior to and 16 posterior to pelvic base. This specimen of American shad had striations on gill cover, and one black spot on the back and close to gill cover (Miller and Lea 1972; Whitehead 1985).

From July 2010 to April 2012, La Niña conditions were present across most of the equatorial Pacific Ocean (NOAA 2013). In July 2010, the temperature anomaly dropped to –1.0°C, with the lowest value of –1.5°C from September 2010 to January 2011, and finished in May 2011; another La Niña event began in August

Figure 2. Individual of American shad, *Alosa sapidissima*, captured on June 28, 2012, at Bahía de Todos Santos, Baja California, México.

2011 (< –0.5˚C), with the lowest temperature anomaly at December (–1.5˚C), and weakened in April 2012 to –0.5˚C (NOAA 2013).

DISCUSSION

The American shad may have one or more black spots in a row on their shoulder, and though rare, some shad have two rows of black spots (Ford 2006); this specimen had only one spot. During summer and fall, American shad can be found in coastal waters before entering rivers to spawn (Eddy 1957; Ford 2006). The presence of this fish species during June 2012 at Bahía de Todos Santos coincides with their coastal movements during summer, and according to tagging studies, their migrations in schools is sometimes thousands of kilometers during one season, closely correlated with sea surface or bottom isotherms (Leggett and Whitney 1972). However, data from commercial and sport landings of American shad along the Pacific Coast indicate no evidence for large-scale seasonal migrations as reported along the Atlantic coast (Pearcy and Fisher 2011); this probably is the reason for the record of only one individual of American shad by a fishing boat, at the south end of their distribution that is Bahía de Todos Santos.

The American shad in the Pacific Ocean migrates long distances within their preferred SST range of 13–18˚C, and between 7-13˚C on bottom (Pearcy and Fisher 2011); this range is similar to those temperatures (11.3–15.7˚C) found at Bahía de Todos Santos on June 2012. The migration of American shad is from south of Point Conception into southern California and Baja California, México during January–June, followed by migrations far to the north during July–October (Leggett and Whitney 1972; Moyle 2002). American shad along the Pacific Coast have adapted to the prevailing environmental conditions, and they rapidly were dispersed, and expanded their range over 5,000 km of coastline from México to Russia. American shad increased dramatically in abundance and now comprise the largest spawning run of anadromous fish in the Columbia River (>4 million fish annually), constituting a remarkable biological invasion (Hasselman et al. 2012).

American shad is a planktivorous species, and is considered an alien fish in marine habitats of California together with the striped bass (*Morone saxatilis*), because both were introduced from Atlantic coastal waters to Sacramento River and San Francisco Bay, respectively (Allen et al. 2006). The American shad is classified as a marine migrant fish species, also an anadromous (estuarine and nearshore species) that pass through estuaries on spawning migrations, and is an inhabitant from northern and central California waters but not for southern California (Allen and Pondella 2006); no negative impacts of this planktivorous species on native fishes have been documented (Allen et al. 2006).

With respect to the possible record of an individual of American shad from Bahía de Todos Santos in 1958 (Claussen 1959), in July 1958 the neutral conditions had just begun with a sea surface temperature anomaly of +0.49°C, and those conditions continued until October 1958 with an anomaly of +0.35°C (NOAA 2013). This probably influenced the American shad presence at the Bahía de Todos Santos or in other sites around the bay.

The fish studies at the Bahía de Todos Santos (31°49' 11.33"N, 116°38'40.53"W) began in the early 1980s at kelp beds (Díaz-Díaz and Hammann 1987), sandy bottoms (Hammann and Rosales-Casián 1990), and the sportfishing catch (Rodriguez-Medrano 1993). In addition, research on the fish community of the systems Bahía de Todos Santos-Estero de Punta Banda, and Bahía de San Quintín and their adjacent coast (30°23'14.59"N, 115°59'29.11"W) was conducted between 1992 to 1995 using beam trawl, otter trawl, beach seine, gill net, and hook and line (Rosales-Casián 1997; Rosales-Casián 2004a). The artisanal coastal fishery was studied at eight fishing camps along northwestern coast of Baja California (Rosales-Casián and Gonzalez-Camacho 2003), from Santo Tomas (31°33'4.78"N, 116°40'35.78"W) to Punta Canoas (29°25'42.72"N, 115°10'50.39"W). Other studied sites were Bahía El Rosario (29°57'4.11"N, 115°47'56.35"W), a bay protected by Punta Baja (Rosales-Casián 2011), and Bahía Santa Rosalillita (fig. 1) as the farthest south site, 28°39'34.01"N, 114°14'13.81"W (my unpublished data). The Seafood Market of Ensenada Port has been surveyed monthly since September 2000 to 2004 (Hernández-Hernández 2002; Rosales-Casián and Ruz-Cruz 2003), and from 2008 until now. All those studies failed to collect any specimen of American shad except in Hammann and Rosales-Casián (1990) where the presence of an individual of American shad in the seafood market is mentioned without specifying the capture site.

The cold conditions during the two years of La Niña (2010–12) that were present in the region probably helped to the southward movement of the American shad, to keep it into the Bahía de Todos Santos until June 2012. During 2010–11, the lowest temperature anomaly was –1.5°C and was considered a strong La Niña event, and during 2011–12 the lowest anomaly was –1.0°C (NOAA 2013). Northern fish species can migrate southward during cold periods (Rosales-Casián and Almeda-Jauregui 2009), in a similar way to movements of tropical fish species northward during El Niño conditions (Rosales-Casián 2004b; Rosales-Casián 2013).

The record of American shad is important because it is an evidence of northern fish species movements to Bahía de Todos Santos during La Niña conditions, similar to southward migration movements of other anadromous fish species like the white sturgeon (*Acipenser trasmontanus*) registered in the bay (Rosales-Casián and Ruz Cruz 2005; Ruiz-Campos et al. 2011), and the green sturgeons (*Acipenser medirostris*) that have been registered in the bay and the southern site of the El Socorro, B.C., 200 km south (Rosales-Casián and Almeda-Jauregui 2009). Also, it reconfirms the southern limit distribution for the American shad species at Bahía de Todos Santos, Baja California (México), and increases the fish species list from the bay.

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LITERATURE CITED

Allen, L. G., and D. Pondella. 2006. Ecological classification. *In* The Ecology of Marine Fishes: California and Adjacent Waters. Allen, L. G., D. J. Pondella, II, and M. H. Horn, eds. University of California Press, Berkeley and Los Angeles, pp. 81–113.

Allen, L. G., M. A. Yoklavich, G. M. Cailliet, and M. H. Horn. 2006. Bays and estuaries. *In* The Ecology of Marine Fishes: California and Adjacent Waters. Allen, L. G., D. J. Pondella, II, and M. H. Horn, eds. University of California Press, Berkeley and Los Angeles, pp. 119–148.

Beltrán-Felix, J. L., M. G. Hammann, A. Chagoya-Guzmán, and S. Álvarez-Borrego. 1986. Ichthyofauna of Estero de Punta Banda, Ensenada, Baja California, México, before a major dredging operation. Ciencias Marinas. 11:79–92.

Claussen, L. G. 1959. A southern range extension of the American shad to Todos Santos Bay, Baja California, México. California Fish & Game. 45:217.

Díaz-Díaz, M. E., and M. G. Hammann. 1987. Relaciones tróficos de los peces asociadas a un manto de *Macrocystis pyrifera* en la Bahía de Todos Santos, Baja California, México. Ciencias Marinas. 13:81-96.

Eddy, S. 1957. How to Know the Freshwater Fishes. WMC Brown Company, Iowa. 253 pp.

Ford, F. 2006. 77 Great Fish of North America. Thomas Allen & Sons Limited, Ontario. 208 pp.

Glebe, B. 1981. Latitudinal differences in energy allocation and use during the freshwater migrations of American shad (*Alosa sapidissima*) and their life history consequences. Canadian Journal of Fisheries and Aquatic Sciences. 38:806–820.

Hammann, M. G., and J. A. Rosales Casián. 1990. Taxonomía y estructura de la comunidad de peces del Estero de Punta Banda y Bahía de Todos Santos, Baja California, México. *In* Temas de Oceanografía Biológica en México, Rosa Vélez J. and F. González Farías, eds. Universidad Autónoma de Baja California, Ensenada, pp. 153–192.

Hasselman, D. J., R. A. Hinrichsen, B. A. Shields, and C. C. Ebbesmeyer. 2012. The rapid establishment, dispersal, and increased abundance of invasive American shad in the Pacific Northwest. Fisheries. 37:103–114.

Hendricks, M. L, and J. D. Tryninewski. 2011. Life History, Conservation and Management Strategies for the American shad (*Alosa sapidissima*) of the Susquehanna River in Pennsylvania. Division of Fish Production Services, Anadromous Fish Restoration Unit, Pennsylvania Fish and Boat Commission. State College, Pennsylvania.

Hernández-Hernández, A. 2002. Composición específica de los peces escama comercializados en el Mercado de Mariscos del Puerto de Ensenada, Baja California, México. B.S. Dissertation, Universidad Autónoma del Estado de Morelos, Cuernavaca, 60 pp.

Leggett, W. C., and R. R. Whitney. 1972. Water temperature and the migrations of American shad. Fishery Bulletin. 70:659–670.

Love, M. 2011. Certainly more than you want to know about the fishes of the Pacific coast. Really Big Press, Santa Barbara, 649 pp.

Miller, D. J,. and R. N. Lea. 1972. Guide to the coastal marine fishes of California. Bulletin of the California Department of Fish and Game, No. 157.

Moyle, P. B. 2002. Herrings, Clupeidae. *In* Inland Fishes of California: Revised and Expanded, P. B. Moyle, ed. University of California Press, Berkeley, pp. 114–120.

NOAA. 2013. ENSO Cycle: Recent evolution, current status and predictions. Available from: http://www.elnino.noaa.gov/ (accessed August 2014).

Rodriguez-Medrano, M. C. 1993. Descripción y análisis biológico de la pesca deportiva en la Bahía de Todos Santos, Ensenada Baja California. M. S. Dissertation, Centro de Investigación Científica y de Educación Superior de Ensenada, B.C., Ensenada, 88 pp.

Rosales-Casián, J. A. 1997. Estructura de la comunidad de peces y el uso de los ambientes de bahías, lagunas y costa abierta en el Pacífico Norte de Baja California. Ph.D. Dissertation, Centro de Investigación Científica y de Educación Superior de Ensenada, B.C. México. 201 pp.

Rosales Casián, J. A. 2011. The fish assemblages from the nearshore area of Punta Baja, B.C., México, the southern limit of the Southern California bight. CalCOFI Reports. 52: 168-181.

Rosales-Casián, J. A., and J. R. González-Camacho. 2003. Abundance and importance of fish species from the artisanal fishery on the Pacific Coast of Northern Baja California. Bulletin of the Southern California Academy of Sciences. 102:51–65.

Rosales-Casián, J. A. 2004a. Composition, importance and movement of fishes from San Quintín Bay, Baja California, México. Ciencias Marinas. 30 (1A):109–117.

Rosales-Casián, J. A. 2004b. Tropical fish species as indicador of 1997–98 El Niño in Bahía de San Quintín, Baja California, México. Bulletin of the Southern California Academy of Sciences. 103:20–23.

Rosales-Casián, J. A., and R. Ruz-Cruz. 2005. Record of a white sturgeon, from Bahía de Todos Santos, Baja California, México, Found at the Ensenada Sea Food Market. Bulletin of the Southern California Academy of Sciences. 104:153–155.

Rosales-Casián, J. A., and C. Almeda-Jauregui. 2009. Unusual occurrence of a green sturgeon, *Acipenser medirostris*, at El Socorro, Baja California, México. Calif. Coop. Oceanic Fish. Invest. Rep. 50:169–171.

Rosales-Casián, J. A. 2013. Finescale triggerfish (*Balistes polylepis*) and roosterfish (*Nematistius pectoralis*) presence in temperate waters off Baja California, México, evidence of El Niño conditions. Calif. Coop. Oceanic Fish. Invest. Rep. 54:81–84.

Ruiz-Campos, G., J. L. Castro-Aguirre, and F. J. García-De León. 2011. First specimen of the white sturgeon (*Acipenser transmontanus* Richardson, 1836) in coastal waters of México with data on its genetic identity. California Fish & Game. 97:36–42.

Schroeter, R. E., and P. B. Moyle. 2006. Alien fishes. *In* The Ecology of Marine Fishes: California and Adjacent Waters. Allen, L. G., D. J. Pondella, II, and M. H. Horn, eds. University of California Press, Berkeley and Los Angeles, pp. 611–620.

Whitehead, P. J. P. 1985. Clupeoid Fishes of the World (suborder Clupeioidei). An annotated and illustrated catalogue of the herrings, sardines, pilchards, sprats, shads, anchovies and wolf-herrings. FAO Species Catalogue. Vol. 7. Part 1–Chirocentridae, Clupeidae and Pristigasteridae. FAO Fisheries Synopsis 125. Rome, 303 pp.

THE GENETIC DIVERSITY AND POPULATION STRUCTURE OF BARRED SAND BASS, *PARALABRAX NEBULIFER*: A HISTORICALLY IMPORTANT FISHERIES SPECIES OFF SOUTHERN AND BAJA CALIFORNIA

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ABSTRACT

We examined the contemporary genetic structure of the barred sand bass, *Paralabrax nebulifer*, a commonly fished species in southern California and Baja California, Mexico. Populations of barred sand bass in southern California have experienced severe declines in numbers over the last decade subsequently leading to severely depressed status of the recreational fishery. Such large population declines can lead to an overall decrease in genetic diversity. The present study examined the genetic diversity in this species (N = 365) using both the control region of the mitochondrial DNA and microsatellite markers for locations throughout California and Baja California. Both markers showed a high degree of genetic diversity and genetic mixing however there is some evidence of structuring between locations north and south of the San Quintin upwelling zone. Despite the weak structuring observed around the upwelling zone, barred sand bass throughout the northeastern Pacific likely comprise a single large population.

INTRODUCTION

Molecular genetic techniques have become more widespread in oceanic systems and in fishery management (Ryman 1991; Ensing et al. 2013) due to the ability to identify distinct genetic stocks, the genetic health, and connectivity between stocks (Palsbøll et al. 2007; Dudgeon et al. 2012; Ovenden et al. 2015). Fishery stocks are identified using various life history parameters that do not necessarily reflect the genetic population or stock (Shaklee et al. 1999; Hutchinson et al. 2003; Hutchinson 2008; Reiss et al. 2009). Additionally, boundaries established by state or international borders can divide a biological stock into multiple fishery stocks (Shaklee et al. 1999). Therefore, it is important to understand what constitutes a biological stock to better manage fisheries. A high degree of genetic variation facilitates the adaptation of a species to a variety of environmental or anthropogenic conditions and thus, species (or population) survival (Carvalho and Hauser 1994; Kenchington et al. 2003). Connectivity between populations or stocks is also important for fishery management because it can identify source and sink populations and the potential for replenishment of depleted stocks (Palsbøll et al. 2007). Therefore, it is essential to quantify genetic variation and connectivity within a species to inform management decisions that maintain that variation (Ryman 1991; Airame et al. 2003; Pérez-Ruzafa et al. 2006; Palsbøll et al. 2007).

The barred sand bass, *Paralabrax nebulifer*, ranges from Santa Cruz, CA to the southern tip of the Baja California peninsula in Mexico (Love et al. 1996) and is fished in both countries. Barred sand bass form large spawning aggregations along the coast from late spring to early fall with a peak in July (Love et al. 1996; Baca-Hovey et al. 2002; Mason and Lowe 2010). Individuals exhibit site fidelity during non-spawning months and some exhibit site fidelity year round, not participating in spawning aggregations (Jarvis et al. 2010; Mason and Lowe 2010). The majority of barred sand bass also exhibit a preference for spawning locations from year to year (Jarvis et al. 2010). Barred sand bass migrate moderate distances (average of 15 km ranging from 1 km to 40 km) (Jarvis et al. 2010) to reach spawning locations; however, individuals with overlapping home ranges do not necessarily migrate to the same spawning grounds (Jarvis et al. 2010).

Because of these characteristics of its mating system, barred sand bass comprise one of the most important recreational fisheries in southern California. The species was commercially fished until the 1950s, and since then, it has been recreationally fished off the coast of southern California (Young 1963). The recreational fishery for barred sand bass experienced a collapse in 2003 due to the targeting of spawning aggregations and a decline in landings and biomass estimates (Erisman et al. 2011). In addition to the recreational fishery in California, there is a small scale commercial fishery in Baja California, Mexico. This small scale fishery has the highest catch in tons of any fished species along the Pacific Coast of

Baja California (Rosales-Casian and Gonzalez-Camacho 2003; Erisman et al. 2011).

Several aspects of the biology of the barred sand bass have been studied including life history (Baca-Hovey et al. 2002; Sadovy and Domeier 2005; Jarvis et al. 2010; Cota-Gomez et al. 2013), ecology (Mason and Lowe 2010) and the fishery (Erisman et al. 2011; Miller and Erisman 2014); however, the genetic diversity and population structure of barred sand bass off both southern and Baja California is unknown. One concern for barred sand bass populations is a decline in the genetic diversity due to the fishery collapse in southern California (Smith et al. 1991; Hutchinson et al. 2003) and the potential for reduction in the body size at first reproduction (van Wijk et al. 2013; Alós et al. 2014). In order to determine potential effects of the fishery collapse on the genetic diversity of barred sand bass, we must first determine what the genetic diversity and population structure of barred sand bass is.

Based on what is known about other species of *Paralabrax*, we expect to see a high degree of connectivity due to its reproductive mode and the potential for the larvae to be transported considerable distances via the currents (Selkoe and Toonen 2011). Barred sand bass have a pelagic larval duration (PLD) of 21–30 days (Allen and Block 2012) that is comparable to two congeners: the kelp bass, *P. clathratus*, and the spotted sand bass, *P. maculatofasciatus*. In both of these species there was a high degree of connectivity throughout the region (mtDNA control region; Phalen 1999; Salomon 2005); however, the spotted sand bass shows some evidence for divergent populations between southern California and Baja California that may be due to the San Quintin upwelling zone in Baja California, Mexico (Salomon 2005). Population genetic structure was also low in the kelp bass using microsatellites with a greater degree of structuring in southern California compared with Baja California (Selkoe et al. 2006; Selkoe et al. 2007). This upwelling zone is a known biogeographic barrier for migratory species (Bernardi 2000; Terry et al. 2000; Bernardi et al. 2003; Olivares-Banuelos et al. 2008). The upwelling zone is thought to also be a barrier for larval dispersal (Butler et al. 1982; Shanks and Eckert 2005). Thus, we expected to show a genetic break around the San Quintin upwelling zone in barred sand bass given that this division is seen in its sister species the spotted sand bass.

The goal of this study was to determine the genetic diversity, population structure, and connectivity among localities of barred sand bass to inform the conservation management of genetic stocks. This study used both mitochondrial DNA markers and nuclear DNA markers (microsatellite loci) to determine the population structure of barred sand bass in southern California and Baja California, Mexico. The mitochondrial DNA control region is a common marker for population structure analysis due to the high variability of the region (Magoulas 2005), while microsatellite markers are ideal for population studies due to their high variability (Wirgin and Waldman 2005).

MATERIALS AND METHODS

Collection and Extractions

Tissue samples from either the fin, gill rakers, muscle, or liver tissues of individual barred sand bass were collected using sterile techniques and stored in 95% ethanol and subsequently frozen in a −4°C freezer at California State University, Northridge. Samples from southern California were collected using hook and line from five locations (Ventura, Marina Del Rey, Los Angeles/Long Beach Harbor, San Clemente, and San Diego) and from commercial fishers from eight sites in Baja California, Mexico (Popolta, San Quintin/Camalu, Santa Rosalita, Laguna Manuela, Isla Cedros, Punta Abreojos, and Bahia Magdalena) (fig. 1). Samples from Ventura, Marina Del Rey, Los Angeles/Long Beach Harbor, San Diego, Santa Rosalita, San Quintin, Popolta, Laguna Manuela, and Camalu were collected during the non-spawning season while samples from San Clemente, Isla Cedros, Punta Abreojos, and Bahia Magdalena were sampled during the spawning season. For each site, 7–30 individuals were sampled (Ventura, n = 21; San Quintin, n = 9; Laguna Manuela, n = 9; Popotla, n = 7; all other sites n = 30).

Additional barred sand bass samples that were collected from 1997 to 1999 from Santa Barbara, California to Isla Cedros, Mexico (San Diego, n = 9; Platform Gina, n = 1; Los Angeles/Long Beach Harbor, n = 37; San Quintin, n = 13; Isla San Martin, n = 6; Isla Cedros, n = 2). The samples from Isla San Martin and Isla Cedros were collected during the non-spawning season while the sample from Platform Gina in Santa Barbara was collected during spawning season. Samples from Long Beach were collected in both non-spawning and spawning season. Extractions were carried out using a DNeasy Blood and Tissue Kit (Qiagen) following the manufacturer's protocol.

Mitochondrial DNA Amplification and Sequencing

The mitochondrial DNA control region was amplified in 25 µl polymerase chain reactions (PCR) containing ~100 ng DNA, 1 uM of primer (FWD 5'-TTCCACCTCTAACTCCCAAAGCTAG-3') and reverse (REV 5'-ACGCTGGAAAGAACG CCCGGCATGG-3'; Lee et al. 1995), and 1X EconoTaq® PLUS 2X Master Mix (Lucigen). PCR conditions consisted of an initial denaturation at 94°C for two minutes, followed

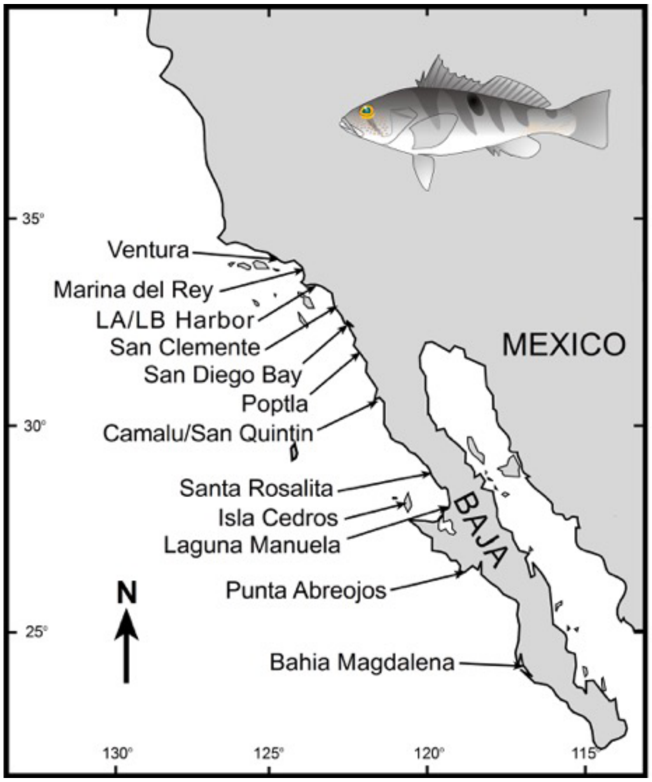

Figure 1. Map of sampling locations of *Paralabrax nebulifer*. Sampling covers the range in which *Paralabrax nebulifer* is commonly found. Sampling was performed using hook and line or from small scale trap fishermen.

by 30 cycles of 94°C denaturation for 30 seconds, 58°C annealing for 30 seconds, 72°C extension for 30 seconds, and a final extension of 72°C for 10 minutes. Amplicons were purified and sequenced by BigDye v3.1 (Applied Biosystems) dye-determination using nested primers from Lee et al. (1995; FWD 5'-GGGCGGATCCCACCACTAGCTCCCAAA-3'; REV 5'-CCTGAAGTAGGAACCAGATG-3') at Laragen, Inc. (Culver City, CA).

Mitochondrial DNA Analysis

For each sample, the forward and reverse sequences were aligned and manually cleaned up using Sequencher 5.2 (Gene Codes Corporation). Each sequence was assigned a haplotype (1–164) and all sequences were aligned in MEGA 6 (Tamura et al. 2013). Corrections to the alignment were done using Mesquite (Maddison and Maddison 2011). All haplotypes were uploaded to GenBank (NCBI) (KJ935922-KJ936085).

We used JModelTest (Guindon and Gascuel 2003; Darriba et al. 2012) to determine the best evolutionary model for the control region. We used a Tamura Nei model with a gamma correction in MEGA 6 (Tamura et al. 2013). Nucleotide divergence between sampling locations was calculated in MEGA 6. Estimates of pairwise genetic differentiation (pairwise Φ_{ST}) between sampling locations was calculated in Arlequin 3.5 (Excoffier and Lischer 2010) with significance being determined by permutation (10,000 replicates) and the false discovery rate used to correct for multiple tests (Narum 2006).

The genetic structure of barred sand bass populations was determined using nested AMOVAs (Analysis of MOlecular Variance) in Arlequin 3.5 (Excoffier and Lischer 2010). The first AMOVA compared the samples collected in 1997–99 and those collected 2010–13 to determine if samples could be pooled. We then used an AMOVA to compare all sampling locations of barred sand bass. Finally, we quantified genetic differentiation for all barred sand bass samples between the north and south of the San Quintin upwelling zone (north: Ventura, CA to San Quintin, B.C.; south: Santa Rosalita, B.C. to Bahia Magdalena, B.C.). To determine significance, 10,000 permutations were performed for all AMOVAs and the false discovery rate was used to correct for multiple tests. A median-joining haplotype network (Bandelt et al. 1999) was generated using all DNA sequences in NETWORK 4.6.11 (Fluxus-engineering.com). Post processing analysis was carried out to clean up the network (Polzin and Daneschmand 2003).

The relative nucleotide composition, number of polymorphic loci, haplotype diversity (*h*), nucleotide diversity (π), the number of pairwise nucleotide differences, the co-ancestry coefficient (θ_S), Tajima's D (Tajima 1989) and Fu's F_S (Fu 1997) were calculated using Arlequin 3.5 (Excoffier and Lischer 2010). In addition, a Mantel test for an estimate of isolation by distance was done across the range of barred sand bass using GeneAlEx 6.5 (Peakall and Smouse 2006, 2012).

Microsatellite Loci Selection

A microsatellite library for *Paralabrax nebulifer* was generated using 454 sequencing by Cornell University using extracted barred sand bass DNA and tissue samples from California and Mexico. We amplified 12 polymorphic loci using a three primer system where a nucleotide tag was added to the 5' end of each primer (Brownstein et al. 1996; Schuelke 2000). The third primer was fluorescently labeled using 6-FAM or 5-HEX. Each PCR contained 2 μl of the 10 μM pig tail primer, 0.15 μl of the 10 μM long tail primer, 0.05 μl of 10 μM 6-FAM (or 5-HEX), 1X EconoTaq® PLUS 2X Master Mix (Lucigen) and 100 ng of template DNA (10–990 μM). We used a touchdown PCR with the following conditions. An initial denaturation of 95°C for 5 minutes, followed by 35 cycles of denaturation at 95°C for 40 sec; annealing temperatures starting at 61°C for 45 sec with a decrease by 1°C for each of 7 subsequent cycles and the remaining 28 cycles performed at 55°C for 45 sec; extension of 72°C for 45 sec, with a final elongation step

TABLE 1

Microsatellite loci generated for use in *Paralabrax nebulifer*. All loci are in Hardy-Weinberg equilibrium and have no null alleles.

Locus	Forward primer 5'–3'	Reverse primer 5'–3'	Motif	N	Size (bp)	A	H_O	H_E	F_{IS}
*Pne*01CCK17	TGGCCAGTAATTATAATACGCACG	CTTCCTTTCATCATCTACCACCC	$(ATCC)_n$	341	217–273	27	0.876	0.837	–0.047
*Pne*2102	CTTCCCTCTGCCACTTCTTCAC	TCAGAGATCAGAGATGGTTTCGG	$(AACAT)_n$	315	163–203	12	0.712	0.713	0.002
*Pne*01CVDJQ	TTCTTTATAGCACCAGACGCAAC	TTTCTCTTGCTCTTTCTTGGGC	$(AGCC)_n$	317	146–200	13	0.820	0.799	–0.027
*Pne*02IMIH6	GGCAGTTTGAAGTGTGTCCTAG	TCTCATATTCAGCCTTCCTCACC	$(ATCC)_n$	340	150–208	14	0.859	0.830	–0.035
*Pne*5053	ACTTCTTGCATGATAGTTCTGGC	GTCTTTATCCTCAATCCCGAAGC	$(AAAG)_n$	341	384–474	32	0.546	0.609	0.102
*Pne*02JMRK5	ACGGTCAGGGTAAGATTATCAGG	TAGTAAGGTGTCGGGTCATCAAG	$(ATCC)_n$	330	234–462	40	0.898	0.932	0.036

*indicates significant value

at 72°C for 5 min. All PCR products were electrophoresed on an Applied Biosystems 3130XL Genetic Analyzer at California State University, Northridge. Allele sizes were scored by comparison with 500 LIZTM ladder (GeneScan™ ABI) and scored manually in GeneMarker (Softgenetics). To validate the dataset, 14% of the PCRs were reanalyzed for all loci.

Additionally, each locus was tested for applicability in two congeners (*P. clathratus* and *P. maculatofasciatus*) using the same protocols for amplification as described previously. Successful amplification and genotypes were determined using GeneMarker (Softgenetics). All 12 of the microsatellite primers successfully amplified in both *P. clathratus* and *P. maculatofasciatus*.

Microsatellite Analysis

Deviations from Hardy-Weinberg equilibrium for each sampling location were calculated using GenePop (Raymond and Rousset 1995; Rousset 2008) and significance was determined after Bonferroni correction for multiple tests. Each sampling location was checked for null alleles using Micro-Checker (van Oosterhout et al. 2004) and tests of disequilibrium between all pairs of loci over all populations and within populations were calculated using FSTAT 2.9.3.2 (Goudet 2003). Loci not in Hardy-Weinberg equilibrium and with possible null alleles were eliminated from the final analysis. A total of six loci were used for the analysis (*Pne*01CCK17, *Pne*2102, *Pne*02IMIH6, *Pne*5053, *Pne01CVDJQ* and *Pne*02JMRK5) (table 1). Observed heterozygosity (H_O) and expected heterozygosity (H_E) for the loci were calculated using GenAlEx 6.5 (Peakall and Smouse 2006, 2012).

Genetic demes were determined using STRUCTURE 2.3.4 (Pritchard et al. 2000) using an admixture model. The model was run for K = 1–12 with a burn-in length of 100,000 and Monte Carlo Markov Chain of 1,000,000 steps and was repeated 20 times for each K. The Evanno method was implemented using STRUCTURE HARVESTER (Earl and VonHoldt 2012) to determine the best K for barred sand bass (Evanno et al. 2005). Proportion of ancestry for each individual based on the best value of K was visualized in Excel (Microsoft Corporation).

POWSIM 4.1 (Ryman and Palm 2006) was used to estimate the statistical power of the microsatellite loci to detect differentiation among localities. Burn-in consisted of 1,000 steps with 100 batches and 1,000 iterations per batch. A Fisher's and Chi-square test were used to test for significance of a F_{ST} value for each run. Pairwise tests of differentiation (F_{ST}) were calculated using GeneAlEx 6.5 (Peakall and Smouse 2006, 2012). As F_{ST} has been shown to underestimate divergence when estimated from highly polymorphic loci (Hedrick 1999),

TABLE 2
Summary statistics for a) mitochondrial DNA control region and b) microsatellite DNA markers for all locations of *Paralabrax nebulifer*.

a) Mitochondrial DNA control region statistics showing haplotype number, haplotype diversity (*h*), nucleotide diversity (π), mean pairwise difference, coancestry coefficient (θ_S), Tajima's D and Fu's F_S for all populations

Location	Haplotype no.	*h*	π	Mean pairwise difference	θ_S	Tajima's D	Fu's F_S
Platform Gina	1	1.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000	0.000
Ventura	20	0.995 ± 0.017	0.014 ± 0.008	7.448 ± 3.625	14.496 ± 5.149	–1.934*	–13.072*
Marina Del Rey	23	0.984 ± 0.013	0.013 ± 0.007	6.919 ± 3.341	12.167 ± 4.018	–1.608*	–13.794*
LA/LB Harbor	45	0.989 ± 0.005	0.010 ± 0.006	5.557 ± 2.703	10.649 ± 3.098	–1.616*	–25.374*
San Clemente	22	0.994 ± 0.013	0.011 ± 0.006	6.169 ± 3.030	11.353 ± 3.629	–1.664*	–16.287*
San Diego	30	0.988 ± 0.009	0.012 ± 0.006	6.250 ± 3.032	11.353 ± 3.629	–1.650*	–24.603*
Popolta	7	0.964 ± 0.077	0.006 ± 0.004	3.464 ± 1.974	4.242 ± 2.154	–1.210	–2.842
Camalu/San Quintin	30	0.989 ± 0.010	0.013 ± 0.007	7.127 ± 3.422	14.710 ± 4.673	–1.897*	–20.915*
Santa Rosalita	29	1.000 ± 0.009	0.013 ± 0.007	7.042 ± 3.040	13.496 ± 4.508	–1.817*	–25.082*
Isla Cedros	27	0.990 ± 0.011	0.011 ± 0.006	5.966 ± 2.921	9.684 ± 3.854	–1.400	–22.931*
Laguna Manuela	9	1.000 ± 0.052	0.012 ± 0.007	6.444 ± 3.369	8.463 ± 3.854	–1.312	–4.037*
Isla San Martin	4	0.900 ± 0.161	0.006 ± 0.004	3.000 ± 1.874	3.360 ± 2.001	–0.747	–0.331
Punta Abreojos	26	0.994 ± 0.011	0.011 ± 0.006	5.712 ± 2.810	9.932 ± 3.342	–1.612*	–25.345*
Bahia Magdalena	21	0.974 ± 0.019	0.009 ± 0.005	4.902 ± 2.462	7.966 ± 2.819	–1.444	–14.865*
All samples	164	0.998 ± 0.000	0.011 ± 0.006	6.148 ± 2.931	19.449 ± 4.139	–2.059*	–24.568*

b) Microsatellite DNA marker statistics showing number of alleles (A), observed (H_O) and expected (H_E) heterozygosity.

Location	A	H_O	H_E
Ventura	11	0.8781	0.786
Marina Del Rey	13	0.8797	0.824
LA/LB Harbor	15	0.7876	0.822
San Clemente	14	0.8499	0.835
San Diego	13	0.7690	0.779
Popolta	7	0.6458	0.777
Camalu/San Quintin	13	0.7424	0.806
Santa Rosalita	10	0.8617	0.752
Isla Cedros	13	0.8460	0.817
Laguna Manuela	6	0.6852	0.675
Punta Abreojos	13	0.7181	0.780
Bahia Magdalena	12	0.7585	0.791
All samples	12	0.7852	0.787

* indicates significant value

G'_{ST} (Meirmans and Hedrick 2011) and Jost's D (Jost 2008) were also calculated in GenAlEx 6.5 (Peakall and Smouse 2006, 2012). For all pairwise comparisons, 9,999 permutations were performed to determine significance and the false discovery rate was used to correct for multiple tests.

Genetic structure was determined by three AMOVAs performed within GeneAlEx 6.5 (Peakall and Smouse 2006, 2012). The first AMOVA tested the samples collected between 1997 and 1999 to those collected between 2010 and 2013. The second AMOVA compared the variation across the entire range of the species. Finally, the third AMOVA tested the effect of the San Quintin upwelling zone on population connectivity by grouping sampling locations into two large populations north and south of the zone (north: Ventura, CA to San Quintin, B.C.; south: Santa Rosalita, B.C. to Bahia Magdalena, B.C.). To determine significance, 9,999 permutations were performed for all AMOVAs and the false discovery rate was used to correct for multiple tests.

RESULTS

Mitochondrial DNA

We amplified 365 mitochondrial control region sequences and detected 164 unique haplotypes from the study region. Sequences ranged from 382 to 545 base-pairs in length and contained approximately 50 base-pairs of the tRNA-Pro gene at the beginning of the sequence (average composition = 22.06% cytosine, 30.01% thymine, 32.61% adenine, and 15.32% guanine). Barred sand bass haplotypes contained a total of 126 variable sites (table 2a; GenBank Accession Number KJ935922–KJ936085). Of the 164 haplotypes, 53 were shared among locations and 111 were unique to a single individual location.

Over all sampling locations haplotype diversity was high ($h = 0.999 \pm 0.000$) and nucleotide diversity was relatively low ($\pi = 0.011 \pm 0.006$). Haplotype diversity remained high across all sampling sites ranging from 0.900 ± 0.161 to 1.000 ± 0.009 while nucleotide diver-

TABLE 3
Results of three hierarchical AMOVA's for Paralabrax nebulifer based on the mitochondrial control region.

a) For samples collected between 1997-1999 and 2010-2013.

Source of variation		d.f.	Sum of squares	Variance component	Percentage of variation
Among groups		1	2.88	–0.0020	–0.07
Among populations within groups		17	52.72	0.0015	0.05
Within populations		347	1066.68	3.074	100.02
Total		365	1122.28	3.073	
Fixation index (Φ_{CT})	–0.001				

$p > 0.025$

b) For all sampling locations.

Source of variation		d.f.	Sum of squares	Variance component	Percentage of variation
Among Populations		13	43.914	0.01244	0.400
Within Populations		352	1078.122	3.06285	99.600
Total		365	1122.036	3.075	
Fixation index (Φ_{CT})	0.004				

$p > 0.05$

c) Comparing locations north and south of the San Quintin upwelling zone.

Source of variation		d.f.	Sum of squares	Variance component	Percentage of variation
Among groups		1	10.90	0.048	1.56
Among populations within groups		12	33.01	–0.013	–0.410
Within populations		352	1078.12	3.039	98.84
Total		365	1122.04	3.099	
Fixation index (Φ_{CT})	0.016				

$p < 0.025$

TABLE 4
Pairwise Φ_{ST} values between all sampling locations of *Paralabrax nebulifer*. Pairwise Φ_{ST} values below and corresponding p-values above. Significant p-values indicated by +. PG = Platform Gina, VE = Ventura, MD = Marina Del Rey, LA = Los Angeles/Long Beach Harbor, SC = San Clemente, SD = San Diego, PO = Popolta, SQ = San Quintin, SR = Santa Rosalita, IC = Cedros Island, LM = Laguna Manuela, ISM = Isla San Martin, PA = Punta Abreojos, and BM = Bahia Magdalena.

	PG	VE	MD	LA	SC	SD	PO	SQ	SR	IC	LM	ISM	PA	BM
PG		—	—	—	—	—	—	—	—	—	—	—	—	—
VE	–0.251		—	—	—	—	—	—	—	—	—	—	—	—
MD	–0.210	–0.012		—	—	—	—	—	—	—	—	—	—	—
LA	–0.118	0.003	–0.007		—	—	—	—	—	—	—	—	—	—
SC	–0.179	–0.026	–0.021	–0.014		—	—	—	—	—	—	—	—	—
SD	–0.128	–0.022	0.002	0.004	–0.003		—	—	—	—	—	—	—	—
PO	0.044	–0.035	–0.021	–0.019	–0.016	–0.029		—	—	—	—	—	—	—
SQ	–0.216	0.002	0.003	0.001	–0.005	0.004	–0.026		—	—	—	—	—	—
SR	–0.326	–0.001	0.014	0.008	–0.001	0.008	–0.011	0.008		—	—	—	—	—
IC	–0.143	0.016	0.052	0.026	0.024	0.025	0.028	0.018	–0.003		—	—	—	—
LM	–0.160	0.007	–0.001	0.004	–0.009	0.011	0.007	0.003	0.014	0.032		—	—	—
ISM	0.000	–0.056	–0.015	–0.005	–0.011	–0.019	–0.074	–0.038	–0.027	0.007	0.029		—	—
PA	–0.150	0.003	0.040	0.012	0.019	0.010	–0.022	0.014	–0.006	0.005	0.027	–0.022		—
BM	–0.056	0.003	0.024	0.001	0.002	0.018	0.018	0.013	–0.007	–0.007	0.010	0.030	0.001	

$p < 0.001$

sity remained low ranging from 0.006 ± 0.004 to 0.014 ± 0.008 (table 2a). Sequence divergence was low within sampling locations (6.148 ± 2.931) and ranged from 0.000 ± 0.000 to 7.448 ± 3.625 (table 2a). Tajima's D for all populations was –2.059 and ranged from –0.717 to –1.934, indicating a population expansion. Nine of the 14 sampling locations show significant deviation from neutrality and potential population expansion (table 2a). Deviation from neutrality was also seen overall for barred sand bass ($F_S = -24.568$; $p < 0.02$) as well as in 11 of the 14 sampling locations indicating a rapid expansion (table 2a).

Barred sand bass samples collected from our two time points, 1997–99 and 2010–13, showed high within-populations variation and were not different from one another in a pairwise test of genetic differentiation ($\Phi_{CT} = 0.001$; $p = 0.660$) (table 3a). All samples were pooled together by sampling site for the remaining analysis. Testing for differentiation among all sampling locations indicated no significant differences ($\Phi_{CT} = 0.004$; p =

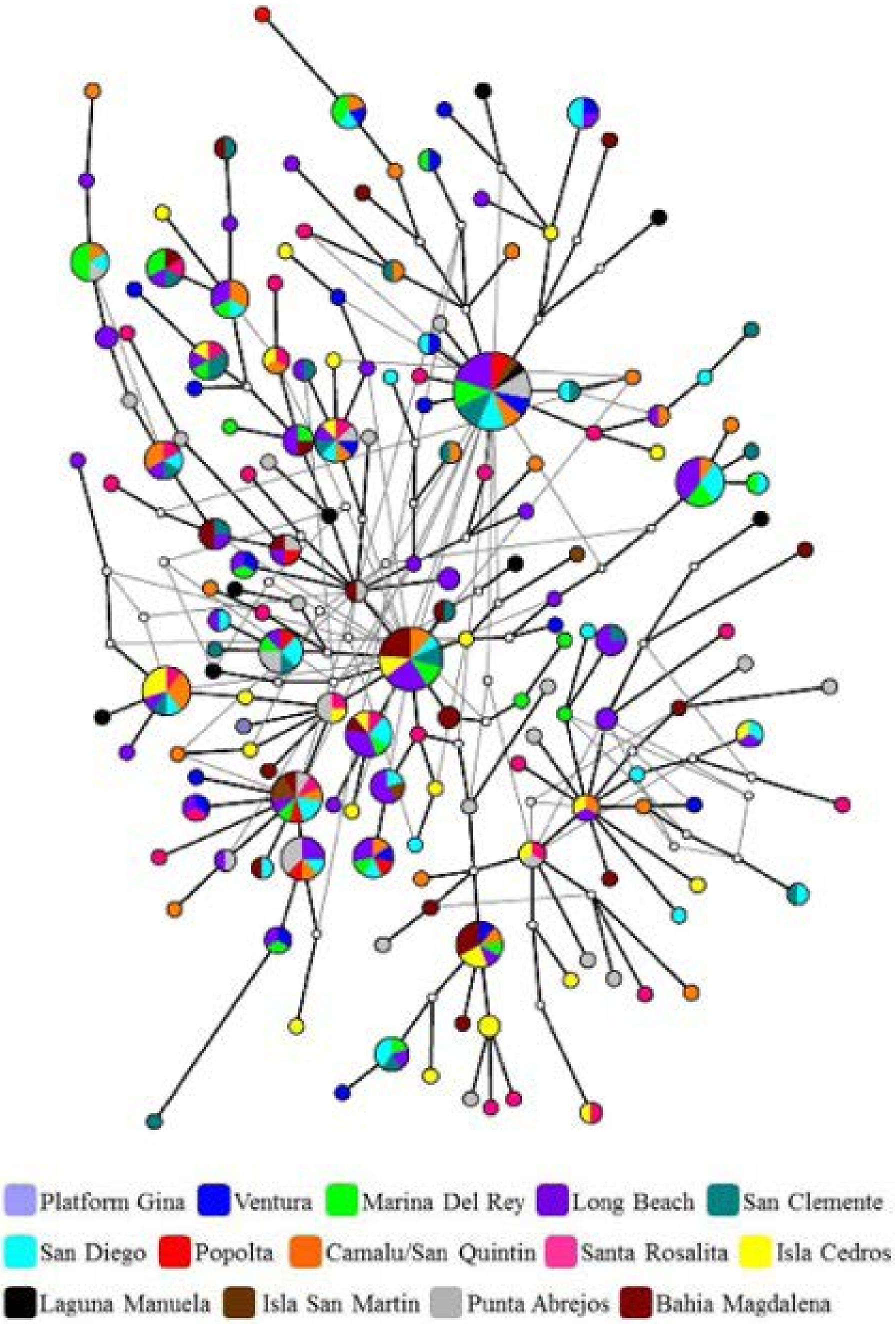

Figure 2. Haplotype network for *Paralabrax nebulifer* in California and Mexico. Each circle represents a haplotype and each color a sampling location found in this study. The bold line represent on of 53 possible Steiner trees while the grey lines represent all other possible trees. All trees are equally likely. A total of 189 haplotypes were found with 51 shared haplotypes. Platform Gina is near Ventura while Isla San Martin is near San Quintin (see fig. 1). Unsampled haplotypes shown as small open circles.

0.156) (table 3b). Similarly, pairwise Φ_{ST} comparisons showed no differentiation among all sampling locations (table 4). However, in testing for the presence of a genetic barrier of the San Quintin upwelling zone there appeared to be a weak but significant difference between samples north and south of the upwelling zone (Φ_{CT} = 0.016; $p < 0.001$) (table 3c). Barred sand bass showed no evidence of isolation by distance for mitochondrial DNA ($R^2 = 0.0002$; $p = 0.164$).

Haplotype network analyses revealed a total of 54 possible Steiner trees where each tree is equally likely (fig. 2). The network revealed no distinct clusters by sampling location or region (north and south of the San Quintin upwelling zone) and revealed no population structure in barred sand bass. This network shows the high number of singletons across the entire range of barred sand bass and historical connectivity among sampling locations.

Microsatellite Markers

The six loci used in the study were highly polymorphic with an average of 23 alleles per locus (range = 12 to 40 alleles). The average observed heterozygosity was 0.785 (0.546–0.898) while the average expected heterozygosity was 0.787 (0.609–0.932) (table 2b). POWSIM indicated that the six loci had the statistical power to detect a significant difference between samples when testing for $F_{ST} \leq 0.05$ (avg. $F_{ST} = 0.0487$ for simulations). Pairwise comparisons of divergence (G'_{ST} and Jost's D) show genetic differentiation between a few population pairs but a pattern of geographic divergence is not clearly discernable (table 5).

As seen with the mitochondrial DNA, samples collected from 1997–99 and 2010–13 were not differentiated from one another ($F_{CT} = -0.001$; $p = 0.777$) (table 6a). Therefore, all samples were pooled together for further analysis. In the AMOVA, we detected weak

TABLE 5

Pairwise G'_{ST} (below the diagonal) and Jost's D (above the diagonal) for all sampling locations of *Paralabrax nebulifer*. Significant p-values are indicated by ⋆. VE = Ventura, MD = Marina Del Rey, LA = Los Angeles/Long Beach Harbor, SC = San Clemente, SD = San Diego, PO = Popolta, SQ = San Quintin, SR = Santa Rosalita, IC = Isla Cedros, LM = Laguna Manuela, PA = Punta Abreojos, and BM = Bahia Magdalena.

	VE	MD	LA	SC	SD	PO	SQ	SR	IC	LM	PA	BM
VE		0.023	0.133⋆	–0.015	0.118⋆	0.103	0.068	0.063	0.036	0.040	0.152⋆	0.097⋆
MD	0.028		0.055⋆	–0.006	0.092⋆	0.013	0.076⋆	0.085⋆	0.020	0.152⋆	0.101⋆	0.037
LA	0.158⋆	0.065⋆		0.041	0.020	–0.038	–0.009	0.061⋆	0.020	0.253⋆	0.028	0.008
SC	–0.018	–0.007	0.049		0.034	–0.003	0.017	0.057⋆	–0.010	0.109	0.089⋆	0.025
SD	0.143⋆	0.110⋆	0.024	0.041		–0.061	–0.008	0.051⋆	0.016	0.247⋆	0.066⋆	0.022
PO	0.123	0.016	–0.046	–0.003	–0.076		–0.045	0.038	0.026	0.259⋆	0.046	–0.003
SQ	0.082	0.090⋆	–0.011	0.020	–0.010	–0.055		0.031	0.008	0.207⋆	0.021	0.010
SR	0.078	0.104⋆	0.076⋆	0.069⋆	0.064	0.048	0.038		0.029	0.150⋆	0.066	0.008
IC	0.044	0.024	0.023	–0.012	0.019	0.031	0.009	0.036		0.167	0.029	–0.012
LM	0.051	0.187⋆	0.304⋆	0.135⋆	0.303⋆	0.311⋆	0.254⋆	0.193⋆	0.206⋆		0.242⋆	0.226⋆
PA	0.183⋆	0.121⋆	0.034⋆	0.107⋆	0.082⋆	0.056	0.026	0.083⋆	0.035	0.296⋆		0.002
BM	0.117⋆	0.045	0.010	0.030	0.028	–0.004	0.013	0.010	–0.015	0.277⋆	0.003	

$p < 0.01$

TABLE 6

Results of three heirarchical AMOVAs for *Paralabrax nebulifer* based on microsatellite loci.

a) For samples collected between 1997-1999 and 2010-2013

Source of variation		d.f.	Sum of squares	Variance component	Percentage of variation	%
Among Regions		1	3.808	3.808	0.000	0%
Among Populations		14	54.929	3.923	0.030	1%
Among Individuals		331	885.280	2.675	0.199	8%
Within Individuals		347	790.000	2.277	2.277	91%
Total		693	1734.016		2.506	100%
Fixation index (F_{ST})	-0.001					

$p > 0.05$

b) For all sampling locations

Source of variation		d.f.	Sum of squares	Variance component	Percentage of variation	%
Among Populations		11	47.325	4.302	0.029	1%
Among Individuals		335	896.691	2.677	0.200	8%
Within Individuals		347	790.000	2.277	2.277	91%
Total		693	1734.016		2.505	100%
Fixation index (F_{ST})	0.012					

$p < 0.05$

c) Comparing locations north and south of the San Quintin upwelling zone.

Source of variation		d.f.	Sum of squares	Variance component	Percentage of variation	%
Among Regions		1	6.100	6.100	0.005	0%
Among Populations		10	41.226	4.123	0.026	1%
Among Individuals		335	896.691	2.677	0.200	8%
Within Individuals		347	790.000	2.277	2.277	91%
Total		693	1734.016		2.508	100%
Fixation index (F_{CT})	0.002					

$p < 0.05$

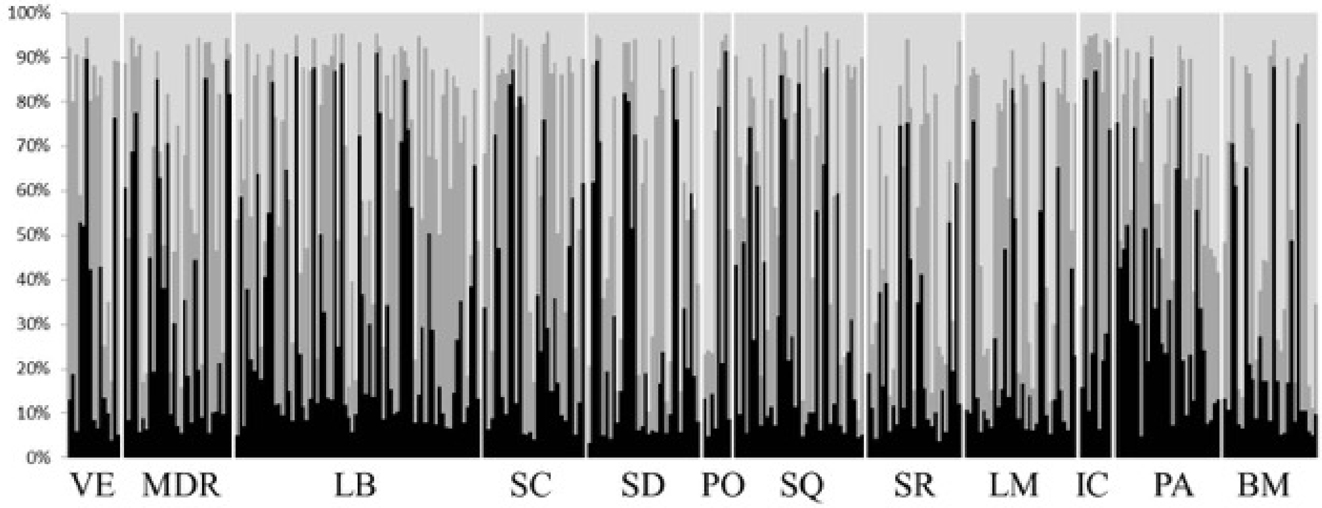

Figure 3. Structure diagram for *Paralabrax nebulifer* with K = 3.

differentiation for all sampling locations pooled together (F_{ST} = 0.012; p = 0.001) (table 6b). Testing specifically for the San Quintin upwelling zone as a genetic barrier showed that there, again, is weak but significant differentiation between sampling locations north and south of the upwelling zone (F_{CT} = 0.002; p = 0.011) (table 6c). The Evanno Method within STRUCTURE HARVESTER determined that three admixed genetic demes was the most probable value of K obtained from the STRUCTURE analysis (Mean LnP(K) = –8713.95; ΔK = 5.488) (fig. 3). However, standard errors associated with mean log likelihood values from the STRUCTURE analysis were highly variable and overlapping for all values of K indicating a failure of the STRUCTURE analysis to resolve the most probable value of K with any certainty.

DISCUSSION

This study found a high degree of genetic diversity for a single population of barred sand bass. While there was a weak but significant difference between sampling locations north and south of the San Quintin upwelling zone for both mitochondrial and nuclear markers, there is still a high degree of connectivity between the two regions. A single, panmictic population is further supported by the STRUCTURE results. While the Evanno method suggested a K of 3 as the most probable number of clusters, standard errors of the log likelihoods from the STRUCTURE analyses were highly variable and overlapped across all estimates of K. The Evanno method may not always determine the most likely K from a STRUCTURE analysis; instead, log likelihood values have been shown to provide reliable estimates of the number of clusters (Duncan et al. 2015). The STRUCTURE histogram generated from a K of 3 (fig. 3) is consistent with a large, single population with high migration as no clear clustering among individuals was observed.

The San Quintin upwelling zone is a seasonal upwelling event along the coast of the Baja California peninsula. This upwelling event occurs regularly in July coinciding with the peak in spawning for all three species of *Paralabrax* (Love et al. 1996; Hovey and Allen 2000; Allen et al. 1995). The San Quintin upwelling zone is also a known barrier to other summer spawning species with a pelagic larval stage such as opaleye, *Girella nigricans* (Terry et al. 2000), white seabass, *Atractoscion nobilis* (Michael P. Franklin pers. comm.), and purple sea urchins, *Strongylocentrotus purpuratus* (Olivares-Banuelos et al. 2008). However, the upwelling zone was not observed as a barrier for all fish along the California coast. Species with a pelagic larval stage that are not exclusively summer spawners like the California halibut, *Paralichthys californicus* (Craig et al. 2011), as well as those without a pelagic larval state such as the brown smoothhound (*Mustelus henlei*) (Chabot et al. 2015) and the round stingray (*Urobatis halleri*) (Plank et al. 2010), did not reveal the San Quintin upwelling zone as a genetic barrier. This suggests that possession of pelagic larvae alone does not predict movement patterns across all fish in this region. The timing of spawning is probably more important.

Seasonal upwelling zones are more effective barriers to larvae than to adults (Gaithier et al. 2009). Eggs of barred sand bass were shown to successfully hatch at a wide range of temperatures, but developed much slower at low temperatures and failed to develop or died at 12°C (Gadomski and Caddell 1996), the mean temperture in July off of San Quintin in July from 1950 to 1978 (Lynn et al. 1982). Furthermore, this was an area of consistently low abundance of serranid larvae in general from 1951 to 1984 (Moser et al 1993). Together these findings imply that barred sand bass larvae are less likely to cross this barrier during the summer months when they are most abundant accounting for the weak, yet significant genetic structuring north and south of the barrier as found in this study. However, all three species of *Paralabrax* off California have a pelagic larval duration of approximately 21–37 days (Allen and Block 2012) and can be in the currents before and after this upwelling event. As a result, the limited larval transport before and after the establishment of the seasonal San Quintin upwelling zone could account for the high degree of gene flow and genetic diversity for barred sand bass. The California Countercurrent generates eddies within the Southern California Bight (Harms and Winant 1998) that has been shown to transport larvae along the coast of southern California and the Channel Islands (Shanks and Eckert 2005; White et al. 2010). Similar patterns of current flow have been shown along Baja California (Bograd and Lynn 2003; Di Lorenzo 2003). Shanks and Eckert (2005) suggested that larvae of nearshore fish species that are pelagic broadcast spawners off the coast of southern California and Baja California were transported widely via the currents and eddies along the eastern Pacific.

In addition to the larval mediated transport, at least some high genetic diversity and site connectivity in barred sand bass can also be attributed to adult migration patterns. Jarvis and colleagues (2010) found that barred sand bass show high spawning site fidelity however not all individuals return to the same spawning site every year and some visit multiple spawning sites in a single spawning season. This migration of just a few individuals per generation can keep the genetic diversity of a population stable (Ryman 1991).

Currently barred sand bass are part of a larger recreational fishery in southern California that includes the kelp and spotted sand bass. All three species are managed together with collective bag limits of 5 fish and a minimum size limit of 14 inches (CDFW). These regulations were increased in March 2013 in response to declining numbers of kelp and barred sand bass, however these regulations do not account for differences in genetic diversity or population structure between the three congeners. A comparison of the diversity of barred sand bass in this study to previous studies of the other two bass species shows that barred sand bass and kelp bass both exhibit high haplotype diversity in the mitochondrial control region (Phalen 1999) while the spotted sand bass shows the opposite (Salomon 2005). However, nucleotide diversity is low for barred sand bass and the spotted sand bass (Salomon 2005) and is high for the kelp bass (Phalen 1999). The differences in haplotype and nucleotide diversity reflect differences in the genetic diversity of the three congers.

Populations that have undergone historic reductions in the past are expected to demonstrate high mitochondrial haplotype diversity and low nucleotide diversity after a demographic expansion from a population of small effective size (Grant and Bowen 1998). Within barred sand bass, high haplotype diversity and low nucleotide diversity were observed in the present study (table 2). Furthermore, significantly negative Tajima's D and Fu's F_S values from the present study (table 2) would seem to support a rapid increase in population size at some point in the past. However, it is important to note that the haplotype network generated in the present study (fig. 2) does not reflect the starburst pattern that is rapidly expanding population. It is possible that the high haplotype diversity observed in barred sand bass in the present study may be a result of the highly mutable nature of this region in teleosts resulting in extreme variability. As a result, the high variability of barred sand bass control region sequences may be masking population structure in the species. Bradman and colleagues (2011) found that the control region in broadbill swordfish, *Xiphias gladius*, was unable to detect population structure on as fine a scale as the NADH dehydrogenase subunit 2 (ND2) region. Based on the limitations imposed by the high variability of the mtCR, this marker may not be the best choice of for detecting population structure in barred sand bass.

Differences in life histories among the congeners of *Paralabrax* appear to have resulted in these observed differences in population genetic structure and diversity. All three species are aggregate broadcast spawners (Allen et al. 1995; Baca-Hovey et al. 2002; Erisman and Allen 2006), however each species differs in where it spawns. Barred sand bass migrate to open soft bottom substrate off the coast (a few km) to spawn (Baca-Hovey et al. 2002) while kelp bass do not migrate large distances to spawn (Erisman and Allen 2006). Spotted sand bass are found within bays and spawn at the mouth of those bays (Hovey and Allen 2000; Allen et al. 1995) which can limit the dispersal of larvae (Levin 1983, 2006).

The barred sand bass is a heavily fished species in both southern California, USA (Erisman et al. 2011) and in Baja California, Mexico (Cota-Nieto et al. 2014; B. Erisman unpublished results). Understanding the life history of the species as well as its population structure is important in the management of both fisheries. Genetic diversity and population structure which informs management of populations and the degree of connectivity between those populations (Shaklee and Bentzen 1998; Airame et al. 2003; Pérez-Ruzafa et al. 2006; Palsbøll et al. 2007). The life history characteristics of barred sand bass have been well studied in southern California (Baca-Hovey et al. 2002; Jarvis et al. 2010; Mason and Lowe 2010) and are underway in Baja California, Mexico (B. Erisman unpublished results). The results of the present study suggest that barred sand bass consist of one large, panmictic population. This suggests the need for a binational management plan for barred sand bass.

Currently the barred sand bass population exhibits very high genetic diversity (table 2). There is no evidence of a decline in genetic diversity over the last 13 years. Because barred sand bass can live up to 24 years (Love et al. 1996), the genetic consequences to the recreational fishery crash off California in 2004 may simply not have had enough time to manifest. Further sampling 20 or more years after the fishery decline in 2004 may be necessary to reflect any decline in genetic diversity. The present study does provide a baseline for the genetic diversity of barred sand bass that can then be used to monitor and detect any future declines in diversity.

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LITERATURE CITED

Airame, S., J. E. Dugan, K. D. Lafferty, H. Leslie, D. A. McArdle, and R. R. Warner. 2003. Applying ecological criteria to marine reserve design: a case study from the Californa Channel Islands. Ecological Applications 13:170–184.

Allen, L. G., and H. E. Block. 2012. Planktonic larval duration, settlement, and growth rates of the young-of-the-year of two sand basses (*Paralabrax nebulifer* and *P. maculatofasciatus*: fam. Serranidae) from Southern California. Bulletin, Southern California Academy of Sciences 111:15–21.

Allen, L. G., T. E. Hovey, M. S. Love, and J. T. W. Smith. 1995. The life history of the spotted sand bass (*Paralabrax maculatofasciatus*) within the Southern California Bight. CalCOFI Report 36:193–203.

Alós, J., M. Palmer, I. Catalan, A. Alonso-Fernández, G. Basterretxea, A. Jordi, L. Buttay, B. Morales-Nin, and R. Arlinghaus. 2014. Selective exploitation of spatially structured coastal fish populations by recreational anglers may lead to evolutionary downsizing of adults. Marine Ecology Progress Series 503:219–233.

Baca-Hovey, C., L. G. Allen, and T. E. Hovey. 2002. The reproductive pattern of barred sand bass (*Paralabrax nebulifer*). CalCOFI Report 43:174–181.

Bandelt, H. J., P. Forster, and A. Rohl. 1999. Median-Joining networks for inferring intraspecific phylogenies. Molecular Biology and Evolution 16:37–48.

Bernardi, G. 2000. Barriers to gene flow in *Embiotoca jacksoni*, a marine fish lacking a pelagic larval stage. Evolution 54:226–237.

Bernardi, G., L. Findley, and A. Rocha-Olivares. 2003. Vicariance and dispersal across Baja California in disjunct marine fish populations. Evolution 57:1599–1609.

Bograd, S. J., and R. J. Lynn. 2003. Long-term variability in the Southern California Current System. Deep Sea Research II 50:2355–2370.

Bradman, H., P. Grewe, and B. Appleton. 2011. Direct comparison of mitochondrial markers for the analysis of swordfish population structure. Fisheries Research. 109:95–99.

Brownstein, M. J., J. D. Carpten, and J. R. Smith. 1996. Modulation of non-templated nucleotide addition by taq DNA polymerase: primer modification that facilitate genotyping. BioTechniques 20:1004–1010.

Butler, J. L., G. Moser, G. S. Hageman, and L. E. Nordgren. 1982. Developmental stages of three california sea basses (*Paralabrax*, Pisces, Serranidae). CalCOFI Report XXIII:252–268.

Carvalho, G. R., and L. Hauser. 1994. Molecular genetics and the stock concept in fisheries. Reviews in Fish Biology and Fisheries 4:326–350.

Chabot, C. L., M. Espinoza, I. Mascareñas-Osorio, and A. Rocha-Olivares. 2015. The effect of biogeographic and phylogeographic barriers on gene flow in the brown smoothhound shark, *Mustelus henlei*, in the northeastern Pacific. Ecology and Evolution. 5(8): 1585–1600. doi: 10.1002/ece3.1358

Cota-Gomez, V. M., G. De La Cruz-Aguero, F. J. Garcia-Rodriguez, and J. De La Cruz-Aguero. 2013. Length-weight relations for 14 fish species of La Paz Bay, Baja California Sur, Mexico. ACTA Ichthyologica et Piscatoria 43:297–298.

Cota-Nieto, J. J., B. Erisman, O. Aburto-Oropeza, M. Moreno-Baez, and G. Hinojosa-Arango. 2014. Characterization of coastal fisheries in Punta Abrejos, Pacific Coast of the Peninsula of Baja California Sur, Mexico. Pages 1–24.

Craig, M. T., F. J. Fodrie, L. G. Allen, L. A. Chartier, and R. J. Toonen. 2011. Discordant phylogeographic and biogeographic breaks in California Halibut. Bulletin, Southern California Academy of Sciences 110:141–151.

Darriba, D., G. L. Taboada, R. Doallo, and D. Posada. 2012. jModelTest 2: more models, new heuristics and parallel computing. Nature Methods 9:772.

Di Lorenzo, E. 2003. Seasonal dynamics of the surface circulation in the Southern California Current System. Deep Sea Research II 50:2371–2388.

Dudgeon, C. L., D. C. Blower, D. Broderick, J. L. Giles, B. J. Holmes, T. Kashiwagi, N. C. Krück, J. A. T. Morgan, B. J. Tillett, and J. R. Ovenden. 2012. A review of the application of molecular genetics for fisheries management and conservation of sharks and rays. Journal of Fish Biology. 80(5):1789–1843.

Duncan, M., N. James, S. T. Fennessy, R. J. Mutombene, and M. Mwale. 2015. Genetic structure and consequences of stock exploitation of *Chrysoblephus puniceus*, a commercially important sparid in the South West Indian Ocean. Fisheries Research. 165:64–72.

Earl, D., and B. VonHoldt. 2012. STRUCTURE HARVESTER: a website and program for visualizing STRUCTURE output and implementing the Evanno method. Conservation Genetics. 4(2):359–361.

Ensing, D., W. W. Crozier, P. Boylan, N. O'Maoileidigh, and P. McGinnity. 2013. An Analysis of genetic stock identification on a small geographical scale using microsatellite markers, and its application in the management of a mixed-stock fishery for Atlantic *Salmon salmo* in Ireland. Journal of Fish Biology. 82(6):2080–2094. doi:10.1111/jfb.12139.

Erisman, B. E., and L. G. Allen. 2006. Reproductive behaviour of a temperate serranid fish, *Paralabrax clathratus* (Girard), from Santa Catalina Island, California, U.S.A. Journal of Fish Biology 68:157–184.

Erisman, B. E., L. G. Allen, J. T. Claisse, D. J. Pondella II, E. F. Miller, and J. H. Murray. 2011. The illusion of plenty : hyperstability masks collapses in two recreational fisheries that target fish spawning aggregations. Canadian Journal of Fisheries and Aquatic Sciences 68:1705–1716.

Erisman B. E., G. A Paredes., T. Plomozo-Lugo, J. Cota-Nieto, P. A. Hastings, and O. Aburto-Oropeza. 2011. Spatial structure of commercial marine fisheries in Northwest Mexico. ICES J. Mar. Sci. 68:564–571.

Evanno, G., S. Regnaut, and J. Goudet. 2005. Detecting the number of clusters of individuals using the software STRUCTURE: a simulatio study. Molecular Ecology. 14(8):2611–2620.

Excoffier, L., and H. E. L. Lischer. 2010. Arlequin suite ver 3.5: A new series of programs to perform population genetics analysis under Linux and Windows. Molecular Ecology Resources 10:564–567.

Fu, Y. X. 1997. Statistical tests of neutrality of mutations against population growth, hitchhiking and background selection. Genetics 147:915–925.

Gadomski, D. M., and S. M. Caddell. 1996. Effects of temperature on the development and survival of eggs of four coastal California fishes. Fishery Bulletin 94:41–48.

Grant, W. S., and B. W. Bowen. 1998. Shallow population histories in deep evolutionary lineages of marine fishes: Insights from sardines and anchovies and lessons for conservation. The Journal of Heredity. 89(5):415–426.

Goudet, J. 2003. FSTAT version 2.9.3.2: a program to estimate and test population genetics parameters. Updated from Goudet [1995].

Guindon, S., and O. Gascuel. 2003. A simple, fast and accurate method to estimate large phylogenies by maximum-likelihood. Systematic Biology 52:696–704.

Harms, S., and C. D. Winant. 1998. Characteristic patterns of the circulation in the Santa Barbara Channel. Journal of Geophysical Research 103:3041–3065.

Hedrick, P. W. 1999. Highly variable loci and their interpretation evolution and conservation. Evolution 53:313–318.

Hovey, T. E., and L. G. Allen. 2000. Reproductive patterns of six populations of the spotted sand bass, *Paralabrax maculatofasciatus*, from Southern and Baja California. Copeia 2:459–468.

Hutchinson, W. F., C. van Oosterhout, S. I. Rogers, and G. R. Carvalho. 2003. Temporal analysis of archived samples indicates marked genetic changes in declining North Sea cod (*Gadus morhua*). Proceedings. Biological sciences/ The Royal Society 270:2125–32.

Hutchinson, W. F. 2008. The dangers of ignoring stock complexity in fishery management: the case of the North Sea cod. Biology Letters. 4(6):693–695. doi:10.1098/rsbl.2008.0443.

Jarvis, E. T., C. Linardich, and C. F. Valle. 2010. Spawning-related movements of barred sand bass, *Paralabrax nebulifer*, in Southern California: interpretations from two decades of historical tag and recapture data. Bulletin, Southern California Academy of Sciences 109:123–143.

Jost, L. 2008. G_{ST} and its relatives do not measure differentiation. Molecular Ecology 17:4015–4026.

Kenchington, E., M. Heino, and E. E. Nielsen. 2003. Managing marine genetic diversity: time for action? ICES Journal of Marine Science 60:1172–1176.

Lee, W. J., J. Conroy, W. H. Howell, and T. D. Kocher. 1995. Structure and evolution of teleost mitochondrial control regions. Journal of Molecular Evolution 41:54–66.

Levin, L. A. 1983. Drift tube studies of bay-ocean water for exchange and implications larval dispersal. Estuaries 6:364–371.

Levin, L. A. 2006. Recent progress in understanding larval dispersal: new directions and digressions. Integrative and Comparative Biology 46:282–297.

Love, M. S., D. Busatto, J. Stephens, and P. A. Gregory. 1996. Aspects of the life histories of the kelp bass, *Paralabrax clathratus*, and barred sand bass, *P. nebulifer*, from the Southern California Bight. Fishery Bulletin 94:472–481.

Lynn, R. J., K. A. Bliss, and L. E. Eber. 1982. Vertical and horizontal distributions of seasonal mean temperature, salinity, sigma-t, stability, dynamic height, oxygen, and oxygen saturation in the California Current, 1950–78. CalCOFI Atlas 30, 513 pp.

Maddison, W. P., and D. R. Maddison. 2011. Mesquite: a modular system for evolutionary analysis. Version 1.01. http://mesquiteproject.org.

Magoulas, A. 2005. Mitochondrial DNA. Pages 311–330 in S. X. Cadrin, K. D. Friedland, and J. R. Waldman, editors. Stock identification methods: Applications in fishery science. Academic Press, Burlington, MA.

Mason, T. J., and C. G. Lowe. 2010. Home range, habitat use, and site fidelity of barred sand bass within a southern California marine protected area. Fisheries Research 106:93–101.

Meirmans, P. G., and P. W. Hedrick. 2011. Assessing population structure: F_{ST} and related measures. Molecuar Ecology 11:5–18.

Miller, E. F., and B. Erisman. 2014. Long-term trends of southern California's kelp and barred sand bass populations: a fishery-independent assesment. CalCOFI Report. 55: 119–127.

Moser, H. G., R. L. Charter, P. E. Smith, D. A. Ambrose, S. R. Charter, C. A. Meyer, E. M. Sandknop, and W. Watson. 1993. p. 66–67 in: Distributional atlas of fish larvae and eggs in the California Current region: taxa with 1000 or more total larvae, 1951–84. CalCOFI Atlas 31, 233 pp.

Narum, S. R. 2006. Beyond Bonferroni: Less conservative analysis for conservation genetics. Conservation Genetics 7:783–787. DOI: 10.1007/s10592-005-9056-y.

Olivares-Banuelos, N. C., L. M. Enrique-Paredes, L. B. Ladah, and J. de la Rosa-Velez. 2008. Population structure of purple sea urchin *Strongylocentrotus purpuratus* along the Baja California peninsula. Fisheries Science 74:804–812.

Ovenden, J. R., O. Berry, D. J. Welch, R. C. Buckworth, and C. M. Dichmont. 2015. Ocean's eleven: a critical evaluation of the role of population, evolutionary and molecular genetics in the management of wild fisheries. Fish and Fisheries. 16(1): 125–159. doi: 10.1111/faf.12052.

Palsbøll, P. J., M. Bérubé, and F. W. Allendorf. 2007. Identification of management units using population genetic data. Trends in Ecology and Evolution 22:11–6.

Peakall, R., and P. E. Smouse. 2006. GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. Molecular Ecology Notes 6:288–295.

Peakall, R., and P. E. Smouse. 2012. GenAlEx 6.5: genetic analysis in Excel. Population genetic software for teaching and research—an update. Bioinformatics 28:2537–2539.

Pérez-Ruzafa, Á., M. González-Wangüemert, P. Lenfant, C. Marcos, and J. A. García-Charton. 2006. Effects of fishing protection on the genetic structure of fish populations. Biological Conservation 129:244–255.

Phalen, C. M. 1999. Genetic variation among kelp bass (*Paralabrax clathratus*) from seven locations throughout their natural range. M.S. Thesis, California State University, Northridge, 60 pp.

Plank, S. M., C. G. Lowe, K. A. Feldheim, R. R. Wilson, and J. A. Brusslan. 2010. Population genetic structure of the round stingray *Urobatis halleri* (Elasmobranchii: Rajiformes) in southern California and the Gulf of California. Journal of Fish Biology 77:329–40.

Polzin, T., and S. V. Daneschmand. 2003. On Steiner trees and minimum spannning trees in hypergraphs. Operations Research Letters 31:21–20.

Pritchard, J. K., M. Stephens, and P. Donnelly. 2000. Inference of population structure using multilocus genotype data. Genetics. 155(2):945–959.

Raymond, M., and F. Rousset. 1995. GENEPOP (version 1.2): population genetics software for exact tests and ecumenicism. Journal of Heredity 86:248–249.

Reiss, H., G. Hoarau, M. Dickey-Collas, and W. J. Wolff. 2009. Genetic population structure of marine fish: mismatch between biological and fisheries management units. Fish and Fisheries. 10(4):361–395.

Rosales-Casian, J. A., and J. R. Gonzalez-Camacho. 2003. Abundance and importance of fish species from the artisanal fishery on the Pacific Coast of Northern Baja California, Bulletin of the Southern California Academy of Sciences 102(2): 51–65.

Rousset, F. 2008. Genepop'007: a complete reimplementation of the Genepop software for Windows and Linux. Molecular Ecology Resources 8:103–106.

Ryman, N. 1991. Conservation genetics considerations in fishery management. Journal of Fish Biology 39:211–224.

Ryman, N., and S. Palm. 2006. POWSIM: a computer program for assessing statistical power when testing for genetic homogeneity. Molecular Ecology Notes 6:600–602.

Sadovy, Y., and M. L. Domeier. 2005. Perplexing problems of sexual patterns in the fish genus *Paralabrax* (Serranidae, Serraninae). Journal of Zoology 267:121.

Salomon, M. P. 2005. Gene flow among populations of the spotted sand bass, *Paralabrax maculatofasciatus*, from southern California and two populations along the Pacific coast of Baja California. M.S. Thesis, California State University, Northridge, 37 pp.

Schuelke, M. 2000. An economic method for the fluorescent labeling of PCR fragments: A poor man's approach to genotyping for research and high-throughput diagnostics. Nature Biotechnology 18:233–234.

Selkoe, K. A., S. D. Gaines, J. E. Caselle, and R. R. Warner. 2006. Current shifts and kin aggregation explain genetic patchiness in fish recruits. Ecology 87:3082–94.

Selkoe, K. A., A. Vogel, and S. D. Gaines. 2007. Effects of ephemeral circulation on recuritment and connectivity of nearshore fish populations spanning Southern and Baja California. Marine Ecology Progress Series. 351:209–220. doi: 10.3354/meps07157.

Selkoe, K., and R. Toonen. 2011. Marine connectivity: a new look at pelagic larval duration and genetic metrics of dispersal. Marine Ecology Progress Series. 436: 291–305.

Shaklee, J. B., and P. Bentzen. 1998. Genetic identification of stocks of marine fish and shellfish. Bulletin of Marine Science 62:589–621.

Shaklee, J. B., T. D. Beacham, L. Seeb, and B. A. White. 1999. Managing fisheries using genetic data: case studies from four species of Pacific salmon. Fisheries Research 43:45–78.

Shanks, A. L., and G. L. Eckert. 2005. Population persistence of California Current fishes and benthic crustaceans: a marine drift paradox. Ecological Monographs 75:505–524.

Smith, P. J., R. I. C. C. Francis, and M. McVeagh. 1991. Loss of genetic diversity due to fishing pressure. Fisheries Research 10(3–4): 309–316. Doi: 10.1016/0165-7836(91)90082-Q.

Tajima, F. 1989. Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. Genetics 123:585–595.

Tamura, K., G. Stecher, D. Peterson, A. Filipski, and S. Kumar. 2013. MEGA6: Molecular Evolutionary Genetics Analysis version 6.0. Molecular Biology and Evolution 30:2725–2729.

Terry, A., G. Bucciarelli, and G. Bernardi. 2000. Restricted gene flow and incipient speciation in disjunct Pacific Ocean and Sea of Cortez populations of a reef fish species, *Girella nigricans*. Evolution 54:652–659.

van Oosterhout, C., W. F. Hutchinson, D. P. M. Wills, and P. Shipley. 2004. Micro-Checker: software for identifying and correcting genotyping errors in microsatellite data. Molecular Ecology Notes 4:535–538.

van Wijk, S. J., M. I. Taylor, S. Creer, C. Dreyer, F. M. Rodrigues, I. W. Ramnarine, C. van Oosterhout, and G. R. Carvalho. 2013. Experimental harvesting of fish populations drives genetically based shifts in body size and maturation. Frontiers in Ecology and the Environment 11:181–187.

White, C., K. A. Selkoe, J. Watson, D. A. Siegel, D. C. Zacherl, and R. J. Toonen 2010. Ocean currents help explain population genetic structure. Proc. Biol. Sci. 277(1688): 1685–1694.

Wirgin, I., and J. R. Waldman. 2005. Use of nuclear DNA in stock identification: single-copy and repetitive sequence markers. Pages 331–370 *in* S. Cadrin, K. D. Friedland, and J. Waldman, editors. Stock identification methods: Applications in fishery science. Academic Press, Burlington, MA.

Young, P. H. 1963. The kelp bass (*Paralabrax clathratus*) and its fishery, 1947–1958. Fish Bulletin:1947–1958.

GROWTH, MORTALITY, AND REPRODUCTIVE SEASONALITY OF CALIFORNIA HALIBUT (*PARALICHTHYS CALIFORNICUS*): A BIOGEOGRAPHIC APPROACH

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ABSTRACT

Differences in key biological processes, such as growth and reproduction, can greatly influence localized population dynamics. Thus, it is important to characterize spatial variation in life history traits of harvested species to develop management plans that maximize fishery sustainability. We estimated sex- and region-specific growth, total mortality, and reproductive seasonality to assess biogeographic differences in California Halibut life history. We found that central California Halibut grew faster but attained smaller maximum sizes than those from southern California. Catch curve analysis illustrated no difference in total mortality by sex or region, though females lived longer than males. Year-class frequency distributions suggested greater recruitment variability in central California, where abiotic factors (e.g., upwelling strength, sea surface temperature) are likely drivers. Reproductive data indicated that summer spawning seasons peak earliest in Mexico, followed by southern and central California. These results demonstrate a need to assess and manage California Halibut at the regional scale.

INTRODUCTION

Biogeographic differences in growth, mortality, and reproduction can result in disproportionate effects of fishing (Rice et al. 2005). However, fisheries are often managed at relatively broad (e.g., statewide/nationwide) spatial scales. Although averaging the condition of a species across its range simplifies resource management, spatiotemporal changes in key biological processes can result in localized over- or under-utilization of the resource (Prince 2010). This is because many fish stocks consist of metapopulations (i.e., groups of individuals that are interconnected through larval dispersal, yet exhibit distinct population dynamics), which are differentially affected by fishing pressure (Levins 1969; Adams 1980; Orensanz et al. 2005; Pascoe et al. 2009). Thus, it is important to understand spatial variation in the life history traits of harvested species, especially those that exhibit widespread distributions spanning multiple biogeographic regions.

California Halibut, *Paralichthys californicus* (family Paralichthyidae), is an economically important species that can be found as far north as the Quillayute River in Washington and as far south as Magdalena Bay in Baja California Sur, Mexico (Allen 1990). However, most individuals in U.S. waters are encountered between Bodega Bay, California and the US-Mexico border. After a short larval duration of 20 to 29 d, juveniles settle into bays, estuaries, and shallow waters of the open coast (Allen 1988; Kramer 1990). Adults are primarily found nearshore (typically less than 60 m water depth) over sandy habitats that are adjacent to hard substrate or biogenic structures (e.g., sand dollar, *Dendraster excentricus*, beds) (Allen 1988; Allen 1990). Female California Halibut grow faster and mature later than male conspecifics (Haaker 1975; MacNair et al. 2001). Males reach sexual maturity between 19 and 32 cm (1 to 3 yr), whereas females mature between 36 and 59 cm (2 to 7 yr) (Love and Brooks 1990). California Halibut are multiple, broadcast spawners that have been noted as living to 30 yr, though recent data have demonstrated a lifespan of only 23 yr (CDFW unpublished data [2007 to 2014]).

In 2011, the California Department of Fish and Wildlife (CDFW, formerly California Department of Fish and Game) conducted its first comprehensive stock assessment for California Halibut to determine population size and the effectiveness of existing management actions (Maunder et al. 2011). As part of the assessment, fishery-independent and -dependent data were synthesized and incorporated into statistical models developed for two separate stocks, one north and one south of Point Conception (a well-known biogeographic boundary between central and southern California). Although substantial amounts of biological information were made available during the assessment, life history data pertained primarily to fish collected off southern California (e.g., Allen 1988; Allen and Herbinson 1990; Allen et al. 1990; Kramer 1990; Domeier and Chun 1995; Valle et al. 1998; MacNair et al. 2001). This forced assessment scientists to parameterize both stock models based primarily on the southern California population. To assess the effect of biogeography on California Halibut life history characteristics, we estimated sex-specific growth and instantaneous total mortality for fish collected both north and south of Point Conception. We also compared

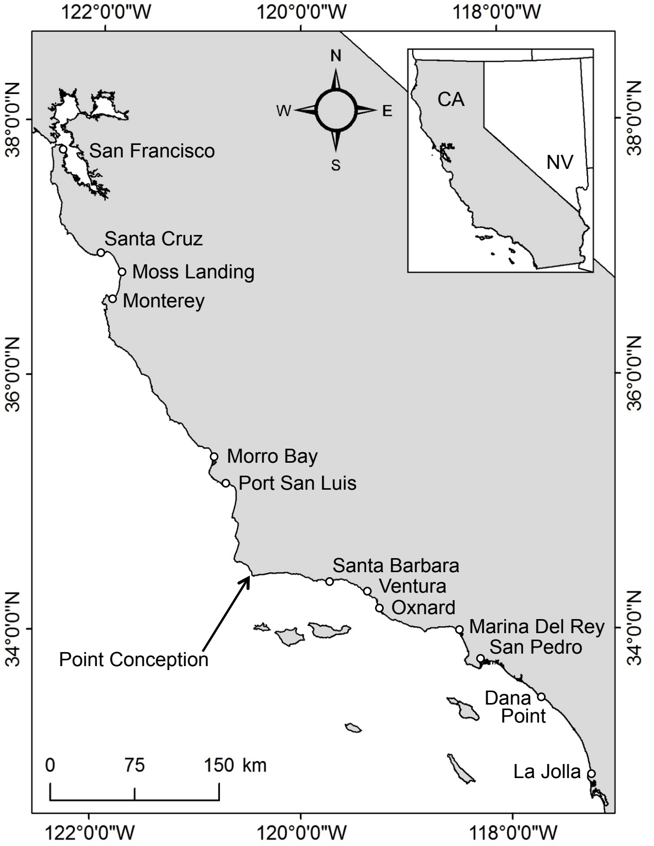

Figure 1. Primary locations used to sample California Halibut, *Paralichthys californicus*. Point Conception (indicated by the black arrow) denotes the boundary between central and southern California sites.

region-specific estimates of reproductive seasonality by evaluating temporal changes in gonadosomatic index for females collected off central California and corrected larval density data obtained by California Cooperative Oceanic Fisheries Investigations (CalCOFI) surveys along southern California and Mexico.

MATERIALS AND METHODS

California Halibut were collected between San Francisco Bay, CA and the US–Mexico border from 2007 to 2014 (fig. 1). Fish were collected using both fishery-independent and fishery-dependent sampling methods. A diversity of gear types (i.e., hook and line, trawl, gill net, seine, and spear) was used to collect fishes of both sexes and from various size classes. Although fishery-independent methods were used, we (CDFW [2007 to 2014] and Moss Landing Marine Laboratories [MLML, 2012 and 2013]) procured most specimens from commercial and recreational fisheries using a combination of stratified random and opportunistic sampling designs (CDFW 2013; Barnes 2015). Fish from central California were collected in nearly equal proportions from commercial and recreational fisheries, whereas the majority of fish from southern California were obtained from commercial fisheries (table 1).

TABLE 1
Sample Sizes of California Halibut Collected by Region, Sex, and Fishery.

	Central California		Southern California	
	Female (n = 743)	Male (n = 556)	Female (n = 615)	Male (n = 145)
Commercial	293	269	571	134
Recreational	359	219	19	1
Research	72	53	23	10
Incidental	19	15	2	0

Date, location, fishery (i.e., commercial or recreational), gear type, sex, fork length (mm), and wet body weight (kg) were recorded in the field. The majority of fork lengths were obtained from whole fish sampled at shore-based facilities. However, a number of California Halibut were received from recreational fishers as filleted carcasses. Fork lengths for filleted fish were recorded and converted to pre-fillet lengths using the relationship $y = 1.37 + 0.99x$ ($R^2 = 0.999$, $p < 0.001$), where x represents post-fillet fork length (mm) and y represents pre-fillet fork length (mm).

In the laboratory, sagittal otoliths were extracted and thin-sectioned according to procedures outlined by the Committee of Age Reading Experts (CARE 2006). Because eyed-side otoliths tended to exhibit distorted patterns of growth, blind-side otoliths were selected for ageing whenever possible. Without prior knowledge of size or sex, two or three readers independently aged each fish to the nearest year. Rounding decisions were based upon the amount of marginal growth relative to immediately adjacent annuli (i.e., otoliths with a margin representing greater than half the distance between neighboring annuli were rounded up and margins representing less than half the distance between neighboring annuli were rounded down). From 2007 to 2011 and again in 2014, two CDFW staff independently read each otolith until a minimum of two identical (within-reader) age estimates were made. If age determinations by the two readers did not agree, a digital image of the thin section was prepared and both readers discussed the various aspects of the otolith until a final age was agreed upon or they decided to exclude the otolith from analyses due to issues associated with poor readability. In 2012 and 2013, one CDFW and one MLML reader followed the same procedures detailed above. However, if reader-specific age determinations conflicted with one another during these years, a third (CDFW) reader was introduced to settle the disagreement. If the third reader did not agree with either of the other two readers, a digital image of the thin section was prepared and all readers either came to a unanimous agreement or decided to exclude the otolith from analyses. Finally, age estimates and capture dates were used to assign a year-class to all fish.

Growth

Sex- and region-specific growth rates were estimated using length-at-age data and the von Bertalanffy growth equation $L_t = L_\infty(1-e^{-K(t-t_0)})$, where L_t is the predicted length at age t, L_∞ represents the theoretical maximum length, K is the growth coefficient, and t_0 indicates the predicted age at a length equal to zero (von Bertalanffy 1938). Parameters L_∞ and K were estimated using least-squares regression techniques and the Excel add-in "Solver." Because our collection methods yielded few fish under 200 mm, we fixed the parameter t_0 at zero (e.g., Robertson et al. 2005; Caselle et al. 2011). Maximum likelihood techniques described by Kimura (1980) were then used to estimate and compare 95% confidence intervals surrounding the intersection of K and L_∞ (R 3.1.1). Statistical significance was determined by evaluating spatial overlap between sex- and region-specific confidence intervals (i.e., overlapping confidence intervals indicated no difference in growth and spatially explicit confidence intervals demonstrated a significant difference).

Mortality

Catch curve analysis was employed to estimate instantaneous total mortality (Z) using the equation $N(t) = N_0 e^{-Zt}$, where N(t) is the number of individuals collected within a particular year-class at age t and N_0 represents the number of individuals from the same year-class at age zero (Ricker 1975). This equation was rewritten as $\ln N(t) = \ln N_0 - Zt$, enabling the use of linear regression on log-transformed age frequency data to solve for N_0 (y intercept) and Z (slope). Because we could not sample the entire range of California Halibut ages (e.g., due to size-based gear selectivity, release of fish measuring less than the minimum legal size, ontogenetic shifts in habitat use or spatial distributions), only data from age classes greater than or equal to the mode were included. ANCOVA (Model III), using age as a covariate, was used to test for differences in slopes and y-intercepts (SPSS 22.0).

We also evaluated differences in year-class frequency distributions to gain a basic understanding of spatiotemporal variation in the survival of young California Halibut. A two-sample Kolmogorov-Smirnov (KS) test was used to compare region-specific differences in year-class strength, a proxy for recruitment (SPSS 22.0). Measures of kurtosis and skewness were also calculated to quantitatively characterize the shape (i.e., peakedness and degree of symmetry) of year-class frequency distributions for each region. Years with the greatest number of fish sampled in each region were selected for these analyses (i.e., 2013 for central California [n = 587] and 2012 for southern California [n = 265]). Year-class frequencies between 1993 and 2007 were analyzed.

Reproductive Seasonality

Duration and peak of the summer spawning season were estimated for central California females using reproductive data collected in 2012 and 2013 (Barnes 2015). Ovaries from sampled fish were removed and weighed to calculate gonadosomatic index (GSI), represented by the equation

$$GSI = \frac{\text{ovary mass (g)}}{\text{body mass (g)} - \text{ovary mass (g)}} * 100$$

(Le Cren 1951; Delahunty and de Vlaming 1980; de Vlaming et al. 1982). Ovaries were then preserved in 10% formalin, stored in 70% ethanol, and processed using histological methods described by Luna (1968). Microscopic maturity stages were determined based, in part, upon descriptions by Murua et al. (2003). The incidence of spawning females (i.e., those possessing hydrated oocytes and/or new postovulatory follicles) was used to estimate the duration of the spawning season, whereas peaks in reproductive activity were identified by fluctuations in GSI (Le Cren 1951; Delahunty and de Vlaming 1980; Almatar et al. 2004).

Reproductive data similar to those described above were not available south of Point Conception. Therefore, temporal changes in larval densities obtained from CalCOFI ichthyoplankton surveys (1980 to 2011) were used to approximate peaks in reproductive activity off of southern California and Mexico. Additionally, we applied a one-month correction to CalCOFI data to account for California Halibut's 20 to 29 d larval duration and approximate the time at which spawning occurred. Because California Halibut spawn in shallow waters, exhibit a relatively short larval duration, and settle into nearshore environments (Allen 1988), the farther offshore and more infrequent CalCOFI surveys conducted north of Point Conception were not appropriate for assessing the reproductive patterns of this species. Therefore, spatiotemporal trends in reproductive activity were assessed by plotting mean monthly GSI for fish collected off of central California and corrected mean monthly larval densities from southern California and Mexico.

RESULTS

In total, 2059 California Halibut (1299 central California, 760 southern California) were collected as part of this study. Fork lengths ranged from 85 to 1346 mm and ages ranged from 1 to 23 yr (tables 2 and 3). The overall mean length (± SE) was 680 ± 4.3 mm and the overall mean age (± SE) was 6.5 ± 0.1 yr. The sex ratio

TABLE 2
Minimum, Mean (Standard Error), and Maximum Fork Lengths (mm) for California Halibut, by Region and Sex. Sample Sizes are Indicated for Each Group.

	Central California		Southern California	
	Female (n = 743)	Male (n = 556)	Female (n = 615)	Male (n = 145)
Minimum	186	130	85	152
Mean (SE)	748 (7)	634 (6)	679 (8)	518 (17)
Maximum	1171	1047	1346	1065

TABLE 3
Minimum, Mean (Standard Error), and Maximum Ages (yr) for California Halibut, by Region and Sex. Sample Sizes are Indicated for Each Group.

	Central California		Southern California	
	Female (n = 743)	Male (n = 556)	Female (n = 614)	Male (n = 145)
Minimum	1	1	1	1
Mean (SE)	6.8 (0.1)	6.7 (0.1)	6.4 (0.1)	4.9 (0.2)
Maximum	19	16	23	14

TABLE 4
Von Bertalanffy Growth Parameters L_∞ and K for California Halibut, by Sex and Region. Standard Errors are Shown in Parentheses.

	Female		Male	
Growth Parameter	Central CA	Southern CA	Central CA	Southern CA
L_∞	1049 (15)	1304 (35)	820 (14)	1048 (60)
K	0.21 (0.01)	0.12 (0.01)	0.25 (0.01)	0.15 (0.01)

was skewed toward females in both regions and was calculated at 1.4:1 (X^2_{11297} = 26.290, $p < 0.001$) in central California and 4.3:1 (X^2_{1759} = 291.512, $p < 0.001$) in southern California. Additionally, contingency table results demonstrated a significant difference in sex ratio between the two regions (X^2_1 = 12.556, $p < 0.001$).

Growth

Sex-specific von Bertalanffy growth equations were estimated to be $L(t)_{female} = 1049\ (1 - e^{-0.21t})$ and $L(t)_{male} = 820\ (1 - e^{-0.25t})$ for central California and $L(t)_{female} = 1304\ (1 - e^{-0.12t})$ and $L(t)_{male} = 1048\ (1 - e^{-0.15t})$ for southern California (table 4). Lifetime growth curves and 95% confidence intervals surrounding parameters K and L_∞ indicate that females grow faster and attain larger maximum sizes than males, and that central California Halibut grow faster but smaller maximum sizes than southern California Halibut (figs. 2 and 3). Based upon the von Bertalanffy growth equations above, central California Halibut typically recruit to the fishery (i.e., reach the minimum legal size limit of 559 mm) at 3.7 yr for females and 4.6 yr for males. In southern California, females recruit to the fishery at 4.6 yr and males recruit to the fishery at 5.0 yr.

Mortality

Statistical comparisons of catch-at-age data indicated no difference in instantaneous total mortality (Z) between male and female California Halibut (central California: $F_{1,12} = 0.166$, $p = 0.691$; southern California: $F_{1,13} = 0.006$, $p = 0.937$). Sex-specific estimates of Z for southern California Halibut were very similar to one another ($Z_{male} = 0.35$, $Z_{female} = 0.36$). In central California, however, the total mortality estimate for males ($Z = 0.42$) was considerably greater than that of females ($Z = 0.34$). When comparing sex-specific estimates of total mortality by region, we found no significant difference between females collected from central and southern California ($F_{1,16} = 0.035$, $p = 0.854$) and an apparent, but nonsignificant difference between males ($F_{1,9} = 0.123$, $p = 0.734$) (fig. 4). Additionally, the number of

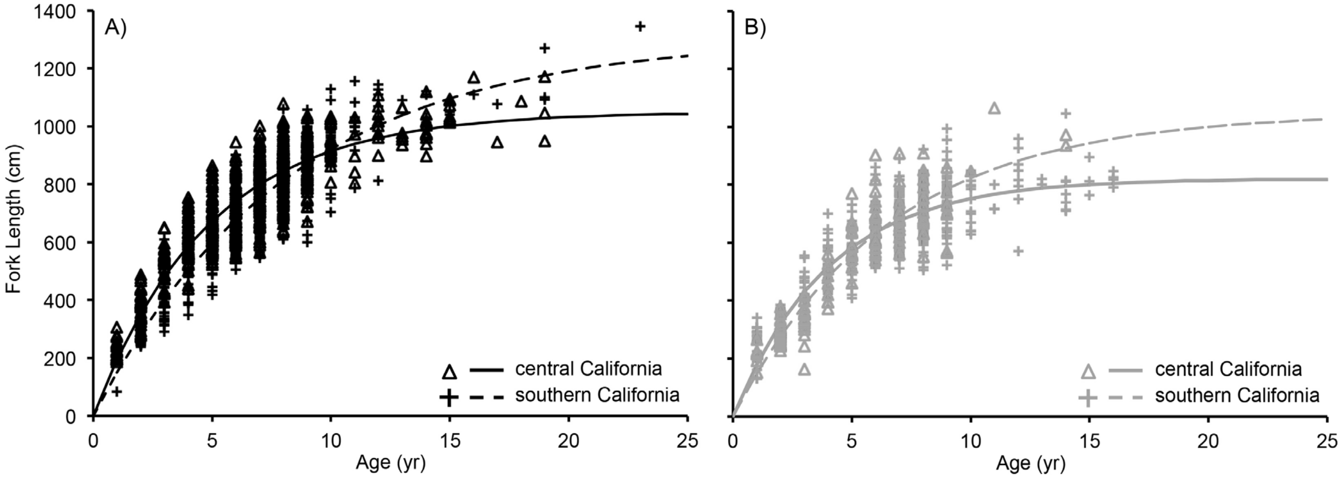

Figure 2. Length-at-age data and von Bertalanffy growth curves for female (A) and male (B) California Halibut. Fish from central California are indicated by open triangles (observed) and solid lines (predicted), whereas fish from southern California are indicated by crosses (observed) and dashed lines (predicted).

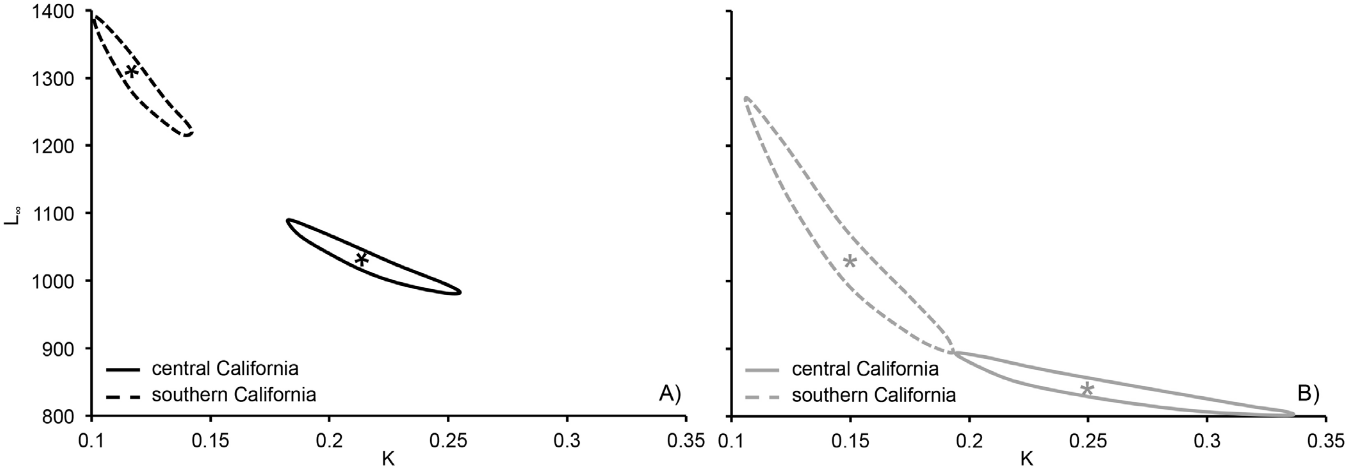

Figure 3. Von Bertalanffy growth parameters K and L∞ for female (A) and male (B) California Halibut. Ellipses represent sex- and region-specific 95% confidence intervals. Fish from central California are indicated by solid lines and fish from southern California are indicated by dashed lines.

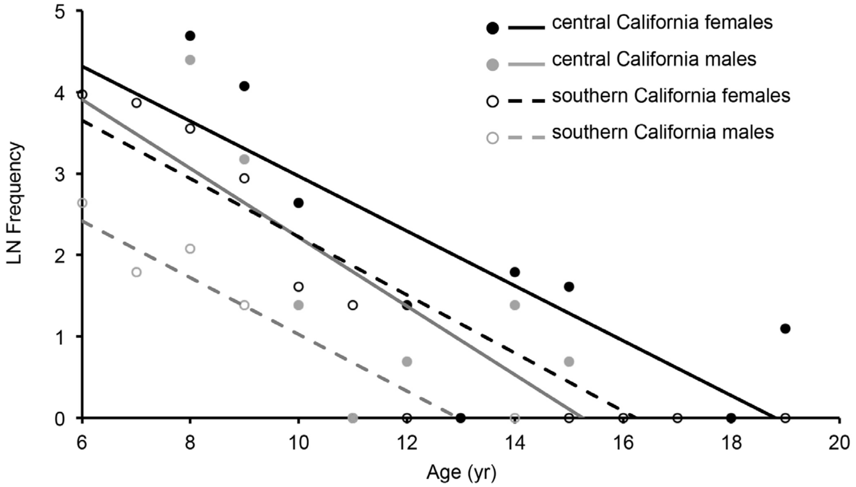

Figure 4. Instantaneous total mortality for California Halibut collected from central California in 2013 (solid) and southern California in 2012 (dashed). Females are shown in black and males are shown in gray.

southern California males sampled was significantly less (as indicated by a difference in the y-intercept) than females from the same region ($F_{1,14} = 69.150$, $p = 0.004$).

When comparing region-specific year-class frequency distributions, we found no significant difference between central and southern California Halibut ($D = 0.250$, $p = 0.847$). However, there were noticeable peaks in year-class frequencies (a proxy for recruitment) in central California in 1998, 1999, and 2005 (fig. 5). Corresponding peaks were absent from southern California, where we observed a relatively normal distribution surrounding the 2006 year-class. The central California year-class frequency distribution ($n = 12$) was leptokurtic (kurtosis = 3.195 ± 1.23), denoting the presence of a sharper than normal peak in the 2005 year-class. Conversely, the year-class frequency distribution for southern California ($n = 12$) was platykurtic (kurtosis = - 0.515 ± 1.23), which indicates a broader than normal shape lacking any significant peaks. Both populations were skewed to the right ($\text{skewness}_{\text{central}} = 1.899 \pm 0.64$, $\text{skewness}_{\text{southern}} = 0.970 \pm 0.64$), though the central California Halibut year-class frequency distribution exhibited a greater probability of encountering relatively old fish.

Reproductive Seasonality

We observed spawning females in central California from mid-June to the beginning of September in 2012 and 2013. From these data, we estimated the duration of the summer spawning season to be 79 ± 3 d (SE). This duration was also supported by relatively low mean GSI of mature females (2.9 ± 0.5 [SE]) in May and September. Additionally, increases in mean GSI to 4.7 ± 0.3 (SE) demonstrated a peak in reproductive effort in central California in July. Because large quantities of California Halibut are not caught between October and April north of Point Conception (CDFW 2014), we have no data with which to evaluate reproductive activity in central California outside of the summer months.

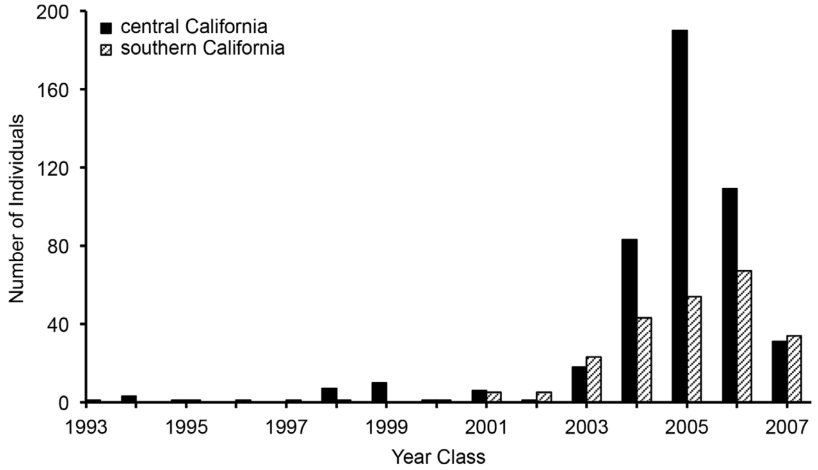

Figure 5. Year-class frequency distributions for central (solid) and southern (dashed) California Halibut, 1993 to 2007.

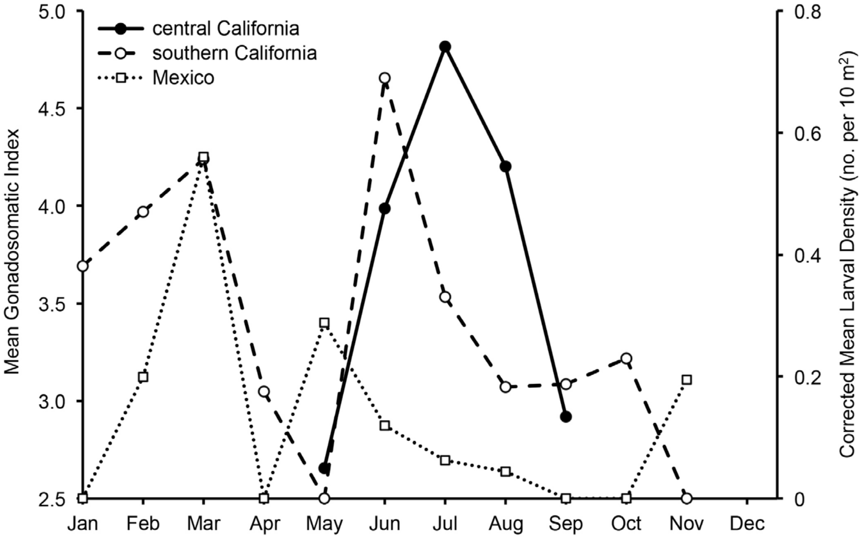

Figure 6. Mean gonadosomatic index for mature California Halibut females collected from central California in 2013 (closed circles, solid line) and corrected mean larval densities (number per 10 m^2, wet displacement volume) for southern California (open circles, dashed line) and Mexico (open squares, dotted line) by month. Larval density data were collected by CalCOFI from 1980 to 2011. Error bars have been omitted for clarity.

Based upon the incidence of larvae obtained from CalCOFI ichthyoplankton surveys in nearshore waters, we know that California Halibut spawn year-round in southern California and Mexico. The greatest larval densities (number of larvae per 10 m^2) of California Halibut can be found in April (0.56 ± 0.19 [SE]) and June (0.29 ± 0.15 [SE]) in Mexico and in April (0.56 ± 0.18 [SE]) and July (0.69 ± 0.20 [SE]) in southern California (CalCOFI 2014). Given the approximate one-month lag between spawning and late larval phase, we inferred that peak spring spawning occurs in Mexico and southern California in March. Additionally, corrected larval density data indicate that peak summer spawning takes place in Mexico in May and in southern California in June. When comparing this information with our observed peak spawning in central California in July, we found that California Halibut display a latitudinal gradient in timing of reproduction, with spawning taking place earlier to the south and later to the north (fig. 6).

DISCUSSION

Our estimated female to male sex ratios of 1.4:1 for central California and 4.3:1 for southern California differ from previous approximations for smaller fish from the same regions (1.1:1 and 1:2.2, respectively; MacNair et al. 2001). However, the 4.3:1 sex ratio for southern California Halibut matches a previous estimate obtained from similarly sized individuals (Sunada et al. 1990). The relatively greater difference in the number of males and females collected off of southern California Halibut may be a result of sampling bias from fishing activities that target larger (typically female) fish. It may also be due to sampling fish within an area where there are sex-structured spatial distributions (e.g., more females found nearshore, as indicated by Sunada et al. 1990). Investigations into sex-specific habitat associations and movement patterns of California Halibut may elucidate potential mechanisms for the observed difference in sex ratio by region.

Growth

Consistent with the scientific literature, female California Halibut collected as part of this study grew faster and to larger sizes than male conspecifics (Haaker 1975; Hammann and Ramirez-Gonzalez 1990; Sunada et al. 1990; MacNair et al. 2001). However, contrary to the only other regional comparison of California Halibut growth (MacNair et al. 2001), our data show that central California Halibut grow faster, but attain smaller maximum sizes than those from southern California. Conflicting results between MacNair et al. (2001) and our study are likely due to different size and age ranges of fish sampled. MacNair et al. (2001) used a single gear type (i.e., trawl with a 8.5 cm mesh cod end), which resulted in the collection of smaller sex- and region-specific median sizes (ranging from 387 to 544 mm) and younger maximum ages (from 12 to 13 yr) of California Halibut. Because our study incorporated numerous gear types (i.e., trawl, gill net, hook and line, spear, seine), we were able to sample a wider size range of fish, with larger sex- and region-specific median sizes (ranging from 559 to 780) and older maximum ages (between 14 and 23 yr) of California Halibut. The truncated size and age distributions of fish collected by MacNair et al. (2001) generated estimates of L_∞ and K that were more theoretical, whereas our estimates were corroborated by length-at-age data for a wider age range of fish, including older fish. Additionally, without having sampled large quantities of small (<200 mm) fish, we found that it was more appropriate to fix t_0 at zero for our study because doing so produced more biologically realistic growth curves that intersected at the origin.

Mortality

Despite observing sex- and region-specific differences in growth, statistical analyses indicated no differences in instantaneous total mortality. Although we did not detect statistical differences, estimates of Z suggested greater mortality for male California Halibut found north of Point Conception ($Z = 0.42$) as compared to females from the same region ($Z = 0.34$) and males from southern California ($Z = 0.35$). Greater calculations of Z for central California males may be due to a combination of several factors. First, catch curve analysis is limited to fish greater than or equal to the mode age sampled. Because of issues associated with selective fishing imposed by a minimum size limit of 559 mm and a sampling scheme that was primarily fishery-dependent, we were limited to fish greater than 6 yr. Additionally, a strong 2005 year-class in central California shifted the mode of age frequencies to the right, preventing catch curve analysis for 6 and 7 yr old fish north of Point Conception. Finally, male California Halibut exhibit a shorter lifespan than females, further reducing the number of data points used in catch curve analysis of this sex. It is probable that each of these factors compounded upon one another to increase the variation in our age frequency data for central California males. As such, continued sampling is necessary to improve our understanding of Z for male California Halibut caught north of Point Conception.

Our estimate of instantaneous total mortality for southern California Halibut females ($Z = 0.36$) was much less than the only other estimate ($Z = 0.53$), which was calculated for fish collected between 1985 and 1988 (Reilly et al. 2008). The greater estimate of total mortality for southern California females may be attributed to the inclusion of particularly strong year-classes resulting from the 1982–83 El Niño event. This, along with some uncertainty surrounding our estimates of Z for central California males, reiterates the need to conduct catch curve analysis over longer time series that account for various levels of year-class strength.

When evaluating spatiotemporal variation in survival of young California Halibut, we observed greater variation in year-class frequency distributions (i.e., recruitment) north of Point Conception. With a pelagic larval phase, young California Halibut are susceptible to advection offshore during periods of intense and persistent upwelling, as has been found in other species resident to eastern boundary currents (e.g., Parrish et al. 1981; Cury and Roy 1989; Gibson 1994; Wilderbuer et al. 2002). Additionally, periods of strong upwelling may decrease sea surface temperatures below a threshold at which young California Halibut can survive. We observed stronger recruitment for California Halibut during weaker upwelling years (1998, 1999, and 2005) and weaker recruitment during stronger upwelling years (2000 to 2002) in central California (Auth 2008; Caselle et al. 2010; Ralston et al. 2013). This variation in California Halibut recruitment is out of synchrony with rockfish recruitment north of Point Conception, which is strongest during colder SST and stronger upwelling (Caselle et al. 2010; Ralston et al. 2013). The opposing patterns of California Halibut and rockfish recruitment in central California may have implications for the nearshore ecosystem as a whole (e.g., California Halibut and similarly influenced species serving as important food sources during periods of poor rockfish recruitment) and, therefore, are important to better understand.

In southern California, a change in current direction produces relatively weak upwelling year-round. This more static upwelling state, combined with generally warmer sea surface temperatures, can offer an explanation for regular recruitment of California Halibut (as evidenced by a more normal distribution of year-classes) south of Point Conception. With more favorable abiotic conditions, it is probable that density dependent processes (e.g., competition, predation) are more important for recruitment of southern California Halibut (Lasker 1981; Cushing 1990; Searcy and Sponaugle 2001). Although we believe that these regional differences in California Halibut recruitment are real, longer time series of year-class frequency data would enhance our understanding about potential environmental and ecological drivers.

Reproductive Seasonality

California Halibut have previously been described as exhibiting year-round reproduction, with peak activity in late winter and spring (Haaker 1975; Lavenberg et al. 1986; Love and Brooks 1990). Recent ichthyoplankton surveys confirmed year-round reproduction south of Point Conception, with greatest densities of California Halibut larvae occurring in April, June, and July (CalCOFI 2014). However, in analyzing GSI data obtained north of Point Conception, we found that California Halibut spawn later and likely for a shorter duration in central California.

Limited quantities of commercially or recreationally caught fish between October and April precluded reproductive analyses outside of the summer months in central California (CDFW 2014). The absence of halibut caught during winter may be indicative of seasonal migrations related to spawning, though movement data are necessary in order to evaluate this hypothesis. Nevertheless, reproductive effort from all three regions (i.e., corrected larval densities from southern California and Mexico and GSI from central California) illustrated a latitudinal gradient in summer spawning. Although this pattern matches that of other West Coast flatfishes (e.g., *Citharichthys* spp., Chamberlain 1979), it opposes temporal trends observed for other *Paralichthys* spp. studied along the east coast of the United States, where spawning takes place earliest in northerly regions (e.g., *Paralichthys dentatus*, Smith 1973).

Temperature and photoperiod have been implicated as potentially important factors in California Halibut reproduction (Caddell et al. 1990). In a laboratory study, Caddell et al. (1990) observed spawning activity at temperatures between 15.0° and 16.5°C and during day lengths greater than or equal to 10.5 hr. Our results indicated that spawning occurs in waters as cold as 13.0°C in central California, though day lengths are comparable to the laboratory study. This indicates that temperature thresholds for reproduction are lower than previously estimated for California Halibut and that some other factor (e.g., planktonic food supply) effects the timing of spawning.

The estimates of growth, total mortality, and reproductive seasonality that we have provided not only enhance our understanding about spatiotemporal effects on the life history traits of nearshore fish species, they also provide sex- and region-specific data for reparameterization of the stock models developed specifically for California Halibut. As such, incorporation of our results into future stock assessments should improve model outputs and reduce uncertainty concerning the sustainability of California Halibut within state waters.

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LITERATURE CITED

Adams, P. B. 1980. Life history patterns in marine fishes and their consequences for fisheries management. U.S. Fish. Bull. 78:1–12.

Allen, L. G. 1988. Recruitment, distribution, and feeding habits of young-of-the-year California Halibut (*Paralichthys californicus*) in the vicinity of Alamitos Bay–Long Beach Harbor, California, 1983–85. Bull. South. Calif. Acad. Sci. 87:19–30.

Allen, L. G., R. E. Jensen, and J. R. Sears. 1990. Research Note: Open coast settlement and distribution of young-of the-year California Halibut (*Paralichthys californicus*) along the southern California coast between Point Conception and San Mateo Point, June–October, 1988. In: C.W. Haugen (ed.), The California Halibut, *Paralichthys californicus*, resource and fisheries. Calif. Fish Game Fish Bull. 174:145–152.

Allen, M. J. 1990. The biological environment of the California Halibut, *Paralichthys californicus*. In: C.W. Haugen (ed.), The California Halibut, *Paralichthys californicus*, resource and fisheries. Calif. Fish Game Fish Bull. 174:7–29.

Allen, M. J., and K. T. Herbinson. 1990. Settlement of juvenile California Halibut, *Paralichthys californicus*, along the coasts of Los Angeles, Orange, and San Diego counties in 1989. Calif. Coop. Oceanic Fish. Invest. Rep. 31:84–96.

Almatar, S. M., K. P. Lone, T. S. Abu-Rezq, and A. A. Yousef. 2004. Spawning frequency, fecundity, egg weight and spawning type of Silver Pomfret, *Pampus argentus* (Euphrasen) Stromateidae), in Kuwait waters. J. Appl. Ichthyol. 20:176–188.

Auth, T. D. 2008. Distribution and community structure of ichthyoplankton from the northern and central California current in May 2004–06. Fish. Oceanogr. 17:316–331.

Barnes, C. L. 2015. Growth, mortality, and reproductive potential of California Halibut (*Paralichthys californicus*) off central California. MS Thesis. Moss Landing Marine Laboratories. Moss Landing, CA.

Caddell, S. M., D. M. Gadomski, and L. R. Abbott. 1990. Induced spawning of the California Halibut, *Paralichthys californicus*, (Pisces: Paralichthyidae) under artificial and natural conditions. In: C.W. Haugen (ed.), The California Halibut, *Paralichthys californicus*, resource and fisheries. Calif. Fish Game Fish Bull. 174:175–198.

California Cooperative Oceanic Fisheries Investigation (CalCOFI). 2014. California Halibut, *Paralichthys californicus*, ichthyoplankton data, 1980 to 2011. https://oceaninformatics.ucsd.edu/ichthyoplankton/. Accessed October 2014.

California Department of Fish and Wildlife (CDFW). 2013. 2013 CRFS Sampling Manual: California Recreational Fisheries Survey. CDFW, PSMFC, NOAA Fisheries, Sport Fish Restoration Act. https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=62348&inline=true.

California Department of Fish and Wildlife (CDFW). 2014. Recreational and commercial landings data for California Halibut, 2004 to 2013. Recreational Fisheries Information Network (RecFIN), http://www.recfin.org/sample-data. Accessed October 2014.

Caselle, J. E., M. H. Carr, D. P. Malone, J. R. Wilson, and D. E. Wendt. 2010. Can we predict interannual and regional variation in delivery of pelagic juveniles to nearshore populations of rockfishes (genus *Sebastes*) using simple proxies of ocean conditions? Calif. Coop. Oceanic Fish. Invest. Rep. 51:91–105.

Caselle, J. E., S. L. Hamilton, D. M. Schroeder, M. S. Love, J. D. Standish, J. A. Rosales-Casian, and O. Sosa-Nishizaki. 2011. Geographic variation in density, demography, and life history traits of a harvested, sex-changing, temperate reef fish. Can. J. Fish. Aquat. Sci. 68:288–303.

Chamberlain, D. W. 1979. Histology of the reproductive systems and comparison of selected morphological characters in four Easter Pacific species of *Citharichthys* (Pisces: Bothidae). PhD Dissertation. University of Southern California. 297 pp.

Committee of Age Reading Experts (CARE). 2006. Manual on generalized age determination: procedures for groundfish. Pacific States Marine Fisheries Commission. 57 pp.

Cury, P., and C. Roy. 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. Can. J. Fish. Aquat. Sci. 670–680.

Cushing, D. H. 1990. Plankton production and year class strength in fish populations: an update of the match/mismatch hypothesis. Adv. Mar. Biol. 26:249–293.

Delahunty, G., and V. L. de Vlaming. 1980. Seasonal relationship of ovary weight, liver weight and fat stores with body weight in the Goldfish, *Carassius auratus* (L.) J. Fish Biol. 16:5–13.

de Vlaming, V., G. Grossman, and F. Chapman. 1982. On the use of gonadosomatic index. Comp. Biochem. Physiol. 73A:31–39.

Domeier, M. L. and C. S. Y. Chun. 1995. A tagging study of the California Halibut (*Paralichthys californicus*). Calif. Coop. Oceanic Fish. Invest. Rep. 36:204–207.

Gibson, R. N. 1994. Impact of habitat quality and quantity on the recruitment of juvenile flatfishes. Neth. J. Sea Res. 32:191–206.

Haaker, P. L. 1975. The biology of the California Halibut, *Paralichthys californicus* (Ayres) in Anaheim Bay. In: E. D. Lane and C. W. Hill (eds.), The Marine Resources of Anaheim Bay, California. Calif. Fish Game Fish Bull. 165:137–151.

Hammann, M. G., and A. A. Ramirez-Gonzalez. 1990. California Halibut, *Paralichthys californicus*, in Todos Santos Bay, Baja, Mexico. In: C.W. Haugen (ed.), The California Halibut, *Paralichthys californicus*, resource and fisheries. Calif. Fish Game Fish Bull. 174:127–144.

Kimura, D. K. 1980. Likelihood methods for the von Bertalanffy growth curve. U. S. Fish. Bull. 77:765–776.

Kramer, S. H. 1990. Distribution and abundance of juvenile California Halibut, *Paralichthys californicus*, in shallow waters of San Diego County. In: C.W. Haugen (ed.), The California Halibut, *Paralichthys californicus*, resource and fisheries. Calif. Fish Game Fish Bull. 174:99–126.

Lasker, R. 1981. Factors contributing to variable recruitment of the Northern Anchovy (*Engraulis mordax*) in the California Current: contrasting years, 1975 through 1978. Conseil international pour l' Exploration de la Mer 178:375–388.

Lavenberg, R. J., G. E. McGowen, A. E. Jahn, J. H. Petersen, and T. C. Sciarrotta. 1986. Abundance of southern California nearshore ichthyoplankton: 1978–84. Calif. Coop. Oceanic Fish. Invest. Rep. 27:53–64.

Le Cren, E. D. 1951. The length-weight relationship and seasonal cycle in gonad weight and condition in the Perch (*Perca fluviatilis*). J. Anim. Ecol. 20:201–219.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bull. Entomol. Soc. Am. 15:237–240.

Love, M. S. and A. Brooks. 1990. Size and age at first maturity of the California Halibut, *Paralichthys californicus*, in the Southern California Bight. In: C. W. Haugen (ed)., The California Halibut, *Paralichthys californicus*, resource and fisheries. Calif. Fish Game. Fish Bull. 174:167–174.

Luna, L. G. 1968. Manual of histologic staining methods of the armed forces institute of pathology, third edition. McGraw-Hill. New York, NY. 258 pp.

MacNair, L. S., M. L. Domeier, and C. S. Y. Chuen. 2001. Age, growth, and mortality of California Halibut, *Paralichthys californicus*, along southern and central California. U.S. Fish. Bull. 99:588–600.

Maunder, M., P. Reilly, T. Tanaka, G. Schmidt and K. Penttila. 2011. California Halibut stock assessment. Calif. Fish Game. https://www.dfg.ca.gov/marine/sfmp/halibut-assessment.asp.

Murua, H., G. Kraus, F. Saborido-Rey, P. R. Witthames, A. Thorsen, and S. Junquera. 2003. Procedures to estimate fecundity of marine fish species in relation to their reproductive strategy. J. Northwest. Atl. Fish. Sci. 33:33–54.

Orensanz, J. M., A. M. Parma, G. Jerez, N. Barahona, M. Montecinos, and I. Elías. 2005. What are the key elements for the sustainability of 'S-fisheries'? Insights from South America. Bull. Mar. Sci. 76(2):527–556.

Parrish, R. H., C. S. Nelson, and A. Bakun. 1981. Transport mechanisms and reproductive success of fishes in the California Current. Biol. Oceanogr. 1:175–203.

Pascoe, S., R. Bustamante, C. Wilcox, and M. Gibbs. 2009. Spatial fisheries management: a framework for multi-objective qualitative assessment. Ocean Coast. Manage. 52:130–138.

Prince, J. 2010. Rescaling fisheries assessment and management: a generic approach, access rights, change agents, and toolboxes. Bull. Mar. Sci. 86:197–219.

Ralston S., K. M. Sakuma, and J. C. Field. 2013. Interannual variation in pelagic juvenile rockfish (*Sebastes* spp.) abundance—going with the flow. Fish. Oceanogr. 22:288–308.

Reilly, P., T. Tanaka, K. Penttila, G. Schmidt, J. Weinstein, and M. Key. 2008. Applications of some recommended analytical methods from data-poor workshop. Calif. Fish Game. 17 pp. https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=39601.

Rice, J., S. X. Cadrin, and W. G. Clark. 2005. Assessment and management of flatfish stocks. In: R. N. Gibson (ed.). Flatfishes, Biology and Exploitation. Blackwell Science Ltd. Oxford, UK. 319–346.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191:1–382.

Robertson, D. R., J. L. Ackerman, J. H. Choat, J. M. Posada, and J. Pitt. 2005. Ocean Surgeonfish *Acanthurus bahianus*. I. The geography and demography. Mar. Ecol. Prog. Ser. 295:229–244.

Searcy, S. P., and S. Sponaugle. 2001. Selective mortality during the larval-juvenile transition in two coral reef fishes. Ecol. 82:2452–2470.

Smith, W. G. 1973. The distribution of Summer Flounder, *Paralichthys dentatus*, eggs and larvae on the continental shelf between Cape Cod and Cape Lookout, 1965–66. U.S. Fish Bull. 71:527–548.

Sunada, J. S., P. V. Velez, and C. A. Pattison. 1990. Age, size, and sex composition of California Halibut in southern California commercial fishery landings, 1983–88. In: C. W. Haugen (ed)., The California Halibut, *Paralichthys californicus*, resource and fisheries. Calif. Fish Game. Fish Bull. 174:303–320.

Valle, C. F., J. W. O'Brien, and K. B. Wiese. 1998. Differential habitat use by California Halibut, *Paralichthys californicus*, Barred Sand Bass, *Paralabrax nebulifer*, and other juvenile fishes in Alamitos Bay, California. Calif. Fish Game Fish Bull. 97:646–660.

von Bertalanffy, L. 1938. A quantitative theory of organic growth. Hum. Biol. 10:181–213.

Wilderbuer, T. K., A. B. Hollowed, W. J. Ingraham Jr., P. D. Spencer, M. E. Connors, N. A. Bond, and G. E. Walters. 2002. Flatfish recruitment to decadal climatic variability and ocean conditions in the eastern Bering Sea. Prog. Oceanogr. 55:235–247.

CHANGES IN SIZE COMPOSITION AND RELATIVE ABUNDANCE OF FISHES IN CENTRAL CALIFORNIA AFTER A DECADE OF SPATIAL FISHING CLOSURES

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ABSTRACT

Rockfish Conservation Areas (RCAs) were implemented in 2000 to 2003 along the West Coast of the United States to reduce fishing mortality on rockfish (*Sebastes* spp.) and other groundfish species that had recently been declared overfished. In 2012, we initiated a study to compare recent catch rates, species compositions and length frequencies of fishes inside and outside the RCAs with data collected in central California between 1995 and 1998. At all sites surveyed, total catch rates from the new surveys (2012–14) were significantly higher than catch rates from before RCA implementation (1995–98). The majority of the differences were due to the increased relative abundance of yellowtail rockfish (*Sebastes flavidus*), although other species, including the overfished canary rockfish (*Sebastes pinniger*), also increased. Differences in the size composition of species between the two time periods reflected both the increased survival of older fishes and higher recruitment success in the past decade.

INTRODUCTION

After receiving subsidies to develop domestic fishing capability in the 1970s, the US West Coast fishing fleet became overcapitalized in the 1980s, resulting in fishing mortality rates that were unsustainable (Ralston 2002; Melnychuk et al. 2013). As a consequence of the combined effects of overexploitation and poor recruitment conditions throughout the 1990s, seven species of rockfish (*Sebastes* spp.), as well as lingcod (*Ophiodon elongatus*) and Pacific hake (*Merluccius productus*) were declared overfished in West Coast waters during the late 1990s and early 2000s (Berkeley et al. 2004; PFMC 2003). In an effort to protect and rebuild overfished species, while allowing for some harvest of healthy stocks, a broad set of spatial area closures was implemented between 2000 and 2003 to minimize fishing mortality on rebuilding species. These areas are known as Rockfish Conservation Areas (RCAs), i.e., areas on the continental shelf and slope closed to specific recreational and commercial fishing activities. In US waters, the RCAs extend along the entire West Coast from the Mexican border to the Canadian border, and fishing prohibitions continue to date.

The regulatory boundaries of RCAs are lines that generally follow depth contours. The precise boundaries vary both over time (season and year), gear type used, and by latitude in different areas of the coast. Recreational fisheries have been constrained to waters shallower than the nearshore boundary of the recreational RCA, while both trawl and fixed gear commercial fisheries are allowed to fish deeper than the seaward boundary of the trawl and non-trawl RCAs (Mason et al. 2012). In California, the recreational RCA has been divided into a number of management areas, such that fishing for groundfish species has been prohibited deeper than 36–110 m (20–60 ftm) on the continental shelf.

Although RCAs are not intended to exclude fishing on a permanent basis, they are intended to provide the benefits of spatial closures often attributed to marine reserves, primarily the severe reduction of fishing effort to rebuild overfished species. Some of these benefits include general increases in population size and biomass, increases in the mean length of fish, and higher reproductive potential (Lester et al. 2009). The latter benefit can occur in situ through increased fish abundance as well as reduced mortality from fishing of larger, older fishes, which may contribute disproportionally to reproductive success (Hixon et al. 2014). In addition, enhanced reproductive potential within a closed area is expected to have "spillover" effects, seeding adjacent areas with both emigrating adults and dispersing progeny from the protected spawning population.

Recent studies have evaluated population trends before and after RCA closures using a combination of onboard observer data for recreational fisheries in areas open to recreational fishing (e.g., Cope et al. 2013) and data from bottom trawl surveys (e.g., Keller et al. 2014). While Keller et al. (2014) documented greater catch rates and larger fish within RCAs for a suite of demersal species, their data set did not include information from the time period prior to RCA establishment, contained minimal coverage of shallower regions targeted by recreational fisheries, and excluded high relief habitats that are inaccessible to trawling. Thus, there remains a need to better quantify changes in the relative abundance of rocky reef fishes in nearshore waters to understand the effects of area closures at fine spatial scales.

A temporally and spatially extensive pre-RCA data set made it possible to assess the effectiveness of the RCAs after a decade of spatial closures. From 1987 to 1998, in response to industry concerns of an apparent decline in the quality of fishing for rockfishes and lingcod in central and northern California waters, the California Department of Fish and Wildlife (CDFW) conducted at-sea sampling of the catch of commercial passenger fishing vessels (CPFVs) (Reilly and Wilson-Vandenberg 1999). During that period, observers accompanied charter-fishing vessels on over 2,200 fishing trips that targeted rockfishes and lingcod, collecting information on over 300,000 fishes. They recorded fishing effort (in units of angler hours spent fishing), species composition, lengths, and coarse fishing location information in every month of the year at sites from Morro Bay to Eureka, CA.

The goal of our research was to evaluate changes in species compositions, catch rates, and lengths of recreationally important species within three different regions of central California in pre-RCA and post-closure data sets. This research was a collaborative effort among the National Marine Fisheries Service (NMFS), CDFW, Moss Landing Marine Laboratories (MLML), California Sea Grant, the central coast CPFV fleet and volunteer anglers recruited through the California Collaborative Fisheries Research Program at MLML for the post-closure surveys. Here we compare fishery metrics calculated from the pre-RCA CDFW data set (1995–98) to a new post-closure data set (2012–14) that was generated by fishing in the same locations and using protocols and techniques similar to those used by Reilly and Wilson-Vandenberg (1999) during the CDFW surveys.

METHODS

Hook and Line Fishing Surveys

1987–98 CDFW Data Set From 1987–98 CDFW selected trips to observe CPFV operations. On each trip, CPFV captains chose the fishing locations, determined drift length and the number of drifts. On selected trips, CDFW observers recorded a latitude and longitude for fishing drifts, the number of active anglers, fishing time, number of each species caught, and whether they were kept or released. This enabled calculations of catch per unit effort (CPUE) for discrete geographic areas. Observers recorded total length (mm) of a subset of retained fishes on the vessel while transiting to port. Thus, length data from 1987–98 do not have associated latitude and longitude coordinates on the fine geographic scale of a fishing drift. As a result, we only compared lengths of fishes from the 1987–98 data set from fishing trips that occurred exclusively at the locations that were sampled in 2012–14. Although the CDFW 1987–98 data have been used to support past stock assessments, information on catches at a greater spatial resolution were recovered as a component of this effort and recently uploaded in 2014 into a relational structured queried language (SQL) database.

2012–14 Fishing Methods Field methods for the 2012–14 surveys followed fishing operations in the 1987–98 CDFW surveys with the exception that we released caught fishes, targeted specific locations where 1987–98 surveys took place, and recruited volunteer anglers. Although the end tackle used by fishers surveyed in the CDFW study was not precisely recorded, discussions with CPFV captains suggested that five-hook shrimp-fly gangions was the gear most commonly used at the time. Therefore, five-hook gangions with shrimp-fly lures were provided for each angler and no subtractions or additions of gear were allowed to enable the calculation of catch rates on a per-hook basis in future comparative studies. Half of the anglers used strips of squid bait on each hook and the other half did not use bait to represent different methods of fishing.

Captains were instructed to conduct fishing drifts as they would on a normal chartered day of fishing. GPS coordinates of CDFW fishing locations were provided to locate areas for fishing to occur. Once in those areas, captains searched for locations to fish, making use of depth sounders as well as their knowledge of the fishing grounds. Captains started and stopped fishing based on drift speed and catch rates, as they would on normal trips. Start and stop times for each drift were recorded to calculate CPUE. Beginning and ending coordinates were recorded and later plotted in GIS to track drift lines in relation to RCA boundaries as well as compare our fishing locations with the CDFW fishing data. Each day consisted of approximately three hours of fishing within the region.

To ensure fish survival upon release, each fish caught was initially placed into an 18-gallon bin filled with fresh seawater. Care was taken to minimize damage to each fish while the hook was removed. Fish were identified to species and we measured fork length to the nearest half-

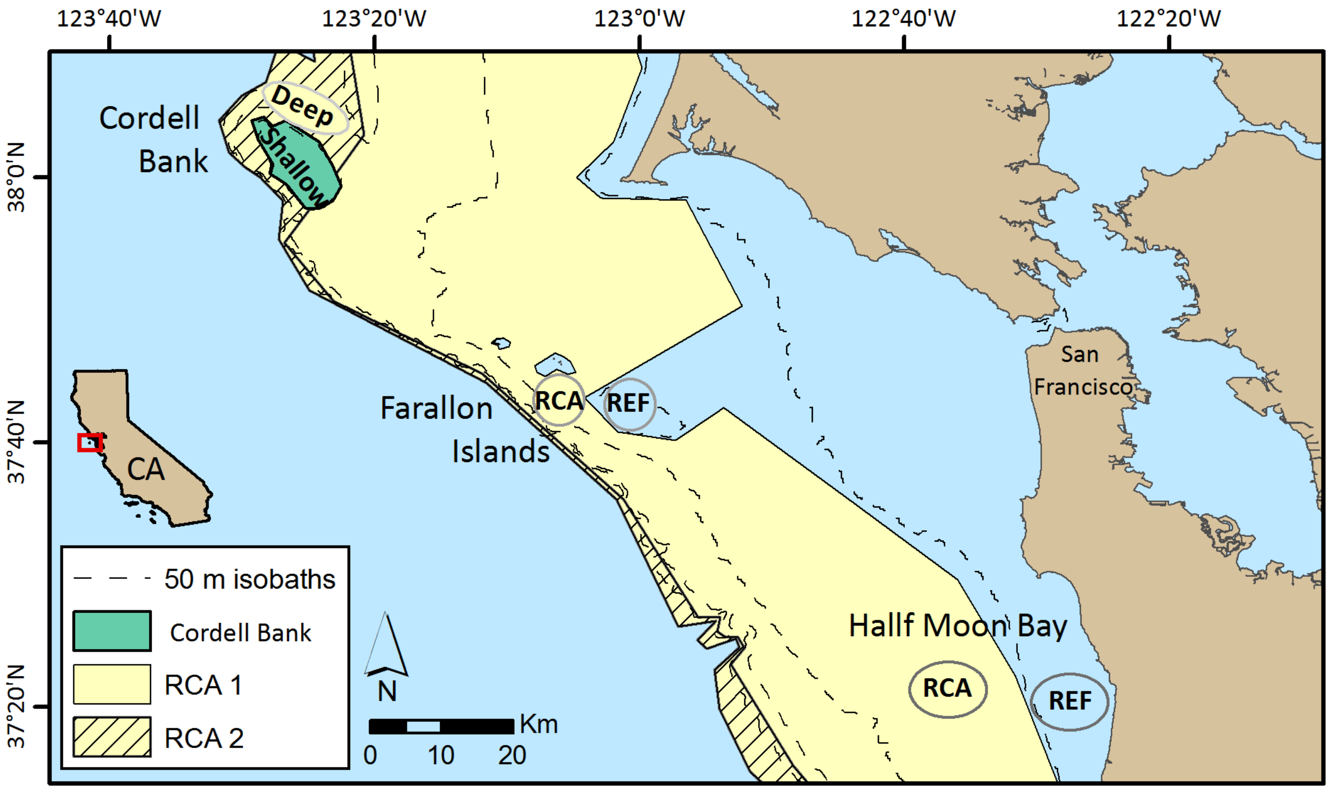

Figure 1. Rockfish Conservation Area boundaries and hook and line fishing sites (RCA, REF, Shallow, Deep) sampled in 1995–98 and 2012–14. Sampling was completed in the regions of Cordell Bank (COR), the Farallon Islands (FAR), and Half Moon Bay (HMB). RCA 1 is the area where recreational fishing and commercial bottom fixed-gear has been prohibited since 2002. RCA 2 is the area where commercial bottom trawling has been prohibited since 2002. These boundaries may change seasonally as well as annually.

centimeter. To enable future studies of fish movements, T-bar anchor tags were inserted into the dorsal muscle of a subset of fishes that displayed little or no signs of barotrauma. The majority of fishes were released back at depths of capture with the aid of descending devices. Subsets of selected species were retained for ongoing studies of reproductive ecology, (e.g., Beyer et al. 2015), age and growth, and isotope/diet analysis.

Fishing Regions and Site Selection

We selected three different regions of central California: Half Moon Bay (HMB), the Farallon Islands (FAR), and Cordell Bank (COR) for comparison of fish communities pre- and post-RCA implementation (fig. 1). All three regions contained popular fishing locations in the 1980s and 1990s, have areas that have been closed since 2002, and were sampled extensively by CDFW between 1987–98. From 2012–14, we fished within RCA sites (closed to recreational fishing) and reference sites (REF, open to fishing) (fig. 1). Sites within the RCA were selected based on their proximity to pre-RCA fishing drifts from the CDFW data set, whereas comparable REF sites were selected based on both their proximity to CDFW fishing drifts and on the fact that they had been fished seasonally since 2002. To select reference fishing sites where recreational fishing continued after 2002 we consulted with local commercial and recreational fishermen in July and August of 2012. The Half Moon Bay and the Farallon Islands regions have sites that have been fished since the implementation of RCAs. However, the surrounding areas of Cordell Bank had no comparable site open to fishing after 2002; therefore we compared "shallow" and "deep" sites to evaluate whether changes in the length and relative abundance of fishes over time varied by depth within this closed region.

As the RCAs are intended to closely approximate depth based spatial closures, the RCA fishing sites were generally deeper than the reference sites in Half Moon Bay and the Farallon Islands. The recreational RCA in the San Francisco Management Area (38˚57.50'N to 37˚11'N) restricted recreational fishing deeper than approximately 55 m (30 ftm) during the 2012–14 surveys. The Half Moon Bay fishing sites were between 4–20 km offshore and included low relief rocky reef habitats. Fishing drifts in the Half Moon Bay RCA site occurred at depths between 55–85 m and drifts within the REF site occurred at depths between 23–52 m. The Farallon Islands fishing sites were distributed between the North Farallon Island and Southeast Farallon Island, approximately 50 km west of San Francisco. Fishing drifts inside the RCA were at depths between 57–73 m and drifts within the REF site were in depths of 27–65 m. Fishing drifts in the REF sites were sometimes deeper than the stated shoreward depth of the RCA because published boundaries do not follow exact isobaths. Cordell Bank is located 40 km west of Point Reyes and is comprised of high relief pinnacles, none reaching closer to the surface than 35 m. The "shallow" fishing sites were all on top of the bank, on the northeast side, at depths between 55–135 m. The "deep" fishing sites were just north of the bank in water depths of 120–190 m.

Analysis

Selection of 1995–98 CDFW data To evaluate the effectiveness of RCA closures, only data from 1995–98 in the CDFW data set were used for comparison with the 2012–14 data set. These years were selected because they were the four years closest to the implementation of the RCAs, and had higher and more consistent number of drifts compared to the 1987–94 data. Individual drifts within the 1995–98 CDFW data set were selected for analyses based on three criteria: recorded amount of time fishing, location, and recorded depth. To minimize the bias caused by short drift times, which might over or underestimate catch rates, we excluded any drifts from catch rate analyses that were less than five minutes in duration for both the 1995–98 and 2012–14 data sets. Additionally, geographic filters were applied to the 1995–98 data set to ensure spatial congruence with the 2012–14 data set. Using ArcGIS, 1 km buffers around all 2012–14 drifts were created and drifts in the 1995–98 data set that did not overlap with the 1 km buffers were excluded from data analyses. Consequently, drifts with incomplete or no spatial information were also excluded. Finally, only 1995–98 drifts that were recorded within a depth of ±10 m of the minimum and maximum depth of 2012–14 drifts within a site were included to maintain similarity between the depths sampled in both time periods.

Catch Rate Analyses We used CPUE, where effort was in units of angler hours, as a metric of relative abundance of fishes. As there was no documentation or records regarding the number of hooks each angler used in the CDFW data set, we measured catch on a per angler basis rather than catch on a per-hook basis. To calculate effort we multiplied the number of anglers observed by the total fishing time for each drift. CPUE was then calculated for each species by dividing the number of fish caught by fishing effort for each drift:

$$\text{CPUE} = \frac{\text{No. of fish caught per drift}}{[\text{No. of anglers}] \times [\text{No. hours fishing}]}$$

We compared species compositions at sites (RCA/REF, deep/shallow) within regions by examining the proportion of catch that each species comprised. The 1995–98 and 2012–14 data sets were compared by calculating the mean CPUE for each species and then determining the fraction of the sum of all mean species CPUE that each species comprised.

To examine how total and species-specific catch rates have changed we used Welch's t-test ($\alpha = 0.05$) to compare CPUE in the 1995–98 and 2012–14 data sets. Welch's t-test was appropriate for these data because our samples were independent, had unequal variances, and sample sizes were high enough that we could assume normality (Ruxton 2006). We also used Welch's t-tests to compare the mean CPUE for each of the six most abundant species, inside and outside of the future RCAs in the 1995–98 data set, to determine if initial differences existed before the implementation of RCAs.

Length Analyses

We compared species mean fork lengths (cm), length frequencies, and the percent of fish larger than the length of 50% maturity to assess overall changes in fish sizes between 1995–98 and 2012–14 data sets. We used Welch's t-test ($\alpha = 0.05$) to compare mean fork lengths of the six most abundant species in both of the time periods combined. Lengths from the 1995–98 data set were converted from total length to fork length using previously published methods (Echeverria and Lenarz 1984; Laidig et al. 1997). Data from Wyllie Echeverria (1987) and Silberberg et al. (2001) provided estimates for length of 50% maturity for species in the geographic region where we collected data. We used a Kolmogorov-Smirnov two-sample test to examine if the length frequency distributions were similar between the 1995–98 and 2012–14 data sets for yellowtail rockfish (*S. flavidus*), canary rockfish (*S. pinniger*), and widow rockfish (*S. entomelas*). Yellowtail rockfish lengths were analyzed because they were exceptionally abundant in field surveys. Canary and widow rockfish were analyzed because they were both federally listed as overfished species and are focal species for management. Statistical analyses were performed in JMP and R (JMP 2012, R Core Team 2014).

RESULTS

The 1995–98 and 2012–14 data sets were comparable in both effort (fishing drifts) and measured fishes in all three regions (tables 1 and 2). For length analyses, we used 6,928 fishes from the 1995–98 data set and measured a total of 7,781 fishes between 2012–14 (table 2).

Species Compositions

Yellowtail rockfish was the most abundant species (measured by mean CPUE) in both the 1995–98 and

TABLE 1
Number of individual fishing drifts by region and site used for CPUE analyses comparing the historical fishing data set (1995–98) and the new data set (2012–14).

		No. of Drifts	
Region	Site	1995–98	2012–14
Cordell Bank	Deep	69	37
	Shallow	61	24
Farallon Islands	RCA	41	30
	REF	42	54
Half Moon Bay	RCA	62	35
	REF	43	59

TABLE 2
Number of fishing trips and counts of fish lengths used in analyses of the historical fishing data set (1995–98) and the new data set (2012–14).

		Fishing Trips		Count of Fish Lengths	
Region	Site	1995–98	2012–14	1995–98	2012–14
Cordell Bank	Deep	8	9	1584	978
	Shallow	6	9	1160	1661
Farallon Islands	RCA	3	8	793	1051
	REF	4	10	985	1169
Half Moon Bay	RCA	11	10	1854	1465
	REF	3	10	552	1457

the 2012–14 data sets (fig. 2). Yellowtail rockfish comprised the largest percentage of CPUE at all sites except the Farallon Islands and Half Moon Bay reference sites in 1995–98, where blue rockfish (*S. mystinus*) were more abundant (fig. 2). The six most abundant species across all regions in the 1995–98 data set were: yellowtail rockfish, blue rockfish, canary rockfish, rosy rockfish (*S. rosaceus*), chilipepper (*S. goodei*), and widow rockfish. Five of these species were also the most abundant in the 2012–14 sampling, although the order of abundance shifted to yellowtail rockfish, blue rockfish, canary rockfish, widow rockfish, rosy rockfish, and lingcod. Species compositions between the 1995–98 and 2012–14 data sets at each site appeared to be more similar than comparisons of paired RCA and reference sites within a region, or deep and shallow sites at Cordell Bank (fig. 2).

Changes in Catch Rates

Farallon Islands and Half Moon Bay Relative to the pre-closure 1995–98 period, total catch rates inside and outside the RCA were significantly higher ($p \leq 0.05$) in the 2012–14 period (fig. 3). This difference was in part attributable to a twofold to threefold increase in the catch

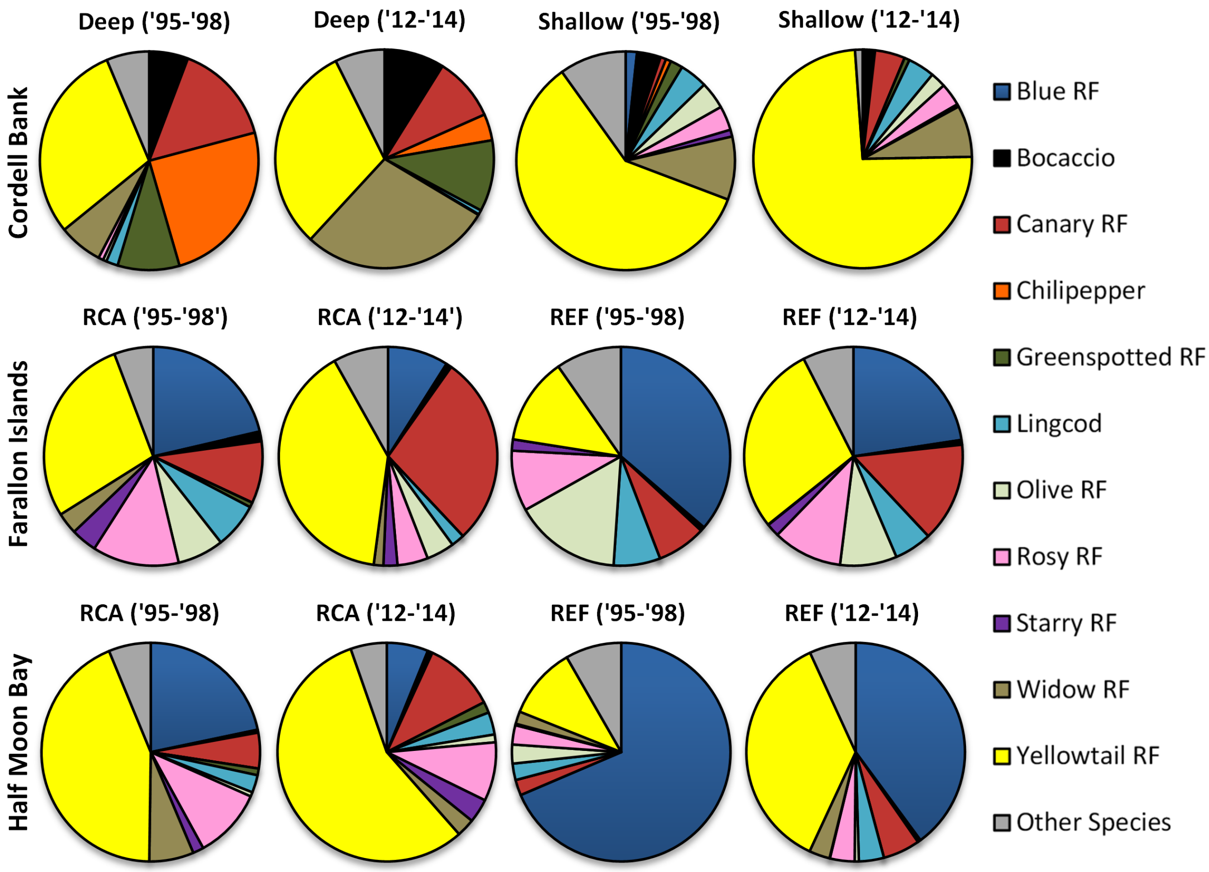

Figure 2. Species compositions calculated as fraction of total CPUE (catch per angler per hour) by site for the historical data set (1995–98) and our recent data set (2012–14) for the 11 most abundant species.

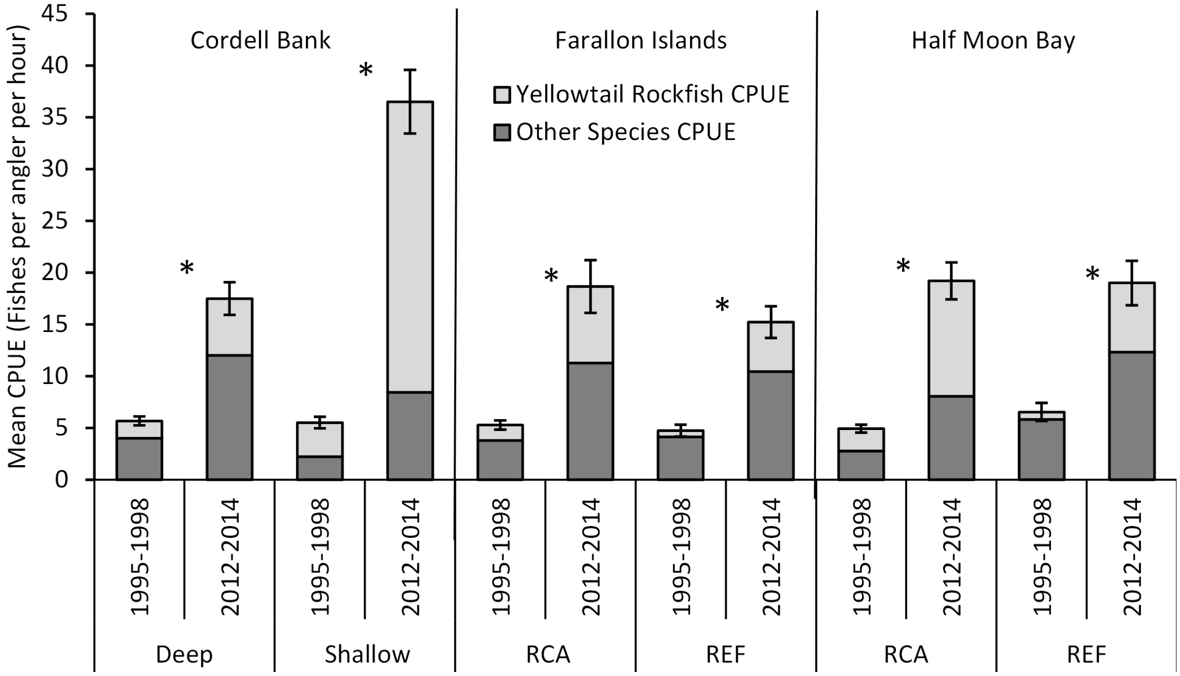

Figure 3. Mean total CPUE (all species caught per angler per hour) shown by site and period of data collection. Yellowtail rockfish CPUE is displayed separately as it represented the single largest proportion of any species caught. Error bars show the standard error of total CPUE. Asterisks indicate a significant mean difference between CPUE for all species combined as well as CPUE without yellowtail rockfish at each site between the 1995–98 and 2012–12 data sets (α = 0.05).

of yellowtail rockfish. However, CPUE was still significantly higher (at some sites doubled) in recent years even when discounting yellowtail rockfish catch (fig. 3). We found significant increases and no significant decreases in CPUE at various sites for all six species (yellowtail rockfish, blue rockfish, canary rockfish, widow rockfish, rosy rockfish, and lingcod) between the 1995–98 and 2012–14 data sets (fig. 4). Canary and yellowtail rockfish CPUE were greater in the 2012–14 data set in all sites at the Farallon Islands and Half Moon Bay (fig. 4).

When comparing total CPUE within each time period we found no significant differences between RCA and reference sites in the Farallon Islands or Half Moon Bay regions (table 3). However, relative differences in CPUE between the RCA and reference sites for individual species changed over time. For example, there was no significant difference in canary rockfish CPUE between the RCA and reference sites in the 1995–98 data set, but the 2012–14 data set showed higher CPUE of canary rockfish in the RCA at both the Farallon Islands and Half Moon Bay regions (fig.4, table 4). Conversely, some trends remained the same in the 1995–98 and 2012–14 data sets. In the Half Moon Bay region, rosy rockfish were more abundant in the RCA and blue rockfish were more abundant in the reference site in both time periods (fig. 4, table 4).

Cordell Bank Similar to the Farallon Islands and Half Moon Bay, total CPUE increased dramatically ($p \leq 0.05$) in both the deep and shallow sites in the 2012–14 data set compared to the 1995–98 data set at Cordell Bank (fig. 3). The shallow site exhibited the greatest increase of all sites in mean CPUE (by approximately six-fold) between the two time periods. Yellowtail rockfish CPUE comprised the majority of this difference (fig. 3). Additionally, compared to the 1995–98 data set, the mean CPUE of lingcod and rosy rockfish at the shallow site and canary rockfish and widow rockfish at the deep site significantly increased in the 2012–14 period (fig. 4). As at the Farallon Islands and Half Moon Bay sites, no significant decreases in CPUE occurred over time at either Cordell Bank site.

For the comparisons between the deep and shallow sites at Cordell Bank, no difference was observed within

TABLE 3

Mean total CPUE differences (Diff.) at sites within each data set, with p-values and degrees of freedom (df). Positive values indicate greater CPUE at deep sites (Cordell Bank) or inside the RCA (Farallon Islands and Half Moon Bay), while negative values denote greater CPUE in shallow/REF sites. Significant differences are shown in bold ($p \leq 0.05$).

	1995–98			2012–14		
Region	Diff. in mean CPUE	p-value	df	Diff. in mean CPUE	p-value	df
Cordell Bank	0.16	0.82	116	**–19.00**	**0.00**	34
Farallon Islands	0.55	0.46	77	3.43	0.25	49
Half Moon Bay	–1.60	0.10	59	0.20	0.94	86

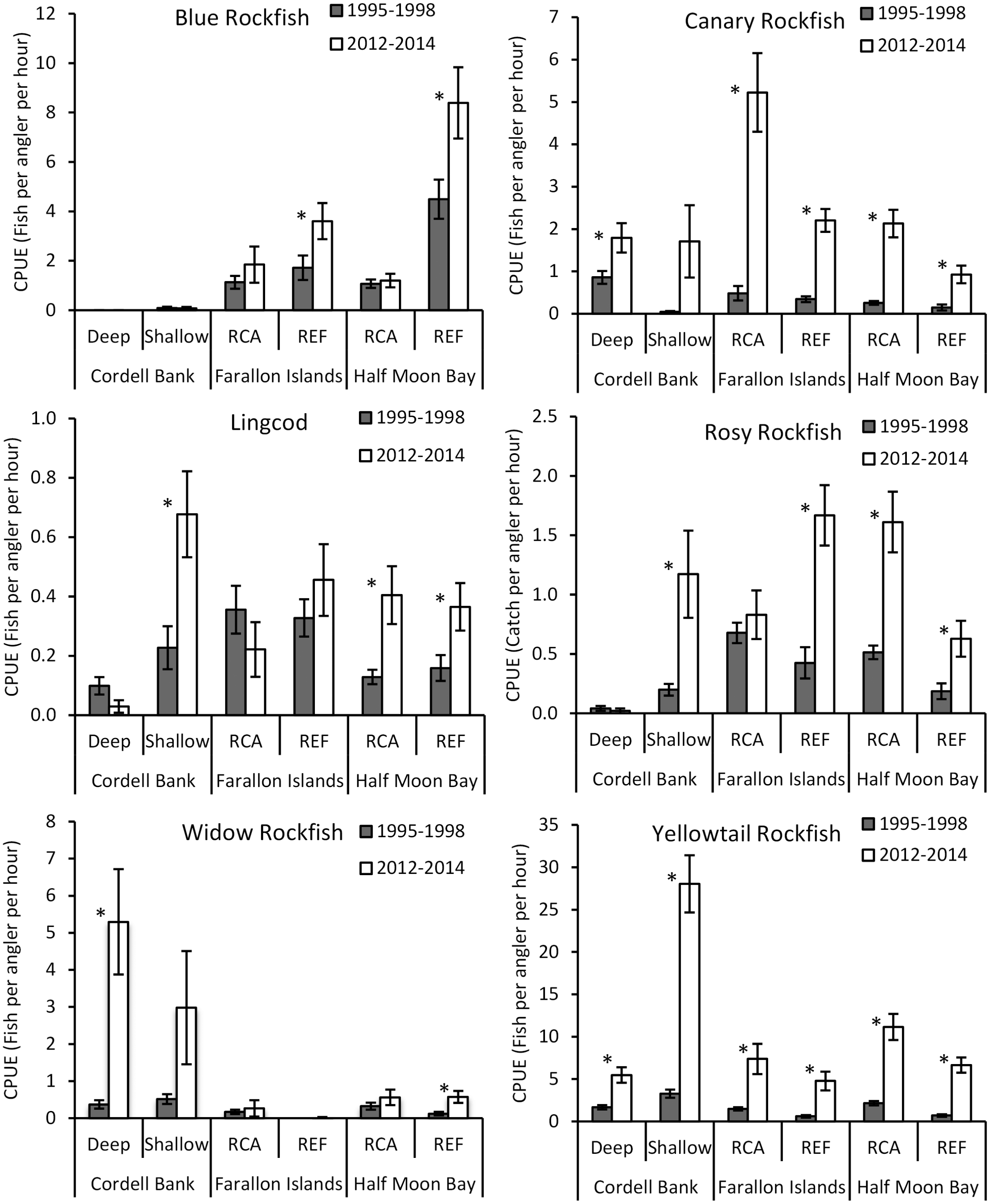

Figure 4. Changes in CPUE of the six most abundant species caught in both the old data set (1995–98) and new data set (2012–14). Error bars represent one standard error from the mean. Asterisks denote significant differences between old and new mean CPUE at each site ($\alpha = 0.05$).

the 1995–98 data set, whereas total CPUE was higher in the shallow site in 2012–14 (fig. 3, table 3). For individual species, canary rockfish were more abundant in the deep site in the 1995–98 data set but did not differ between deep and shallow sites in the 2012–14 data set (fig. 4, table 4). Yellowtail and rosy rockfish remained more abundant in the shallow site in both the 1995–98 and 2012–14 data sets (fig. 4, table 4).

Changes in Size of Fishes

Farallon Islands and Half Moon Bay Mean fork lengths and sample sizes for the top six species at each

TABLE 4

Comparisons of CPUE between RCA and reference sites within the old 1995–98 data set (A) and 2012–14 data set (B) for the six most abundant species across both data sets. Comparisons at Cordell Bank are between "shallow" and "deep" sites. Positive differences in mean CPUE indicate more fish in the RCA/deep site whereas negative values indicate more fish in the REF/shallow site. All significant results are shown in bold (p ≤ 0.05).

(A)

	Blue Rockfish			Canary Rockfish			Lingcod		
1995–98	Diff. in mean CPUE	p-value	df	Diff. in mean CPUE	p-value	df	Diff. in mean CPUE	p-value	df
Cordell Bank	–0.09	0.06	60	**0.81**	**0.00**	70	–0.13	0.10	79
Farallon Islands	–0.59	0.30	62	0.14	0.46	52	0.03	0.79	76
Half Moon Bay	**–3.42**	**0.00**	46	0.11	0.20	74	–0.03	0.54	67

	Rosy Rockfish			Widow Rockfish			Yellowtail Rockfish		
	Diff. in mean CPUE	p-value	df	Diff. in mean CPUE	p-value	df	Diff. in mean CPUE	p-value	df
Cordell Bank	**–0.16**	**0.00**	81	–0.15	0.41	123	**–1.60**	**0.00**	94
Farallon Islands	0.25	0.11	70	**0.17**	**0.01**	40	**0.88**	**0.00**	73
Half Moon Bay	**0.33**	**0.00**	92	0.21	0.06	89	**1.46**	**0.00**	95

(B)

	Blue Rockfish			Canary Rockfish			Lingcod		
2012–14	Diff. in mean CPUE	p-value	df	Diff. in mean CPUE	p-value	df	Diff. in mean CPUE	p-value	df
Cordell Bank	–0.08	0.16	22	0.08	0.93	29	**–0.65**	**0.00**	23
Farallon Islands	–1.75	0.09	73	**3.02**	**0.00**	33	–0.23	0.13	81
Half Moon Bay	**–7.19**	**0.00**	59	**1.20**	**0.00**	58	0.04	0.75	71

	Rosy Rockfish			Widow Rockfish			Yellowtail Rockfish		
	Diff. in mean CPUE	p-value	df	Diff. in mean CPUE	p-value	df	Diff. in mean CPUE	p-value	df
Cordell Bank	**–1.15**	**0.00**	22	2.32	0.27	51	**–22.57**	**0.00**	25
Farallon Islands	**–0.84**	**0.01**	80	0.25	0.26	28	2.59	0.22	50
Half Moon Bay	**0.98**	**0.00**	54	–0.01	0.96	68	**4.48**	**0.02**	54

site in each period are reported in table 5. In contrast to the clear increase in CPUE over time, patterns in fish size were more variable between regions. For example, compared to the 1995–98 data set in Half Moon Bay, mean lengths of yellowtail rockfish were larger during the 2012–14 period both inside and outside the RCA. However, the opposite trend was observed at the Farallon Islands, where mean yellowtail rockfish lengths were significantly larger (p ≤ 0.05) in the 1995–98 period both inside and outside the RCA (table 6). Results from Kolmogrov-Smirnov two-sample test showed that length distributions of yellowtail rockfish were different at all sites between the 1995–98 period and the 2012–14 period (p ≤ 0.05). Almost all of the yellowtail rockfish caught both inside and outside the RCA at the Farallon Island and Half Moon Bay regions in the 2012–14 data set were below the length at 50% maturity (fig. 5A and fig. 6). Similarly, most canary rockfish caught in both the Farallon Islands and Half Moon Bay regions were smaller than the length at 50% maturity and were distributed similarly across size classes between the two time periods (fig. 5B and fig. 6). Mean lengths of widow rockfish were significantly larger (p ≤ 0.05) in the Half Moon Bay RCA in the 2012–14 period (3.8 cm larger mean size), but the majority of the widow rockfish caught from 2012–14 at Half Moon Bay and the Farallon Islands were smaller than the size at 50% maturity (fig. 5C and fig. 6). The mean length of lingcod was greater in the 1995–98 data set than the 2012–14 data set both inside and outside the RCA at the Farallon Islands as well as outside the RCA in Half Moon Bay (table 6).

In general, the mean lengths of species in both the 1995–98 and the 2012–14 data sets were larger in the RCA than in the reference sites at the Farallon Islands and Half Moon Bay (table 7). In both data sets, the mean lengths of blue, canary, and yellowtail rockfish were greater in the RCA than in the reference site (table 7). Additionally, in the 2012–14 data set, mean length of

Figure 5 (on following page). Yellowtail (A), Canary (B), and Widow (C) rockfish length frequencies by region and site. Lengths (x-axis) are classified by two cm bins of fork length. Length frequencies are normalized and displayed as the proportion of fish in each length bin (y-axis). Vertical dashed lines indicate fork length at 50% maturity; 35 cm, 42 cm, 35 cm respectively, converted from total lengths in Wyllie Echeverria (1987) using methods from Echeverria and Lenarz (1984). Asterisks indicate results from Kolmogorov-Smirnov two-sample test of differences in distributions between the old data set (1995–98) and new data set (2012–14). ** p ≤ 0.001, *p ≤ 0.05. See Table 5 for sample sizes.

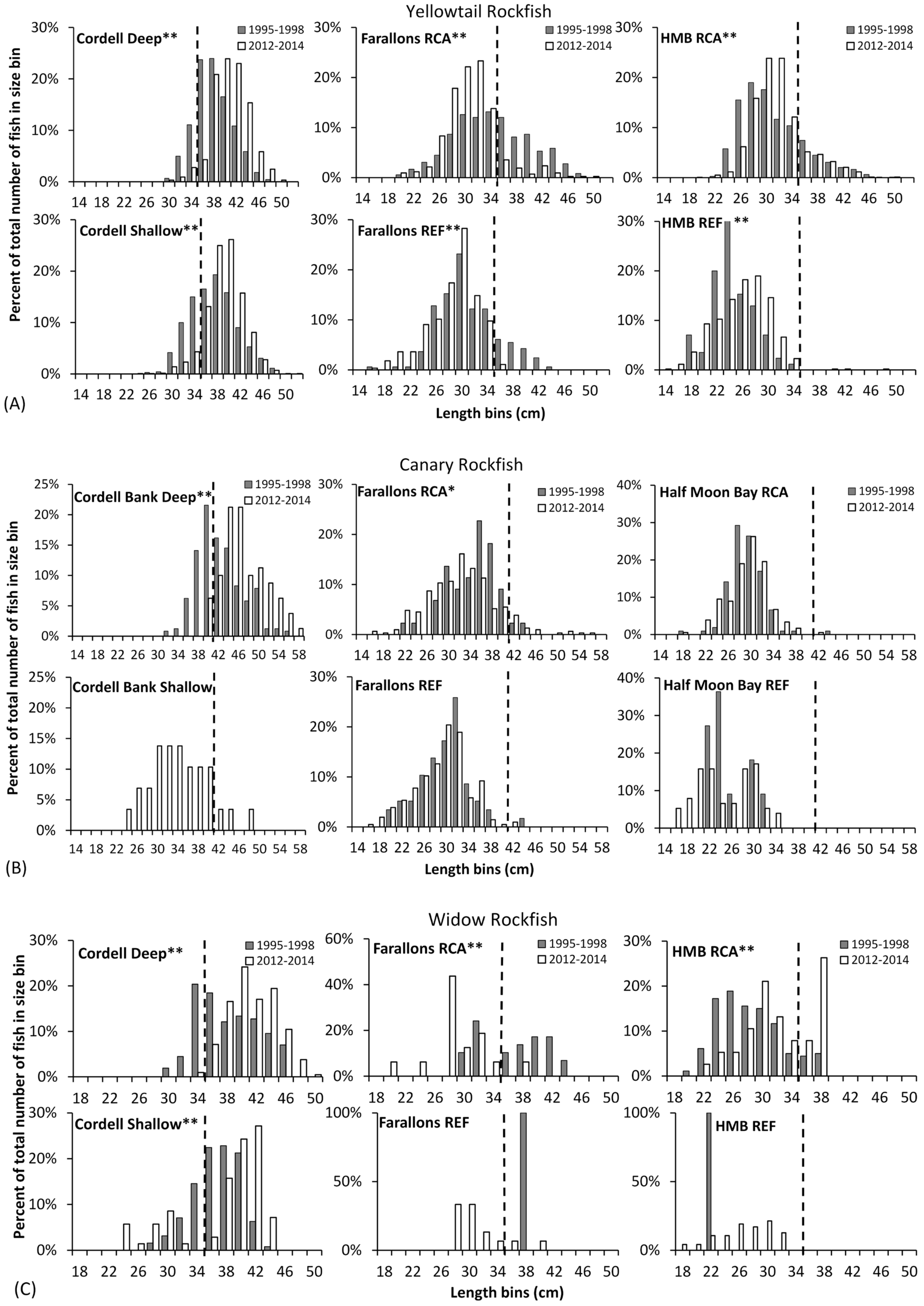
Yellowtail Rockfish
Cordell Deep**
Farallons RCA**
HMB RCA**
Cordell Shallow**
Farallons REF**
HMB REF **
1995-1998
2012-2014
Percent of total number of fish in size bin
Length bins (cm)
(A)
Canary Rockfish
Cordell Bank Deep**
Farallons RCA*
Half Moon Bay RCA
Cordell Bank Shallow
Farallons REF
Half Moon Bay REF
(B)
Widow Rockfish
Cordell Deep**
Farallons RCA**
HMB RCA**
Cordell Shallow**
Farallons REF
HMB REF
(C)
0%
10%
20%
30%
40%
50%
60%
100%
5%
15%
25%
14 18 22 26 30 34 38 42 46 50 54 58

TABLE 5
Number (n) of fish measured and mean fork length (cm) by site and years of data collection. Species shown are the six most abundant species caught in both old and new data sets.

			Blue Rockfish			Canary Rockfish			Lingcod			Rosy Rockfish			Widow Rockfish			Yellowtail Rockfish		
Region	Site	Data set	mean size (cm)	SE	n	mean size (cm)	SE	n	mean size (cm)	SE	n	mean size (cm)	SE	n	mean size (cm)	SE	n	mean size (cm)	SE	n
Cordell Bank	Deep	1995–98	—	—	—	43.5	0.3	241	70.8	1.5	16	23.9	1.6	7	39.4	0.3	157	39.0	0.2	442
		2012–14	—	—	—	47.7	0.5	80	77.0	3.9	8	22.5	0.7	3	42.1	0.2	211	41.6	0.2	326
	Shallow	1995–98	33.7	0.4	79			—	70.2	0.8	7	22.2	0.9	7	37.9	0.2	254	38.4	0.2	720
		2012–14	35.0	1.0	11	35.0	0.7	58	59.6	1.1	69	20.9	0.4	54	38.3	0.7	70	40.0	0.1	1297
Farallon Island	RCA	1995–98	32.6	0.3	224	35.6	0.7	44	68.5	2.2	17	21.3	0.4	48	37.9	0.9	29	35.4	0.3	357
		2012–14	31.0	0.5	95	33.0	0.4	310	47.7	2.6	23	21.6	0.4	46	29.8	1.0	16	31.7	0.2	420
	REF	1995–98	29.1	0.2	454	33.0	0.6	58	66.3	1.4	32	23.2	0.3	56	40.0	—	1	32.1	0.4	164
		2012–14	29.5	0.2	276	31.9	0.3	206	49.8	1.0	82	23.0	0.2	114	29.5	—	1	29.4	0.2	276
Half Moon Bay	RCA	1995–98	29.2	0.2	526	32.6	0.3	106	70.6	2.0	23	20.5	0.3	54	29.3	0.3	180	32.0	0.2	779
		2012–14	33.8	0.3	103	32.1	0.3	179	56.3	1.3	45	20.5	0.2	111	33.1	0.8	38	32.5	0.1	776
	REF	1995–98	27.0	0.2	412	28.3	1.1	11	57.1	0.5	2	21.5	0.1	2	22.6	—	1	25.6	0.4	85
		2012–14	27.0	0.2	573	27.5	0.6	76	54.2	1.5	52	19.6	0.3	57	27.6	0.6	47	26.8	0.2	527

widow rockfish was greater in the RCA than in the reference site in Half Moon Bay.

Cordell Bank The highest percent of mature yellowtail rockfish in both data sets were observed at Cordell Bank (fig. 5A and fig. 6). Additionally, compared to 1995–98, the mean lengths of yellowtail rockfish were significantly larger ($p \leq 0.05$) in 2012–14 in both the deep and shallow sites (table 6). The Cordell Bank deep site was the only site with more than 10% of canary rockfish that were greater than the length at 50% maturity (fig. 5B and fig. 6). Canary rockfish were an average of 12.8 cm larger in the deep site than the shallow site in the 2012–14 data set (table 7). Compared to the 1995–98 data set, the six most abundant species had a higher percentage of fishes over the length at 50% maturity at Cordell Bank in the 2012–14 data set; however, this trend was not seen in the Farallon Islands and Half Moon Bay regions (fig. 6).

DISCUSSION

Overall, catch rates in the 2012–14 period were two to six times higher (depending on the site) than those observed in the 1995–98 period, suggesting striking increases in total abundance of demersal species in central California shelf habitats. Significant increases, at least at some of the sites, were observed for three of the species designated as overfished prior to establishment of the RCAs; canary rockfish, widow rockfish, and lingcod (other overfished species are typically uncommon at the depths included in our study). Our sampling in 2012–14 was designed to mimic the CDFW 1990s effort as closely as possible to allow direct comparison of CPUE. Although the gear used in the earlier study was not explicitly recorded by observers, we believe our assumption of five-hook gangions is reasonable and possibly conservative since there was no hook limit in effect at that time. If a high proportion of anglers were using more than five-hook gangions then our results would underestimate the extent of the increase in CPUE.

The marked increase in rockfish and other demersal species in the last decade is consistent with many other sources of fishery dependent data sets, fishery independent data sets, and stock assessment results (e.g., Wallace and Cope 2011; Field 2013; Cope et al. 2013). For example, the abundance of lingcod in California waters was estimated to be at less than 10% of the unfished level in 1998 (the last year of the CDFW study), but above 70% by 2009 (Hamel et al. 2009). In this study, catch rates of Lingcod were greater in the recent period, although their magnitude varied spatially. However, the specific causes of the increased abundance for any given species or region are difficult to conclusively identify, as even with stock assessment models there are no analyses of the relative abundance or contribution to new recruitment

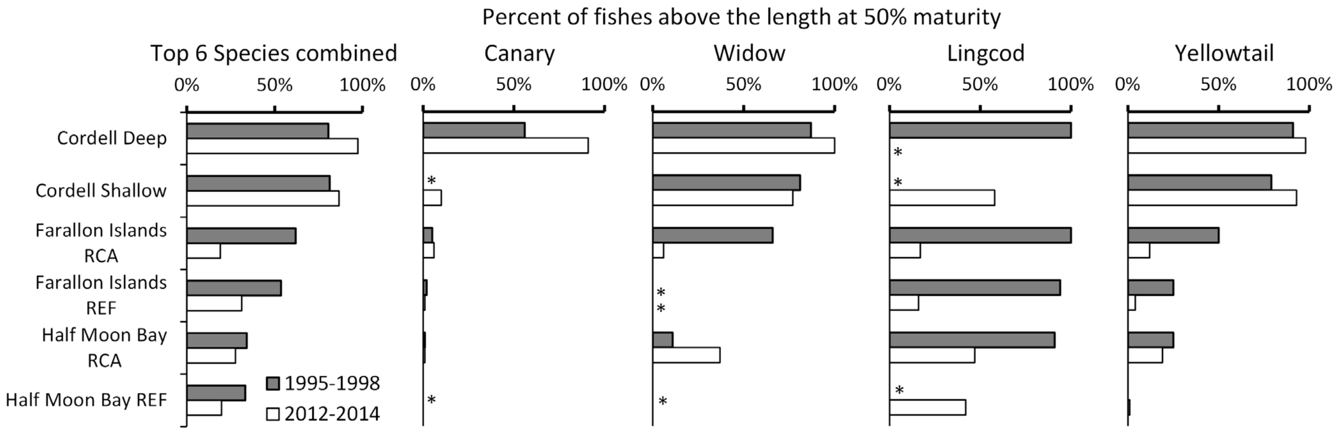

Figure 6. Summary of the percent of fishes caught at each site that were above the length of 50% maturity (Wyllie Echeverria 1987). The combined six species reported here are: canary, widow, yellowtail, blue, and rosy rockfish and lingcod. Asterisks indicate sites at which species counts were less than 15 individual fish.

TABLE 6

Differences in mean fork length between the 1995–98 and 2012–14 data sets and associated p-values for all areas and sites sampled. Positive differences indicate an increase in mean length in the 2012–14 data set, and negative values indicate a decrease in mean length in the 2012–14 data set. All significant results are shown in bold (p ≤ 0.05). Species shown are the top six most abundant species across both data sets.

		Blue Rockfish			Canary Rockfish			Lingcod		
Region	Site	Diff. in mean (cm)	p-value	df	Diff. in mean (cm)	p-value	df	Diff. in mean (cm)	p-value	df
Cordell Bank	Deep	N/A	—	—	**4.2**	**0.00**	142	6.2	0.17	9
	Shallow	1.2	0.29	13	N/A	—	—	**–10.6**	**0.00**	36
Farallon Islands	RCA	**–1.6**	**0.00**	155	**–2.7**	**0.00**	69	**–20.9**	**0.00**	37
	REF	**0.4**	**0.00**	293	–1.12	0.11	100	**–16.5**	**0.00**	63
Half Moon Bay	RCA	**4.6**	**0.00**	156	–0.5	0.25	240	**–14.3**	**0.00**	39
	REF	0	0.97	926	–0.8	0.54	16	N/A	—	—
		Rosy Rockfish			Widow Rockfish			Yellowtail Rockfish		
Region	Site	Diff. in mean (cm)	p-value	df	Diff. in mean (cm)	p-value	df	Diff. in mean (cm)	p-value	df
Cordell Bank	Deep	N/A	—	—	**2.7**	**0.00**	288	**2.6**	**0.00**	716
	Shallow	N/A	—	—	0.4	0.59	80	**1.6**	**0.00**	1249
Farallon Islands	RCA	0.3	0.60	92	**–8.1**	**0.00**	35	**–3.6**	**0.00**	628
	REF	–0.2	0.60	112	N/A	—	—	**–2.8**	**0.00**	293
Half Moon Bay	RCA	–0.1	0.85	103	**3.8**	**0.00**	50	**0.5**	**0.03**	1498
	REF	N/A	—	—	N/A	—	—	**1.2**	**0.00**	130

from fish inside versus outside of closed areas. Consequently, the observation that catch rates have increased both inside and outside of the RCAs could be an indication that either spillover and larval export effects are more than compensating for continued fishing removals in the outside sites, or could simply represent improved recruitment throughout the broader region occupied by lingcod and rockfish. The continuity of the RCA along the entire West Coast and the overall areal extent of the closure provided a high potential for reproductive contributions from inside and outside sites, but overall reductions in fishing mortality rates have clearly contributed to direct population increases of the shelf species whose habitats are closed to fishing. In addition to the additive benefits of these management actions that closed habitats and reduced fishing mortality, ocean conditions through the late 1990s tended to be associated with poor recruitment, whereas a greater fraction of years from 1999 through the period of this study (particularly the 2008–14) have been associated with strong recruitment and reproductive success, with strong year classes often occurring synchronously among species (Ralston et al. 2013; Stachura et al. 2014; Leising et al. 2014). While our results clearly document and quantify the improved status of demersal species in the surveyed regions, the subsequent link to specific management actions or ocean-driven changes in recruitment success is beyond the scope of our analysis.

Although all of our sites were within a relatively small section of the US West Coast, there were clear spatial

TABLE 7

Differences in mean fork length inside and outside the RCA within the 1995–98 data set (A) and the 2012–14 data set (B) for the six most abundant species across both data sets. Comparisons at Cordell Bank are between "shallow" and "deep" sites. Positive differences indicate greater mean fork lengths in deep/RCA sites, whereas negative values indicate smaller fork lengths in RCA/deep sites. All significant results are shown in bold (p ≤ 0.05).

(A)

	Blue Rockfish			Canary Rockfish			Lingcod		
1995–98	Diff. in mean (cm)	p-value	df	Diff. in mean (cm)	p-value	df	Diff. in mean (cm)	p-value	df
Cordell Bank	N/A	—	—	N/A	—	—	0.6	0.69	21
Farallon Islands	**3.6**	**0.00**	511	**2.6**	**0.00**	93	2.2	0.39	29
Half Moon Bay	**2.2**	**0.00**	873	**4.3**	**0.00**	11	N/A	—	—

	Rosy Rockfish			Widow Rockfish			Yellowtail Rockfish		
	Diff. in mean (cm)	p-value	df	Diff. in mean (cm)	p-value	df	Diff. in mean (cm)	p-value	df
Cordell Bank	N/A	—	—	1.5	0.05	267	**0.6**	**0.00**	1077
Farallon Islands	**–1.9**	**0.00**	89	N/A	—	—	**0.1**	**0.00**	389
Half Moon Bay	N/A	—	—	N/A	—	—	**6.5**	**0.00**	126

(B)

	Blue Rockfish			Canary Rockfish			Lingcod		
2012–14	Diff. in mean (cm)	p-value	df	Diff. in mean (cm)	p-value	df	Diff. in mean (cm)	p-value	df
Cordell Bank	N/A	—	—	**12.8**	**0.00**	103	**17.4**	**0.00**	8
Farallon Islands	**1.5**	**0.00**	163	**1.1**	**0.02**	495	–2.2	0.44	28
Half Moon Bay	**6.8**	**0.00**	150	**4.6**	**0.00**	108	2.1	0.28	94

	Rosy Rockfish			Widow Rockfish			Yellowtail Rockfish		
	Diff. in mean (cm)	p-value	df	Diff. in mean (cm)	p-value	df	Diff. in mean (cm)	p-value	df
Cordell Bank	N/A	—	—	**1.6**	**0.00**	84	**1.6**	**0.00**	521
Farallon Islands	**–1.4**	**0.00**	75	N/A	—	—	**2.4**	**0.00**	618
Half Moon Bay	**0.8**	**0.00**	123	**0.8**	**0.00**	71	**5.7**	**0.00**	1094

differences in species compositions and catch rates. After accounting for the differences in relative abundance over the two time periods (1995–98, 2012–14), differences in catch rates were the largest among regions, likely reflecting differences in ocean and/or habitat conditions, with more modest differences in catch rates inside and outside of the recreational RCA boundary. This is consistent with work presented by Starr et al. (2015), who used comparable hook and line fishing inside and outside of the newly created State Marine Protected Areas (MPAs), and showed that area-specific and temporal trends in catch rates tended to be greater than the differences in catch rates inside and outside of MPAs. Over longer time scales differences between closed and open fishing areas are expected to increase, as Starr et al. (2015) found greater differences between exploited areas and adjacent habitats that had been protected for over 20 years as compared to seven years.

The very dramatic increase in catch rates of yellowtail rockfish, which accounted for the overwhelming majority of fishes encountered in this study, is particularly interesting. Although this stock is more abundant and more important to commercial fisheries north of Cape Mendocino, this species was historically a key component of recreational fisheries in central and northern California. Following the implementation of the RCAs, which closed most of the yellowtail rockfish habitat to fishing, catches have been very modest (the average central California catches in 2003–12 period were 12% of the 1993–2002 average, based on catch data reported in Cope et al. 2013). Due to a paucity of fishery-independent data, a stock assessment for yellowtail rockfish has never been conducted south of Cape Mendocino, yet the stock is assumed to be healthy (well above target levels) north of Cape Mendocino (Cope et al. 2013) and the data-poor methods applied to the central California stock have indicated that the stock is above target levels and that both historical and recent catches are far below sustainable levels (Dick and MacCall 2010). Similar to yellowtail rockfish, catch rates of canary rockfish at both the Farallon Islands and Half Moon Bay regions have also increased considerably between the 1995–98 and 2012–14 time period. Our study showed that most canary rockfish tended to be less than the 50% maturity length, which is consistent with earlier stock assessment results that indicated patchiness in the distribution of small canary rockfish relative to larger individuals, with the central California region including a greater fraction of smaller and immature individuals (Wallace and Cope 2011). Given this pattern, the increase in catch rates of canary rockfish indicates strong recruitment in recent years, which is also consistent with results from trawl surveys, stock assessments and pre-recruit surveys (Wallace and Cope 2011; Ralston et al. 2013; Thorson and Wetzel 2015). As it has been shown that catch rates for some rockfish species in recreational fisheries increase substantially following strong recruitment events (Field et al. 2010). More detailed investigations into the interaction between strong recruitment events and catch rates in the recreational fishery should be explored; particularly canary rockfish is a key constraining species for the recreational fishery in this region.

A primary objective of spatial closures is to allow enhanced survival and aging of long-lived species, with the expected result of increased fish sizes. However, recovery of overfished species will be reflected by decreases in mean size as high abundances of juveniles recruit to the population. The conflicting shifts in fish size over time for the most abundant species in this study may reflect the occurrence of both processes. At the Cordell deep site, shifts to larger sizes over time were significant for canary rockfish, widow rockfish, and yellowtail rockfish, and there was a trend toward larger sizes for lingcod. In both data sets the majority of fish at this site were mature adults, potentially suggesting that higher recruitment in recent years would not be evident as young fish have not yet migrated to deeper habitats (Lea et al. 1999; Love et al. 2002). Likewise, at the deeper shelf and slope habitats examined by Keller et al. (2014), fish sizes tended to be larger within the RCAs compared to areas open to trawling. At our other, shallower sites, lingcod sizes decreased markedly over time, presumably indicating successful recruitment. In particular, the 1999 year class was exceptionally strong for Lingcod and likely contributed to our recent catches. In contrast, the dominance of mature lingcod in the late 1990s likely reflected the poor recruitment observed for that stock during that period (Hamel et al. 2009). Canary rockfish likewise were generally smaller in size in the 2012–14 data set and mostly composed of immature fish at all sites other than the Cordell deep site, suggesting successful recruitment and a shift to predominantly younger fish in recent years. Other species had inconsistent shifts in fish size over time at the shallower sites, potentially reflecting a mix of increased survival of older fish and increased recruitment of juveniles.

Because RCAs are depth-based closures, comparisons between the RCA and reference sites at the Farallon Islands and Half Moon Bay for both catch rate and length data may be confounded by depth and habitat differences that influence the distribution of fishes, as many rockfish (as well as lingcod and many other groundfishes), exhibit ontogenetic migrations to deeper water as they increase in size and age (Lea et al. 1999; Love et al. 2002; Love et al. 2009). For that reason, the mean fish length of a given population within a more shallow depth range is likely to decline and their abundance increase in response to strong recruitment events, as those individuals initially recruit to shallower habitats (Love el al. 2009; Jaworski et al. 2010). Our selection of reference sites was somewhat constrained to slightly shallower water since RCA boundaries are generally based on depth. Some efforts to mitigate for these depth differences were taken by attempting to select reference sites closer to RCA boundaries and in more comparable depths where possible, but even slight differences in depth may be influential to our results. For example, blue rockfish typically reside in shallower depths than the other species sampled in our study. At both Half Moon Bay and the Farallon Islands, Blue Rockfish were more abundant at the reference sites than the RCA sites both before and after the RCAs were implemented, and increases in CPUE over time were only evident at the reference sites. The slightly deeper depths of the RCA sites may have reduced the habitat suitability for blue rockfish in contrast to the other species. Similarly, our results showed that both before RCA implementation and ten years after, mean lengths of yellowtail, canary, and blue rockfish were greater inside the RCA, suggesting an ontogenetic pattern unrelated to the fishing closure. Given that the deeper waters were open to fishing historically and are closed now, it is not possible to fully decouple possible reserve effects from the effects of ontogenetic migration and strong recruitment pulses, thus complicating the hypothesis that fish lengths will increase in closed areas as fish are allowed to age and grow.

Regardless of whether or not the trends observed are due to management protection, our results are consistent with stock assessments and others studies demonstrating a strong and sustained recovery of rockfish and other groundfish, and indicate that the existing RCAs tend to be populated by larger individuals, which may have a higher reproductive capacity (Sogard et al. 2008: Hixon et al. 2014). As such, these data will be useful for future stock assessments, as well as for finer-scale evaluations of changes in species composition and spatial variability in both abundance and recruitment. Future analyses are anticipated in combination with analysis of ongoing observer program data, which, combined with these results, should help to address questions relating to stock structure and distribution and lead to improvements and refinements to ongoing spatially explicit management decisions.

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LITERATURE CITED

Berkeley, S. A., M. A. Hixon, R. J. Larson, and M. S. Love. 2004. Fisheries sustainability via protection of age structure and spatial distribution of fish populations. Fisheries. 29: 23–32.

Beyer, S. G., S. M. Sogard, C. J. Harvey, and J. C. Field. 2015. Variability in rockfish (*Sebastes* spp.) fecundity: species contrasts, maternal size effects, and spatial differences. Env. Bio. Fish. 98:81–100.

Cope, J., E. J. Dick, A. D. MacCall, M. Monk, B. Soper, and C. Wetzel. 2013. Data-moderate stock assessments for brown, China, copper, sharpchin, stripetail, and yellowtail rockfishes and English and rex soles in 2013. Stock Assessment and Fishery Evaluation, Pacific Fishery Management Council: Portland, OR.

Dick, E. J., and A. D. MacCall. 2010. Estimates of sustainable yield for 50 data-poor stocks in the Pacific Coast groundfish fishery management plan. NOAA Technical Memorandum NMFS-SWFSC-460.

Field, J. C. 2013. Status of bocaccio, *Sebastes paucispinis*, in the Conception, Monterey and Eureka INPFC areas as evaluated for 2013. Stock Assessment and Fishery Evaluation, Pacific Fishery Management Council: Portland, OR.

Field, J. C., A. D. MacCall, S. Ralston, M. Love, and E. Miller. 2010. Bocaccionomics: the effectiveness of pre-recruit indices for assessment and management of bocaccio. CalCOFI Rep. 51:77–90.

Echeverria, T., and W. H. Lenarz. 1984. Conversions between total, fork and standard length in 35 species of *Sebastes* from California. Fish. Bull. 82(1):249–251.

Hamel, O. S., S. A. Sethi, and T. F. Wadsworth. 2009. Status and future prospects for lingcod in waters off Washington, Oregon, and California as assessed in 2009. Stock Assessment and Fishery Evaluation, Pacific Fishery Management Council: Portland, OR.

Hixon, M. A., D. W. Johnson, and S. M. Sogard. 2014. BOFFFFs: on the importance of conserving old-growth age structure in fishery populations. ICES J. Mar. Sci. 71:2171–2185.

Jaworski, A., J. Solmundsson, and S. A. Ragnarsson. 2010. Fish assemblages inside and outside marine protected areas off northern Iceland: protection effects or environmental confounds? Fish Res. 102(1-2):50–59.

JMP®. 2012. Version v. 10.0.1. SAS Institute Inc., Cary, NC, USA.

Keller, A. A., W. W. Wakefield, C. E. Whitmire, B. H. Horness, M. A. Bellman, and K. L. Bosley. 2014. Distribution of demersal fishes along the US west coast (Canada to Mexico) in relation to spatial fishing closures (2003−11). Mar. Eco. Prog. Ser. 501:169–190.

Laidig, T. E., P. E. Adams, K. R. Silberberg, and H. E. Fish. 1997. Conversions between total, fork, and standard lengths for lingcod, *Ophiodon elongatus.* Calif. Fish Game 83(3):128–129.

Lea, R. N., R. D. McAllister, and D. A. VenTresca. 1999. Biological aspects of nearshore rockfishses of the genus Sebastes from central California. Calif. Dept. Fish and Game, Fish Bull. 177. Sacramento.

Leising, A. W., I. D. Schroeder, S. J. Bograd, E. Bjorkstedt, J. Field, K. Sakuma, J. Abell, R. R. Robertson, J. Tyburczy, W. Peterson, R. D. Brodeur, C. Barcelo, T. D. Auth, E. A. Daly, G. S. Campbell, J. A. Hildebrand, R. M. Suryan, A. J. Gladics, C. A. Horton, M. Kahru, M. Manzano-Sarabia, S. McClatchie, E. D. Weber, W. Watson, J. A. Santora, W. J. Sydeman, S. R. Melin, R. L. DeLong, J. Largier, S. Yong Kim, F. P. Chavez, R. T. Golightly, S. R. Schneider, P. Warzybok, R. Bradley, J. Jahncke, J. Fisher, and J. Peterson. 2014. State of the California Current 2013–14: El Niño looming. CalCOFI Rep. 55:51–87.

Lester, S. E., B. S. Halpern, K. Grorud-Colvert, J. Lubchenco, B. I. Ruttenberg, S. D. Gaines, S. Airame, and R. R. Warner. 2009. Biological effects within no-take marine reserves: a global synthesis. Mar. Ecol. Prog. Ser. 384:33-46.

Love, M. S., M. Yoklavich, and L. Thorsteinson. 2002. The Rockfishes of the Northeast Pacific. Berkeley, Los Angeles, London: University of California Press. 404 pp.

Love, M. S., M. Yoklavich, and D. M. Schroeder. 2009. Demersal fish assemblages in the Southern California Bight based on visual surveys in deep water. Environ. Biol. Fish. 84:55–68.

Mason, J., R. Kosaka, A. Mamula, and C. Speir. 2012. Effort changes around a marine reserve: The case of the California Rockfish Conservation Area. Mar. Pol. 36:1054–1063.

Melnychuk, M. C., J. A. Banobi, and R. Hilborn. 2013. Effects of management tactics on meeting conservation objectives for western North American groundfish fisheries. PLoS ONE 8:2: e56684.

PFMC (Pacific Fishery Management Council). 2003. Status of the Pacific Coast groundfish fishery through 2003 and stock assessment and fishery evaluation. Vol 1. Pacific Fishery Management Council, Portland, Oregon.

R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.

Ralston, S. 2002. West Coast groundfish harvest policy. N. Amer. J. Fish. Mgmt. 22:1:249–250.

Ralston, S., K. M. Sakuma and J. C. Field. 2013. Interannual Variation in Pelagic Juvenile Rockfish Abundance—Going With the Flow. Fish. Oceanogr. 22: 288–308.

Reilly, P., and D. Wilson-Vandenberg. 1999. Central and Northern California Commercial Passenger Fishing Vessel (CPFV) fisheries sampling Final performance report, grant F-50-R-11, Federal Aid in Sport Fish Restoration Act.

Ruxton, G. D. 2006. The unequal variance t-test is an underused alternative to Student's t-test and the Mann-Whitney U test. Behav. Ecol. 17(4):688–690.

Silberberg, K. R., T. E. Laidig, P. B. Adams, and D. Albin. 2001. Analysis of maturity in lingcod, *Ophiodon elongatus*. Calif. Fish. Game Fish Bull. 87:139–152.

Sogard, S. M., S. A. Berkeley, and R. Fisher. 2008. Maternal effects in rockfishes *Sebastes* spp.: a comparion among species. Mar. Ecol. Prog. Ser. 360:227–236.

Stachura, M. M., T. E. Essington, N. J. Mantua, A. B. Hollowed, M. A. Haltuch, P. D. Spencer, T. A. Branch, and M. J. Doyle. 2014. Linking Northeast Pacific recruitment synchrony to environmental variability. Fish. Oceanogr. 23:389–408.

Starr, R. M., D. E. Wendt, C. L. Barnes, C. I. Marks, D. Malone, G. Waltz, K. T. Schmidt, J. Chiu, A. L. Launer, N. C. Hall, and N. Yochum. 2015. Variation in responses of fishes across multiple reserves within a network of marine protected areas in temperate waters. PloS ONE 10:3: e0118502.

Thorson, J., and C. Wetzel. 2015. The status of canary rockfish (*Sebastes pinniger*) in the California Current in 2015. Stock Assessment and Fishery Evaluation, Pacific Fishery Management Council, Portland, OR.

Wallace, J. R., and J. M. Cope. 2011. Status update of the US canary rockfish resource in 2011. Stock Assessment and Fishery Evaluation, Pacific Fishery Management Council, Portland, OR.

Wyllie Echeverria, T. 1987. Thirty-four species of California rockfishes: maturity and seasonality of reproduction. Fish. Bull. 85:229–250.

ECONOMIC ATTRIBUTES OF STAYERS AND LEAVERS IN FOUR CALIFORNIA FISHERIES

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ABSTRACT

We use a simple regulatory event study approach to evaluate hypothesized economic attributes of California commercial fishermen who remain as active fishery participants ("stayers") following regulatory events that attenuate fishing opportunities. The attributes of greater revenue diversification from multi-fishery participation, lower interannual income variation, and higher annual gross fishing income are hypothesized to distinguish stayers from those who leave commercial fishing after a regulatory event. We find consistent and (in many but not all cases) significant associations as hypothesized between these economic attributes of commercial fishermen and their status as a stayer or a leaver, with interannual fishing income stability being the most consistently significant. In light of declining numbers of commercial fishermen in California, and the importance of multi-fishery participation in sustaining those who remain, policy makers should provide for flexible multi-fishery participation when designing fisheries regulations, where possible.

Attributes Distinguishing Stayers from Leavers

What attributes foster sustainability and resilience in the context of heightened restrictions on commercial fishing opportunities in California? As Marshall et al. (2007) note, knowledge of the properties that confer resilience can assist resource managers, communities and resource users to design and implement policies that minimize the impacts on people while maximizing the sustainability of ecosystem goods and services. Building on the seminal work of Holling (1973) on resilience in ecological systems, Marshall et al. use the term "social resilience" to refer to the flexibility with which resource users can cope and adapt to changes in resource policy.

In this paper we consider resilience in the context of persistence in commercial fishing. We use a simple regulatory event study approach to evaluate a number of hypothesized economic attributes of commercial fishers who remain as active fishery participants following regulatory events that attenuate fishing opportunities. Our focus is in evaluating economic characteristics that distinguish "stayers"—commercial fishermen who remain as active fishery participants in a fishery following regulatory events that attenuate fishing opportunities—from "leavers" who exit a fishery under the same regulatory circumstances. These economic attributes are hypothesized to confer advantages that assist commercial fishers in coping with regulatory events and sustaining active participation in a commercial fishery.

There are many attributes of fishers and their households that can be expected to influence the decision to stay or leave as an active participant in a commercial fishery. These include fishing income diversification, stability, and level; market channel relationships that facilitate sales of multiple fish species; age, health, and disability status; educational attainment, experience, and skills that are transferable to non-fishing occupations; spousal income and employment opportunities; and the spatial location of outside work opportunities relative to household mobility. A comprehensive analysis of all these attributes would require detailed confidential household-level data, interview methods that would include measures for intangible and subjective attributes, and historical regional job market analysis. Rather, we took a narrower and more tractable approach that focused on economic attributes linked to commercial fishing data.

We empirically analyze three related economic attributes that are hypothesized to be congruent with successfully coping with attenuated fishing opportunities following a regulatory event. The first of these measurable attributes is meaningful participation in multiple fisheries, sometimes referred to as "combination fishing" (Dory Associates 2009). We hypothesize that stayers will materially participate in a larger number of fisheries than leavers. Participation in multiple fisheries is facilitated by production linkages in vessel, human capital, and gear so that fishermen can relatively easily redirect fishing effort to fisheries that employ similar gear or fishing methods (Hutchinson 2003). Multi-fishery participation may confer a number of economic benefits, including more complete utilization of vessel and other malleable fishing capital, and the capacity to apportion effort across fisheries based on abundance, prices, fishery management, and other factors. We construct a revenue diversity index (RDI), described in greater detail in section 4 below, as a measure of income diversification from multi-fishery participation.

The second attribute we analyze is interannual variation in gross fishing income as measured by the coefficient of variation (CV), which measures the ratio of the standard deviation to the mean. We hypothesize that stayers will have a lower coefficient of variation in interannual gross annual fishing income than leavers. Fishing strategies that reduce interannual variation in income reduce dependence on credit or non-fishing work as a means of smoothing consumption in households dependent upon commercial fishing income. This second economic attribute may derive in part from multi-fishery participation that results in a more diversified portfolio of fishing income sources. Low interannual variation in gross fishing income may also derive from other, more difficult to measure intrinsic attributes of stayers. In years of reduced abundance or lower prices, for example, fishermen with more knowledge, skill, capacity, or commitment to fishing may be better able to smooth their interannual fishing income and sustain participation over time.

The third attribute we analyze is the level of gross annual income from all fishery sources. We hypothesize that stayers will have higher mean gross annual fishing income than leavers. Higher gross annual fishing income may reduce the need for fishers to exit commercial fishing for outside employment in the context of restrictive fishery regulations. As Marshall et al. (2007) note, in addition to their ability to secure outside employment and to remain competitive within the fishing industry, commercial fishermen assess their vulnerability to policy change on the basis of their financial situation. Fishermen with a larger financial buffer feel less vulnerable to policy change. This third attribute may derive in part from multi-fishery participation that provides more sources of fishing income, but (as with low interannual income variation) may also derive from other attributes of stayers.

To empirically analyze these economic attributes and their association with sustaining commercial fishermen, we apply a regulatory event study methodology to four California fisheries that allows for longitudinal analysis of stayers and leavers before and after a regulatory event. The event study approach is based on the idea that in the context of public hearings linked to proposed regulatory rule-making, fishery participants can anticipate the economic consequences of the upcoming regulation and sort themselves as either stayers or leavers. For example, Brandt (2005) looked at the Atlantic surf clam (*Spisula solidissma*) and ocean quahog (*Arctica islandica*) fishery before, during, and after imposition of individual transferable quotas in 1990, and found that participants who had a transition period to negotiate future quota shares acted strategically in anticipation of future regulatory change. And Casey et al. (1995) found substantial evidence of adaptation by fishers and processors to an individual vessel quota system in the British Columbian halibut fishery.

This is not to say that participants will always anticipate the economic effects of regulation. Fishery regulation does not occur in a deterministic environment. Post-regulation adaptation may occur due to unanticipated regulatory impacts, fishery population dynamics, market changes, or broader economic forces.

Fisheries Analyzed

We focus on four California fisheries: Dungeness crab (*Cancer magister*), spot prawn (*Pandalus platyceros*), (California) sheephead (*Semicossyphus pulcher*), and (California) spiny lobster (*Panulirus interruptus*). All had significant restrictive regulatory events since 1980, and all employ trap gear to land live finfish or shellfish (occasionally other gear types are utilized as well, as described below). In large part all of these fisheries also feature relatively high prices per pound that are driven by the growth and development of new markets that increasingly support processing and distribution in live condition.

Hypothesized Attributes of Stayers and Leavers

- Multi-fishery participation (as measured by a revenue diversity index) is associated with a commercial fisher's status as a stayer who continues commercial fishery participation following a regulatory event that attenuates fishing opportunities.
- A lower coefficient of variation (CV) in gross annual fishing income is associated with a commercial fisher's status as a stayer who continues commercial fishery participation following a regulatory event that attenuates fishing opportunities.
- Higher gross annual fishing income is associated with a commercial fisher's status as a stayer who continues commercial fishery participation following a regulatory event that attenuates fishing opportunities.

Research Approaches

The California Department of Fish and Wildlife (CDFW) provided the authors with a time-series commercial landings data set of annual individual landings receipts for 1980 to 2012.

Regulatory events in the four study fisheries were researched for the time period of available CDFW data. Regulatory events that could change a fishermen's behavior include catch limits, restricted access, or season closures. Table A describes the regulatory events identified for each fishery to determine its effect on a fishermen's participation.

Dungeness Crab. Since 1905 the fishery has been regulated by the "3-S" principle: sex, size, and season limits. The 3-S principle allows only male crabs greater

TABLE A
Regulatory Events by Fishery

Fishery	Regulatory Event Year	Regulatory Event Description
Dungeness Crab	1995	Restricted Access Program
Spot Prawn	2002	Restricted Access Program
Sheephead	2001	Catch Quota
Spiny Lobster	1996	Restricted Access Program

than 6.25 inches to be landed during the established season (Dewees et al. 2004). In 1995 California implemented a restricted access program and capped the number of available licenses.

Spot Prawn. This fishery began as a trawl fishery, with the trap fishery developing in the 1980s. The industry experienced modified seasonal closures in locations along the California coast in the 1990s to 2000. California implemented a restricted access program in 2002 that featured a two tier system, with the first tier allowing a number of high-performing vessel permits to be transferable with no landings limit. A second tier of permits were nontransferable, with landings restrictions, and a maximum of 150 traps/vessel.

Sheephead. Sheephead emerged as a specific targeted fishery in the 1980s. Regulations were first enacted with size limits in 1999 to address smaller-sized fish landed for the live fish market. We chose to focus on a catch quota imposed on the fishery at the beginning of 2001 that evolved into bimonthly catch limits. Currently sheephead is a restricted access fishery with catch limits.

Spiny Lobster. Spiny lobster has been fished in southern California since the late 1800s. Prior to 1996, the fishery was regulated by trap design. In 1996 a restricted access program was initiated. Operator permits were nontransferable, which allowed the state to eventually achieve a 225 permit capacity through attrition.

We use a 10-year event window to identify fishermen who stayed or left. Using a longitudinal approach, we tracked individual fishermen's landings five years before the regulatory event, and then determined which fishermen remained or left the fishery within five years after the event (including the event year itself). This event study approach allowed us to determine who was a consistent participant prior to the event, and who dropped out after the event occurred. The study developed criteria for individual fishermen who were considered "stayers" and "leavers" (table B). In order to be considered materially active in a fishery (and thus to be either a stayer or a leaver), a fisherman must make at least $1,000 worth of landings in a fishery in a five-year event period. The nominal $1,000 threshold in ex-vessel landings eliminates the issue of landings of non-target catch confounding participation in one of the four study fisheries.

TABLE B
Criteria for Individual Fishermen Who Were Considered Stayers or Leavers in a Given Fishery:

Stayers	Leavers
• Made at least $1,000 from landings in the fishery in the five-year period prior to the regulatory event, and were active in the fishery in at least three of those five years. • Made at least $1,000 from landings in the fishery in the five-year period during and after the regulatory event, and were active in the fishery in at least three of those five years.	• Made at least $1,000 from landings in the fishery in the five-year period prior to the regulatory event, and were active in the fishery in at least three of those five years. • Did not make any landings in the fishery during and after the regulatory event.

After designating fishermen as a "stayer" or "leaver" in one of the four study fisheries, we calculated each stayer's or leaver's revenue diversity index (RDI). Fishermen's landing records were first categorized into specific fisheries based on previous work done by Hackett et al. (2009) (table C). Once landing records were coded for specific fisheries, we needed to determine whether there were significant or incidental landings in a given fishery. We used $1,000 during the five-year period before the regulatory event, or the five-year period on and after the regulatory event, as the revenue threshold for material participation in a given fishery.

TABLE C
List of California Fisheries

California Fisheries*	
Herring	Anchovies
Salmon	Squid
Albacore	Urchin
Tuna	Sea Cucumber
Spiny Lobster	Swordfish/Shark
Pink Shrimp	Halibut
Dungeness Crab	Nearshore/Groundfish
Sardine	Spot Prawn

*Source: Hackett et al. (2009).

After longitudinal analysis to determine which fisheries individual fishermen participate in for the five-year windows before and during/after the regulatory event, we calculated a fisherman's RDI by simply counting the number of fisheries each fisherman materially participated in. For each of the four study fisheries, the RDIs of all stayers were averaged for the five-year windows before and during/after the regulatory event ("stayers-pre" and "stayers-post," respectively), and the RDIs of all leavers were averaged for the five-year window before the regulatory event ("leavers"). Once mean RDIs for each group of fishermen were calculated in the "pre" and "post" regulatory periods, statistical tests were applied, as described on the next page.

Analysis of Stayers and Leavers

To test whether an attribute (RDI, CV, or gross annual income) for stayers is significantly different from that of leavers, a simple two-sample *t* test procedure is employed. Two-sample *f* tests for variances provided *p* values that determine whether attribute variances between the two groups are significantly different. The outcome of the *f* tests determined whether the *t* tests were done assuming equal or unequal variances. One-tailed *t* tests are appropriate here because each of the alternative hypotheses is directional—mean RDI is larger, CV lower, and gross annual fishing income higher—for stayers relative to leavers in the period prior to regulation.

Before we turn to our results, it is worth explaining why we did not use a logit or probit regression analysis to model the probability of a fisher being a stayer or leaver as a function of various observable explanatory variables. One reason is the correlated nature of RDI, CV, and gross fishing income as explanatory variables in such a regression, which would lead to multicollinearity in the resulting model. In addition, as noted in section 1, we lack observations on other important explanatory variables such as outside ("non-fishing") income, fishers' and their spouses' age, education, training, and employment experience, as well as proximity to relevant employers that presumably would contribute to a household-level understanding of the stay/leave decision. Moreover, low sample sizes for the spot prawn and sheephead fisheries would raise problems with the power of the resulting statistical tests. As a result of these issues we focused on simpler statistical analysis to identify key attributes of stayers and leavers. Results for each of the tests are provided below.

Do Stayers Have Greater Fishing Revenue Diversity? Recall that the revenue diversity index (RDI) is a count of the number of fisheries fishermen participate in. We evaluate this hypothesized attribute using two-sample tests for stayers and leavers for the five-year period prior to imposition of the regulatory event (these two samples are grouped as "stayers-pre" and the "leavers"). Table D summarizes the results. Note that the stayer and leaver samples draw from the five-year period prior to the regulatory event.

The mean RDIs for the two fishermen groups show a consistent pattern of stayers having larger mean RDIs than leavers. In two fisheries (Dungeness crab and sheephead) this difference in mean RDI values across stayer and leaver groups is significant at below the 1% level. In the other two fisheries (spot prawn and spiny lobster) the difference in mean RDI values across stayer and leaver groups has only marginal significance. In the case of spiny lobster, weaker significance is driven by the stayer group participating in on average only about 0.34 more fisheries than leavers in the period prior to regulation. In the case of spot prawn, weaker significance is driven more by the small sample size of the stayer and leaver groups, as the stayers participated in on average about 0.54 more fisheries than leavers prior to regulation.

TABLE D
Tests of Hypothesized Revenue Diversity Attribute

Fishery	Groups	Sample Size	Mean RDI	*P* Value, Difference in Means*
Dungeness Crab	Stayers	363	2.71	< 1%
	Leavers	161	2.05	
Spot Prawn	Stayers	24	3.67	11.66%
	Leavers	23	3.13	
Sheephead	Stayers	59	4.80	< 1%
	Leavers	28	2.68	
Spiny Lobster	Stayers	139	2.44	9.41%
	Leavers	40	2.10	

**P* values derive from two-sample, one-tailed *t* tests. *F* tests for equality of variances (5% critical value) resulted in the use of *t* tests assuming equal variances in all four fisheries.

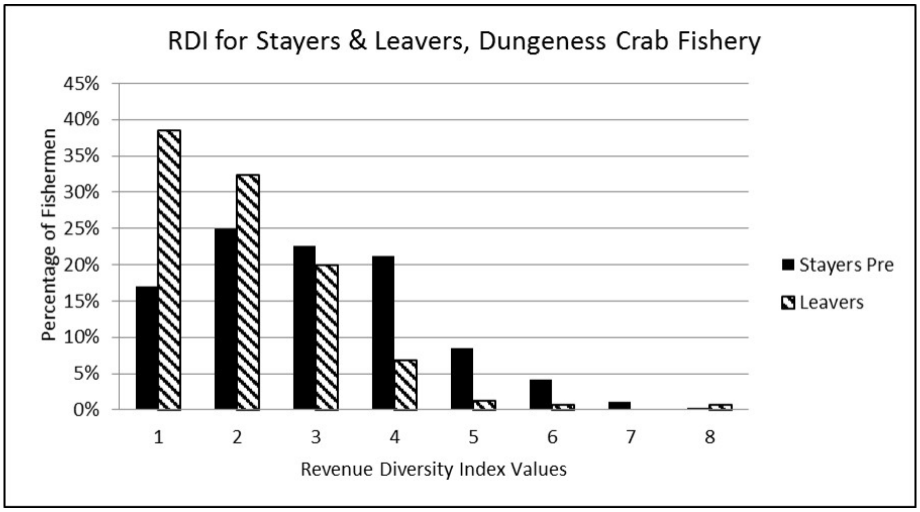

Figure 1.

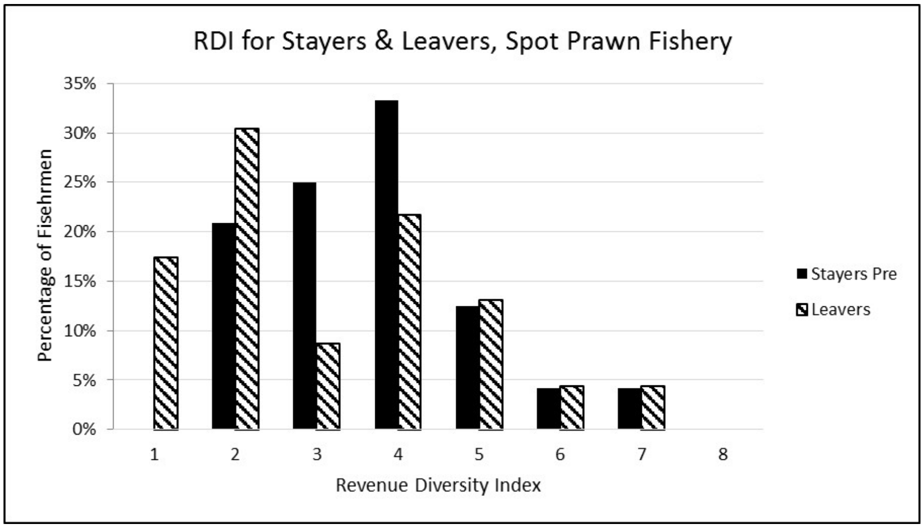

Figure 2.

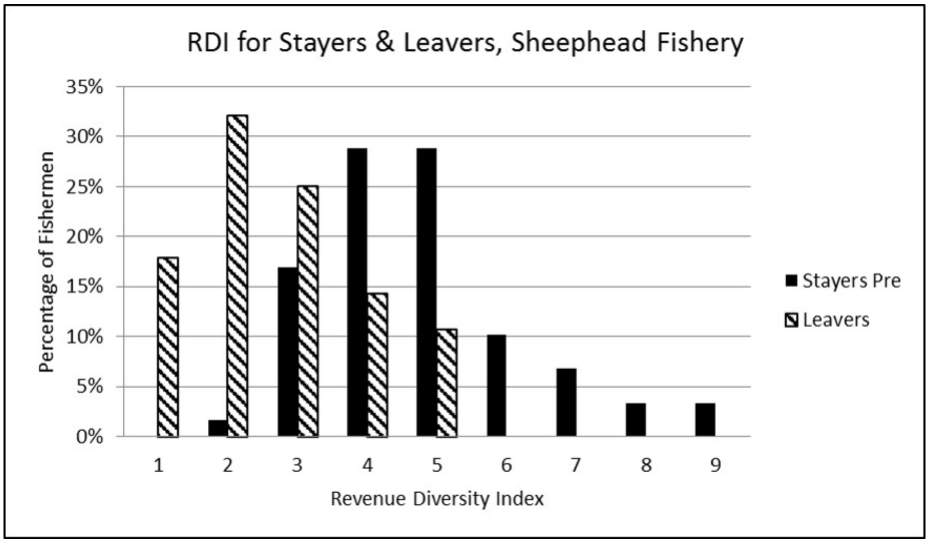

Figure 3.

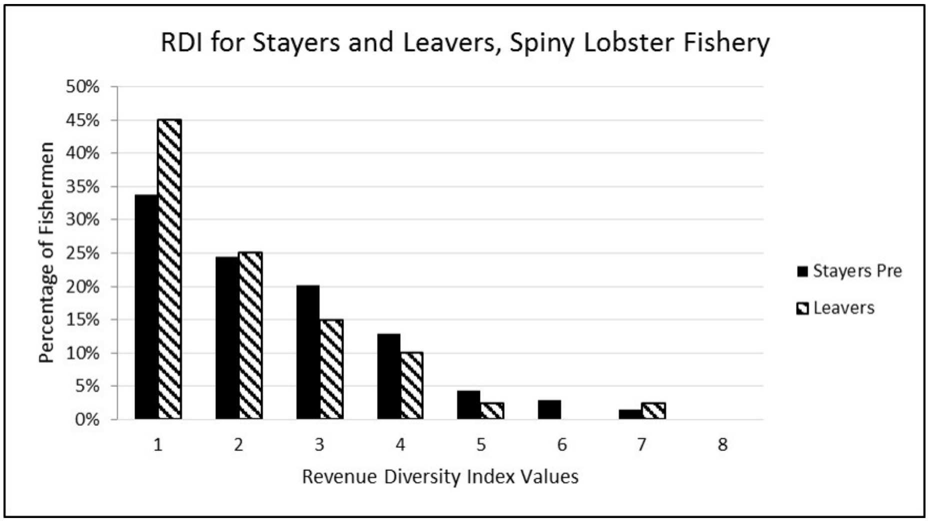

Figure 4.

We find consistent support for stayers having greater fishing revenue diversity, with mixed results for significance. Multi-fishery participation is consistently associated with stayers who persist in commercial fishery participation following a restrictive regulatory event.

Additional insight into differences in multi-fishery participation and revenue diversity across stayers and leavers can be gained by looking at RDI density plots for the two groups in the period prior to regulation. Density plots for each fishery show the distribution of RDIs for stayers and leavers in the five-year period prior to imposition of regulation Figures 1 through 4).

From the density plots we can see that some leavers had relatively high RDI values, and some stayers had relatively low RDI values. Clearly revenue diversity is not the only attribute distinguishing stayers from leavers. Some fishermen with high revenue diversity may nevertheless exit a fishery due to age, health, or outside work opportunities, among other reasons. Likewise some stayers may focus on a single fishery due to prices, abundance, fishery-specific skills, or outside income, among other reasons. Nevertheless, in each of the four fisheries prior to the regulatory event, a higher percentage of leavers participated in either a single fishery or at most two fisheries. Moreover, in each of the four fisheries a larger percentage of stayers were diversified into three or more fisheries prior to the regulatory event. The difference in the distribution of RDI values for stayers and leavers from the density plots is strongest for the Dungeness crab and the sheephead fisheries, which is reflected in the *t* test significance levels, though this difference is clearly discernable for all four fisheries.

Do Stayers Have More Stable Fishing Income? We now turn to the hypothesized attribute that stayers will have a significantly lower coefficient of variation (CV) for gross annual fishing revenue than leavers, for the five-year period prior to imposition of regulation. Results for each of the tests are shown in Table E.

TABLE E
Tests of Hypothesized Revenue CV Attribute

Fishery	Groups	Sample Size	Mean Revenue CV	*P* Value, Difference in Means*
Dungeness Crab	Stayers	363	0.542	< 1%
	Leavers	161	0.700	
Spot Prawn	Stayers	24	0.387	< 1%
	Leavers	23	0.618	
Sheephead	Stayers	59	0.441	< 1%
	Leavers	28	0.633	
Spiny Lobster	Stayers	139	0.478	< 1%
	Leavers	40	0.767	

**P* values derive from two-sample, one-tailed *t* tests. *F* tests for equality of variances (5% critical value) resulted in the use of *t* tests assuming equal variances in all but the sheephead fishery, where the *t* test assuming unequal variances was used.

We find strong and consistent support for the hypothesized attribute that stayers will have a lower CV for their fishing income. From Table E, one can see substantially lower CVs for gross annual fishing income for stayers relative to leavers in all four fisheries for the five-year period prior to imposition of regulation. All test results were significant at below the 1% level. These findings are consistent with the idea that low interannual fishing income variation reduces economic stress on the households of commercial fishers, and thus would be associated with economically resilient stayers capable of sustaining participation in a commercial fishery following a regulatory event that attenuates fishing opportunities.

Figure 5 shows mean coefficients of variation (CV) in gross annual fishing income for stayers-pre, stayers-post, and leavers. The mean CV for gross annual fish-

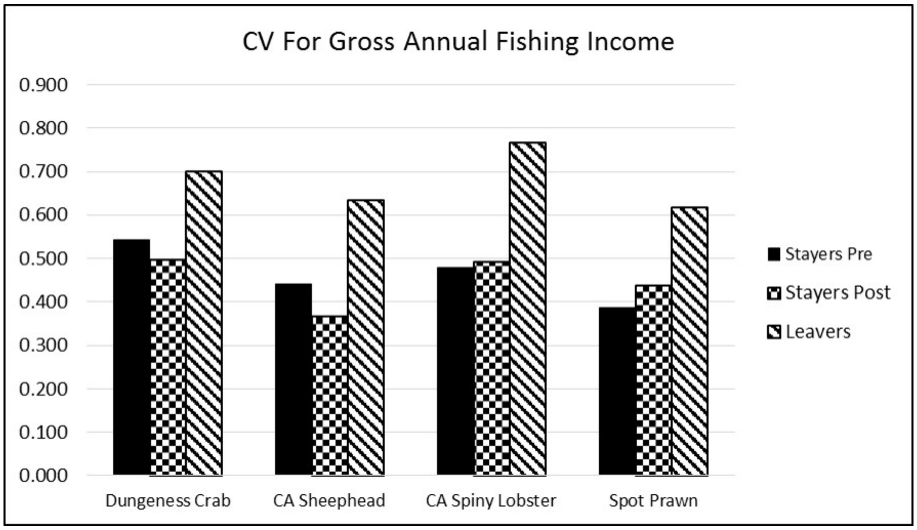

Figure 5.

TABLE F
Tests of Hypothesized Gross Annual Fishing Income Attribute

Fishery	Groups	Sample Size	Mean Gross Annual Fishing Income	*P* Value, Difference in Means*
Dungeness Crab	Stayers	363	$52,223	< 1%
	Leavers	161	$16,239	
Spot Prawn	Stayers	24	$111,751	11.9%
	Leavers	23	$86,134	
Sheephead	Stayers	59	$61,042	< 1%
	Leavers	28	$27,875	
Spiny Lobster	Stayers	139	$32,407	21.47%
	Leavers	40	$26,379	

**P* values derive from two-sample, one-tailed *t* tests. *F* tests for equality of variances (5% critical value) resulted in the use of *t* tests assuming unequal variances in all but the spot prawn fishery, where the *t* test assuming equal variances was used.

ing income for leavers consistently exceeds that of both stayer groups in all four fisheries.

It is also notable that there is no consistent longitudinal pattern to changes in mean CV for gross annual fishing income for stayers before and after the regulatory event. Post-event mean CV of stayers declines for the Dungeness crab and sheephead fisheries (paired two-sample *t* test for difference in means is significant at the 5% level), but increases for the spiny lobster and spot prawn fisheries (though these slight increases are not significant at even the 10% level).

Do Stayers Have Higher Gross Annual Fishing Income? We now turn to our last hypothesis, which is that stayers will have significantly higher gross annual fishing income than leavers. Gross annual fishing income is calculated by summing ex-vessel revenue from all landings receipts for a given fisherman in a particular year. Results are given in Table F. Note that as with the earlier analysis, the stayer and leaver samples draw from the five-year period prior to the regulatory event.

We find a consistent pattern of stayers having a larger mean gross annual fishing income than leavers. Moreover, as with the fishing revenue diversity attribute, the significance of these differences in mean gross annual fishing income is mixed. In two fisheries (Dungeness crab and sheephead) this difference in mean gross annual fishing income across stayer and leaver groups is significant at below the 1% level. In the other two fisheries (spot prawn and spiny lobster), the difference in mean gross annual fishing income across stayer and leaver groups is not significant at the usual 5% level.

Figure 6 shows mean gross annual fishing income for stayers (pre- and post-event) and leavers. One can see that mean gross annual fishing income for stayers consistently exceeds that of leavers in all four fisheries. It is also notable that there is a consistent longitudinal pattern of higher mean annual gross fishing income for stayers during and after the regulatory event relative to before the regulatory event. Paired two-sample *t* tests for difference in mean gross annual fishing income for stayers before and on/after the regulatory event are significant at the 5% level in all four fisheries. Consolidation of commercial fishing activity following exit of leavers resulted in higher mean gross annual fishing income for the stayers who were more resilient to regulatory change and were able to sustain active fishery participation.

The Challenge of Participating in Multiple Fisheries

There are a number of factors that may affect a fisher's capacity for participation in multiple fisheries. One

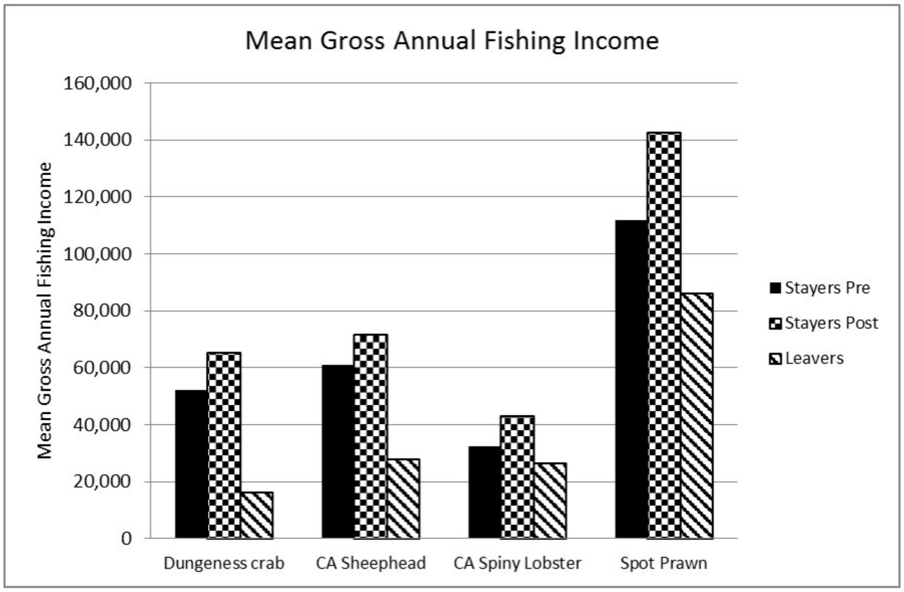

Figure 6.

of these is the extent to which capital (vessel, gear, and human capital) is transferable from one fishery to another. Hutchinson (2003) notes that similar fishing inputs (e.g., gear, vessel, and crew), along with complementary fishing seasons, allowed fishers to participate in multiple fisheries. All four of the fisheries analyzed in this paper are trap fisheries. It should be noted, however, that Dungeness crab, CA sheephead, CA spiny lobster, and spot prawn require different trap configurations in terms of mesh size, escape and entry port size, and location in order to reduce the incidence of bycatch (NOAA 2012). As a result, trap inputs from one fishery cannot be repurposed for another fishery. Although fishery gear is not amenable to transferability, a given vessel configuration can facilitate participation in a variety of live trap fisheries. Stayers who participate in multiple trap fisheries own trap gear unique to each fishery, and simply swap one type of gear out for another (pers. comm. Lia Protopapadakis 2014).

Transferable human capital—skills and experience associated with deploying different types of trap gear and handling different types of live fish and crustaceans—is another important factor associated with participation in multiple fisheries. Durrenberger and Palsson (1983) describe how success can be attributed to a fisherman's expert knowledge gained from experience and active engagement with the environment (Palsson 1994). This would extend beyond fishing into market channel relationships, as reflected by ready access to receiver/processors, direct-to-consumer, fisherman's markets, restaurant accounts, and other channels that can absorb a variety of live species of fish and crustaceans.

Though a substantial proportion of the study's fishermen participate in multiple fisheries, it is not as simple as swapping out one gear configuration for another to meet other target fisheries needs. Many fisheries are under a restricted access, or limited entry, program. Such programs restrict the number of participants by limiting number and size or vessels, necessitating permits, requiring specific gear, or imposing harvest rights such as a quota system. Responding to an upcoming regulatory event by participating in additional fisheries may thus require access to financial capital to acquire limited access permits. Therefore restricted access programs may make it difficult for fishermen to participate in multiple fisheries and can prevent fishermen from making the best strategic choices (Dory Associates 2009).

Participation in multiple fisheries may also be affected by the timing of fishing seasons (Dory Associates 2009). While the Dungeness crab season extends into July, the great majority of landings occur in the first four to six weeks of the season opening (Dewees et al. 2004). Consequently, fisheries with derby characteristics and with temporally conflicting season openings can make multi-fishery participation difficult. The CA spiny lobster fishery has a long closure period. Fishers participating in the spot prawn or CA sheephead fisheries can enter and exit the CA spiny lobster fishery and thereby enhance annual fishing revenue and more fully utilize vessel and related capital.

Spatial considerations are another factor associated with participation in multiple fisheries. For example California's commercial Dungeness crab fishery is located primarily in northern California (and to a limited degree central California). As a result fishers targeting Dungeness crab tend to have home ports in northern California and face considerable transit and other costs if they seek to participate in the more southern California fisheries of CA sheephead, CA spiny lobster, and spot prawn. Instead, fishers targeting Dungeness crab traditionally fish other northern California fisheries that have complimentary seasons such as salmon and groundfish. The southern California CA sheephead, CA spiny lobster, and spot prawn fisheries are spatially proximate and share compatible production linkages such as vessel and captain/crew inputs that allow those fishermen to participate across those fisheries (Hutchinson 2003).

The California Marine Life Management Act (MLMA) has as one of its goals to provide for the long-term interests of fishing-dependent individuals, minimizing adverse impacts through regulatory actions. Our findings point to multi-fishery participation as one potential approach to complying with this goal, as diversity in fishery participation and diversity in marketing arrangements and strategies may be the best solutions to weathering reduced fishing opportunities and other shocks to income. The problem that arises from this is that regulatory hurdles are high, attention to factors with regard to the resource may not considered, and cooperative efforts among fishermen may not be sustainable. Additionally, the strategies are not always adaptable in certain environmental contexts (Tough 1999).

In spite of the complexities associated with a multi-fishery approach to minimizing negative impacts to fishermen, there are several options that the state of California could take in order to comply with the goal of the MLMA outlined above. It could be effective for managers to promote a more collaborative approach, wherein regularly held meetings would be convened with fisheries participants that would take into account needs linked to multi-fishery participation. There is evidence that such a collaborative management approach with practical input provided by fishers may have fruitful outcomes (Cinner et al. 2012). Through this process, deficiencies of information flow could be determined, as well as concerns regarding permits, access, and opportunities that may otherwise be largely unknown. A centralized web-based location clearly outlining regulations for both market-integration (e.g., direct sale) and fisheries permits throughout the state, perhaps with a specific focus on typical multi-fishery combinations, would help consolidate information and eliminate confusion that often leads to frustration and inertia.

Ethnographic data gathered as a different component of our research revealed that as a result of the many regulatory, environmental, and market-based challenges faced by the commercial fishing sector, and the perceived subsequent decline in job satisfaction and general well-being, many fishermen indicate they are unlikely to promote entering the industry to their children, and new entrants are decreasing. State management could alleviate the pressures associated with an aging fleet through establishing financial incentives and educational opportunities for those wishing to enter commercial fishing. While the California Fisheries Fund is helpful in providing loan assistance to fishermen for permits and gear, a model more akin to that of the Nature Conservancy and the Morro Bay, California, commercial fishermen puts less of a financial burden on fishermen and serves as a longer-term investment in the overall health of not just the fishermen and their communities, but the ecosystem on which they depend.

The Morro Bay model originated when the Nature Conservancy purchased permits for fisheries that were near collapse from Morro Bay fishermen who no longer wished to remain in the fishery. They leased the quota back to the fishermen under the condition that they worked collaboratively to innovate sustainable practices. Given the success of this program (e.g., lowering bycatch, increasing catch of target species), the Nature Conservancy ultimately transferred fishing rights back to the Morro Bay Community Quota Fund that now regulates the quota of groundfish among its members and its collaborative scientific board. These types of "community quota entities" are being tested in various locations in the west, though the initial capital outlay and subsequent management of such models requires participation from people other than the fishermen themselves in order to finance and effectively and sustainably manage activities. When successful, as in the case of Morro Bay, this model has the potential to sustain local fishery access to a consortium of community members. The state of California could contribute to the financing of such a program instead of relying on a private entity to finance these programs that directly benefit the state.

Another approach that could be more widely promoted and financed by the state to facilitate multi-fisheries participation is the cooperative model developed by the San Francisco Community Fishing Association. Here, members of the association who may be permitted to fish for different species individually, collectively benefit in revenue sharing, in effect creating multi-fisheries participation through cooperative efforts. Due to the fact that many of the high value California commercial fisheries are now limited entry, and that opening these fisheries to more entrants is not a viable option, it appears as though the collaborative models outlined above may have better potential for success.

The goal of this research was to assess the variables that kept fishermen in the industry in spite of shocks to their fishery after a major regulatory event. These types of events occur regularly throughout the country, as new science emerges, access becomes restricted, or fisheries decline. Since many states, including California, have mandates to minimize the adverse effects of such regulatory events on fishermen, managers will be seeking proven alternative models to integrate into the regulatory process. We have explored the importance of multi-fisheries participation as a means for long-term success in the commercial fishing industry, and explained the challenges associated with the realities of such an approach. While there are successful models engaging this multi-fisheries approach operating throughout the state, they have all required collaborative assistance from state and nongovernmental organizations in terms of financing, technology, and operations in varying degrees. With a goal of the MLMA to insure the long-term sustainability of commercial fishing communities, the state would benefit from creating a streamlined process through which individual fishermen and their communities could locate information related to the models outlined here and related regulatory information. In addition, the state could develop partnerships with organizations experienced in implementing these models and actively promote their integration into the current paradigm.

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REFERENCES CITED

Brandt, S. 2005. A Tale of Two Clams. Regulation 28, Spring, pp. 17–21.

Casey, K., C. Dewees, B. Turris, and J. Wilen. 1995. The Effects of Individual Vessel Quotas in the British Coumbia Halibut Fishery. Marine Resource Economics 10, pp. 211–230.

Cinner, J., J. McClanahan, M. MacNeil, N. Graham, T. Daw, A. Mukminin, D. Feary, A. Rabearisoa, A. Wamukota, N. Jiddawi, S. Campbell, A. Baird, F. Januchowski-Hartley, S. Hamed, R. Lahari, T. Morove, and J. Kuange. 2012. Co-management of Coral Reef Social-Ecological Systems. Proceedings of the National Academy of Sciences of the United States of America 109, pp. 5219–5222.

Dewees, C., K. Sortais, S. Hackett, M. Krachey, and D. Hankin. 2004. Racing for Crabs: Costs and Management Options in Dungeness Crab Fishery. California Agriculture (58): 186–93.

Dory Associates. 2009. Access Restrictions in Alaska's Commercial Fisheries: Trends and Considerations. Technical report, Alaska Marine Conservation Council.

Durrenberger, E. P., and G. Palsson 1983. Riddles of Herring and Rhetorics of Success. Journal of Anthropological Research (39): 323–335.

Hackett, S., D. King, M. Hansen, and E. Price. 2009. The Economic Structure of California's Commercial Fisheries. Technical Report under Contract P0670015, California Department of Fish and Game, Sacramento, CA.

Holling, C. Resilience and stability of ecological systems. Annual Review of Ecological Systems 4, 1973, pp. 1–23.

Hutchinson, S. 2003. An Economic Analysis of Multi-Fishery Participation among Commercial Fishers in South Florida. Dissertation, University of Florida.

Marshall, N., D. Fenton, P. Marshall, and S. Sutton. 2007. How Resource Dependency Can Influence Social Resilience within a Primary Resource Industry. Rural Sociology (72): 359–390.

Marshall, N., and P. Marshall. Conceptualizing and Operationalizing Social Resilience within Commercial Fisheries in Northern Australia. Ecology and Society 12, 2007 (online). URL: http://www.ecologyandsociety.org/vol12/iss1/art1/.

NOAA Protected Species Publication. February 2012. URL: http://www.westcoast.fisheries.noaa.gov/publications/protected_species/marine_mammals/large_whale_entanglement_appendix_a-e.pdf.

Palsson, G. 1994. Enskilment at Sea. Man 29(4): 901-27.

Tough, F. 1999. Depletion by the market: Commercialization and resource management of Manitoba's lake sturgeon (*Acipenser fulvescens*), 1885–1935. Fishing places, fishing people: Traditions and issues in Canadian small-scale fisheries. Eds. Dianne Newell and Rosemary E. Ommer University of Toronto Press, Toronto.

THE NEARSHORE FISHES OF THE CEDROS ARCHIPELAGO (NORTH-EASTERN PACIFIC) AND THEIR BIOGEOGRAPHIC AFFINITIES

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ABSTRACT

Located in the central region of the west coast of Baja California Peninsula, the Cedros Archipelago consists of five continental islands (Cedros Island, Natividad, San Benito Este, Medio, and Oeste), with Cedros being the largest island in the Mexican Pacific. This archipelago represents the biogeographic transition zone between the temperate and subtropical region and hence, the end of the geographic distribution of a large number of species. Based on field surveys, literature, and scientific collection records, an exhaustive species list of fishes associated with the archipelago and their biogeographic relationships is presented. The checklist includes 269 species belonging to 191 genera, 97 families, 31 orders, and 4 classes. Of the total species, 105 species were recorded in the field, 57 were the result of the literature review, and 218 species of the records were obtained from collections. A total of 14 biogeographic affinities are presented, where 51% of the species have warm-temperate or cold-temperate affinity and 37% have tropical-subtropical affinity. This work highlights the fish diversity present in a transition zone within the temperate and subtropical marine areas of the Northeastern Pacific. More importantly, it reveals a biogeographic region where a great number of species converge, and may be related with the evolutionary history of different taxa and the geological history of the region.

INTRODUCTION

The Cedros Archipelago (CEA) includes five continental islands, and is located 10 km off the coast in the east-central region of the Baja California Peninsula (fig. 1). Cedros is the largest island in the Mexican Pacific, and along with San Benito Oeste, Medio, Este, and Natividad Island, represent a land territory of 360.7 km^2. The polygon formed between all of these islands accounts for a marine region of 3,928.9 km^2.

The CEA forms a group of northwestward-trending islands that are considered an extension of the Vizcaino Desert; therefore a subregion of the Sonoran Desert (Oberbauer 1985). The area was separated from the coast of Baja California by a submersion process in the last glacial period (Busby-Spera 1988), resulting in a 200 m deep channel called the Kellet Channel. The archipelago has a complex geologic history, beginning with rock material accumulated in a deep trough in the late Jurassic period, forming the Jurassic Grand Canyon. During the Cretaceous, the formations were folded, faulted, and overlaid by marine deposits. Finally, uplift occurred as recently as the late Pleistocene (Oberbauer 1985; Busby-Spera 1988).

The Pacific islands of the Baja California Peninsula can be considered as among the least degraded ecosystems in continental islands (Littler 1980; Richards 2000; Pondella et al. 2005; Aguirre-Munoz et al. 2008), however unlike their terrestrial biodiversity (Huey 1942; Oberbauer 1985; Mellink 1993; Aguirre-Munoz et al. 2008), the marine diversity has been poorly documented. This contrasts with ecological interest on the central region of the Baja California Peninsula, which represents a transition zone between the San Diegan and the Cortez biogeographic provinces (sensu Horn et al. 2006; Ruiz-Campos et al. 2010). South of the CEA the cold waters from the California Current system converge

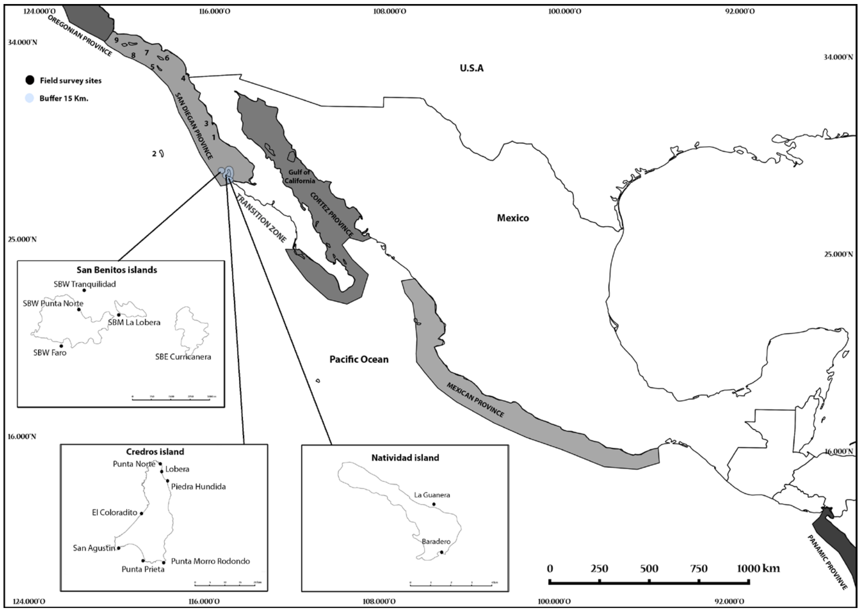

Figure 1. Locations of field surveys at the Cedros Archipelago, México

with the subtropical current system from the south, West Mexican Current (Hubbs 1960; Hickey 1979; Kessler 2006; Taylor et al. 2007), and recently documented intricate eddy motions of ocean water masses in the region contribute to the complexity of the coastal upwelling regime (Miller et al. 1999).

To the north of the CEA, temperate species associated with rocky reefs and kelp forests begin to be dominant until Point Conception, California (Horn et al. 2006). To the south of the CEA, species associated with the tropical Cortez and Mexican provinces begin to appear, mainly associated with mangrove ecosystems in estuaries and bays located in Bahía Magdalena (24°47.6'N, 112°18.2'W). While some species associated with the San Diegan faunistic province can be found as far south as Bahía Magdalena, the transition begins sharply at Punta Eugenia (27°50.7'N, 115°4.84'W), a major mainland landmark in front of the archipelago. Kelp forests do not persist farther south than Punta Eugenia and tropical marine species become more common (Taylor et al. 2007).

The CEA region has been historically relevant for extractive purposes, as archaeological investigations have documented an intensive pre-Hispanic use of marine resources (Des Lauriers 2010), and currently there are fisheries that target on spiny lobster (*Panulirus interruptus*; Randall 1840), green abalone (*Haliotis fulgens*; Philippi 1854), and pink abalone (*H. corrugata*; Gray 1828). Although the finfish fishery has less relevance, some taxa are of artisanal importance (e.g., *Paralabrax nebulifer* [Girard 1854]; *P. clathratus* [Girard 1854]; *Semicossyphus pulcher* [Ayres 1854]; and *Seriola lalandi* [Valenciennes 1833; Rodriguez-Valenica et. al 2004]).

Despite the ecological and economical importance of this region, there is scarce information about the species that inhabit it. In fact, most published species lists of marine groups contain only information from occasional visits or literature reviews (e.g., Hubbs 1960; Miller and Lea 1972; Love et al. 2005). The few studies that have specifically targeted any of the islands of the CEA are focused on particular fish families (Clinidae: Stepien and Rosenblatt 1991), species (*Sardinops* spp.: Felix-Uraga et al. 1996; Quiñonez-Velazquez et al. 2002) or habitats (reef fishes: Pondella et al. 2005; intertidal fishes: Carpizo-Ituarte et al. 2012).

Baseline studies for the CEA are a priority because the region has begun to show signs of environmental decay related to anthropogenic impacts. Among them the overexploitation of the fishing resources, overpopulation of Cedros Island, and the Mitsubishi/Mexican government-owned salt-transshipment facility, which is a source of introduction for exotic species (Mellink 1993; Des Lauriers 2009; Aguilar-Rosas et al. 2011). The lack of a detailed fish checklist hinders the efforts of decision-makers, who require comprehensive baseline data to set adequate protocols for monitoring temporal changes in community composition caused either by anthropogenic or natural forces (Reyes-Bonilla et al. 2010). Furthermore, without a thorough inventory of fish species, any biogeographic analysis of the CEA will be limited in its relevance and outcomes.

The main objective of this work is to provide the first comprehensive, systematic checklist of marine ichthyofauna of the CEA. We performed an overview of the composition of fish community and an analysis of zoo-

TABLE 1

Study sites and habitat in the Cedros Archipelago.
***I=Intertidal, S=Subtidal; **T=Tidepools, K=Kelp forest, R=Rocky reefs, S=Soft bottom.**

	Site	Coordinates	Date	Sampled zone*	Habitat**	Temp C
Cedros Island	Punta Norte	28°21’48.7 N, 115°11’50.7 W	17-May-12	I, S	T, K	14
	Lobera	28°20’12.1 N, 115°11’43.9 W	18-May-12	S	K, R	14
	San Agustin	28°4’48.9 N, 115°20’27.3 W	19-May-12	I, S	T, K	14
	El Coloradito	28°11’54.5 N, 115°15’45.7 W	I	T		
	Punta Prieta	28°2’14.6 N, 115°15’11.9 W	I	T		
	Punta Morro Redondo	28°1’56.7 N, 115°11’18.1 W	I	T		
	Piedra Garropa	28°18’17.5 N, 115°10’19.1 W	18-May-12	S	S, R	14
San Benito	SBE Curricanera	28°17‘38.5 N - 115°32‘28.1 W	20-May-12	I, S	T, K	15
	SBE Tranquilidad	28°19.0‘ N - 115°35.0‘ W	22-May-12	I, S	T, K	14
	SBM La Lobera	28°18‘25 N - 115°34‘11 W	21-May-12	S	T, K, R	16
	SBW Punta Norte	28°18’29.6 N, 115°35’9.5 W	22-May-12	I	T	
	SBW Faro	28°17‘40.7 N - 115°35‘31.1 W	21-May-12	S	R	15
Natividad	Baradero	27°52‘31.4 N - 115°10‘16.8 W		I, S	T, K	15
	La Guanera	27°51‘5.8 N - 115°10‘2.6 W		S	T, K	15

geographic affinity of the species using field surveys, fish collection records, and a full literature review. The results highlight that the relatively high local fish diversity is a result of physical and biological factors determining the transition between warm temperate and subtropical communities in the northeastern Pacific.

MATERIALS AND METHODS

The Cedros Archipelago (CEA) is composed of five islands. Cedros is the dominant topographic feature of a 400 km long submerged ridge, with a maximum height of 1,204 m, encompassing an area of 348.2 km^2 and laying approximately 22 km from the nearest point on the central coast of the Baja California Peninsula (fig. 1). San Benito Archipelago has three small islands situated 31.5 km west of Cedros, encompassing an area of 6 km^2 and with a highest altitude of 212 m. Finally, Natividad is located 7.5 km west of Punta Eugenia and measures 6 km in length and 2.5 km at its maximum width, accounting an area of 7.28 km^2.

In order to compile the fish checklist of the CEA, we followed three steps. First, we gathered information from electronic and in-house scientific collections from institutions in México, the United States, and Canada, encompassing records between 1934 and 2001. In the case of museum data, we reviewed records from thirty collections, either electronically or by direct visits, obtaining records of the following eleven institutions: Universidad Autónoma de Baja California (UABC; Ensenada); Centro Interdisciplinario de Ciencias Marinas (CICIMAR; La Paz); Instituto de Biología de la Universidad Nacional Autónoma de México (México, DF); Scripps Institution of Oceanography (La Jolla); Los Angeles County Natural History Museum (Los Angeles); California Academy of Sciences (San Francisco); National Museum of Natural History, Smithsonian Institution (Washington, DC); American Museum of Natural History (New York); University of Kansas Natural History Museum (Kansas City); University of Florida (Gainesville); and Canadian Museum of Nature Fish Collection (Dartmouth).

Second, we conducted an extensive literature review of the species reported in peer reviewed articles and technical reports from libraries at UABC (Ensenada, México), CICIMAR (La Paz, México), Centro de Investigaciones Biológicas del Noroeste (La Paz, México), Centro de Investigación Científica y de Educación Superior de Ensenada (Ensenada, México), and Scripps Institution of Oceanography (La Jolla, CA).

Finally, we conducted field surveys around the islands between 2010 and 2012 (table 1). Field surveys included intertidal and subtidal samplings. Intertidal fishes were sampled during eight sampling campaigns, carried out between February 2010 to April 2012 in the rocky tidepools of five sites at Cedros Island, two at San Benito, and two at Natividad (fig. 1, table 1). Tidepools were sprayed using manual aspersion pumps containing a solution of 10% eugenol (clove oil) dissolved in ethanol. After 10 minutes, the tidepools were thoroughly checked using dip and hand nets (Ruiz-Campos et al. 2010).

Subtidal fishes were sampled in May 2012 through underwater visual censuses performed by trained scuba divers. Using 30 × 2 m belt transects, we dove at three different depths (10, 15, and 20 m) and three main habitats (kelp forest, rocky reef, and soft-bottom). We carried out a total of 66 transects in four sites at Cedros, four sites at San Benito and two at Natividad. The total surveyed area with visual censuses was 3,960 m^2. Subtidal species were also recorded using the roving dive technique and underwater photography. Voucher specimens of all recorded species in tidepools were kept in the Fish Collection at UABC, while most of the species recorded in the subtidal had in situ photographs taken.

In order to establish which records would be considered as valid for purposes of the study, in a geographical information system (QGIS 2.8) we traced a buffer area of 15 km around the archipelago. The records with coordinates inside the buffer area were considered part of the checklist, independently of the collection method or year of collection.

The taxonomic identification was performed using descriptions by Miller and Lea (1972), Fischer et al. (1995), and Robertson and Allen (2015). A specialized bibliography was also used for some groups (e.g., clingfishes [Briggs 1955]; gobies [Hoese and Reader 2001]; labrisomid blennies [Hubbs 1953]; rays [Castro-Aguirre and Espinoza-Pérez 1996]; sharks [Espinosa-Pérez et al. 2004]; tube blennies [Stephens 1963 and Stephens et al. 1996]). The final checklist follows a systematics order according to Eschmeyer (2015), with modifications by Wiley and Johnson (2010). Genera and species names are presented alphabetically. To eliminate synonyms and generate a systematic list consisting only of valid names, each taxonomic name was corroborated in the Catalog of Fishes of the California Academy of Sciences (Eschmeyer 2015) and common names in Page et al. (2013).

The biogeographic analysis followed three approaches.

1) We created a species presence/absence matrix using the species recorded in our subtidal field surveys at Cedros, San Benito and Natividad Islands, and field records from eight Northeastern Pacific islands gathered from peer review journals (Guadalupe Island, México [Reyes-Bonilla et al. 2010]; San Martin and North Coronado from México; and San Clemente, Santa Catalina, Santa Cruz, Santa Barbara, and San Nicolas from USA [Pondella et al. 2005]). Then, we performed a non-metric multidimensional scaling analysis (nMDS) (Kruskal & Wish, 1978) using the unweighted paired group method and arithmetic averages (UPGMA), based on a Bray-Curtis similarity matrix. SIMPER analysis was used to determine which species contributed with the largest dissimilarity patterns, using the statistical package PRIMER 6.1 (Primer-E Ltd: Plymouth; Clarke and Gorley 2006).
2) Species distributions were plotted using the available information for northern and southern endpoints following Love et al. (2005), and Robertson and Allen (2015). If a species had not been reported at CEA but was observed during field surveys, endpoints were updated with such information. We developed a MATLAB routine to generate latitudinal distribution for the 262 species with known distribution. We defined species with wide distribution those that have a full geographic range covering at least 60 degrees in latitude and which occurred beyond 30 degrees of latitude in both hemispheres.
3) Finally, we assessed the regionalization of the fish species recorded at CEA. The zoogeographic affinity of the ichthyofauna was achieved following Horn et al. (2006) for the North Pacific region, and Hastings (2000) for the Tropical Eastern Pacific, with modifications from Robertson and Cramer (2009). Considering their distribution range, the species were grouped into eight biogeographic provinces from the Eastern Pacific (Briggs 1974), one realm (North Pacific), and three distribution patterns (AmphiAmerican, Circumtropical, and Circumglobal).

RESULTS

The field surveys, museum records, and literature review, taken together helped to construct a list of 269 species of marine fishes of the CEA, from 191 genera, 97 families, 31 orders, and 4 classes (table 2). Perciformes was the most commonly represented order, with 33 families and 106 species in total. Almost half of the families (48) are represented by a single species. The most speciose families were Sebastidae (22 spp.), Myctophidae (16 spp.), and Embiotocidae (10 spp.). The genera with the highest number of species were *Sebastes* (22 spp.) and loosely followed by *Citharichthys* (5 spp.), and *Apogon*, *Halichoeres*, *Paralabrax*, *Icelinus*, *Lepophidium*, and *Pleuronichthys* with 4 species each.

The nMDS ordination plot based on presence/absence data clearly shows a separation of the CEA from the other eight northern islands, located in the California Current system (fig. 2). The fish assemblages from Cedros, Natividad, and San Benito are tightly grouped, indicating high similarities (>50%), while the Channel Islands, North Coronado, and Guadalupe Islands constitute a more spread group with equivalent similarity between fish assemblages (<50%), and San Martin island is separated from the rest.

According to the geographic distribution, 135 species have a temperate affinity (warm-temperate to cold-temperate) and 92 species have a tropical affinity (tropical-subtropical). A third group of 35 species are widely distributed in tropical and subtropical seas, and a geographic distribution was not assigned to seven taxa that were not identified to specific level (fig. 3).

A total of 170 species comes from a single source (field record, scientific collections and literature review) and 100 species came from multiple sources (table 2). Considering all records, 105 species were seen or collected in the field, 57 taxa were cited in the literature review and 218 species had specimens from the CEA housed in scientific collections. Based on our field records, 90 species were recorded in the subtidal (soft bottom [9 spp.]; kelp forest and rocky reefs [84 spp.],

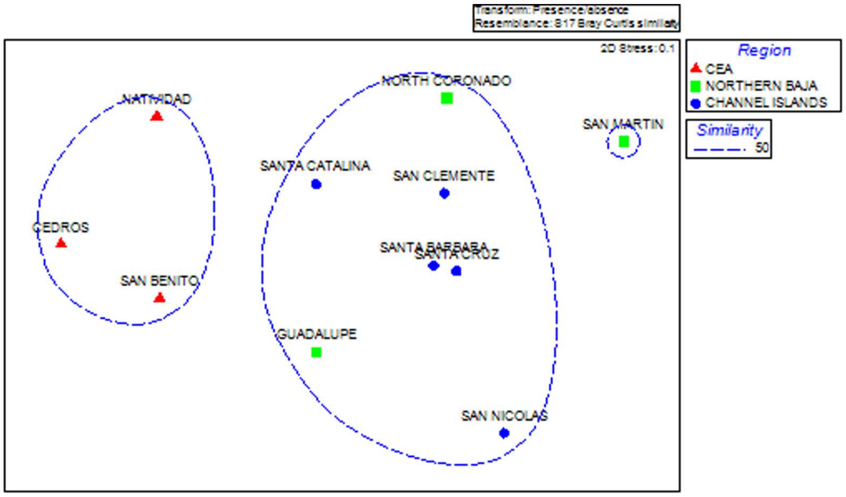

Figure 2. Non-metric Multidimensional Scaling analysis (nMDS) for fish species recorded in the subtidal field surveys at Cedros, Natividad and San Benito, and eight islands in the Pacific coast of Baja California and California [data from Pondella et al. (2005), Reyes-Bonilla et al. (2010) and present study].

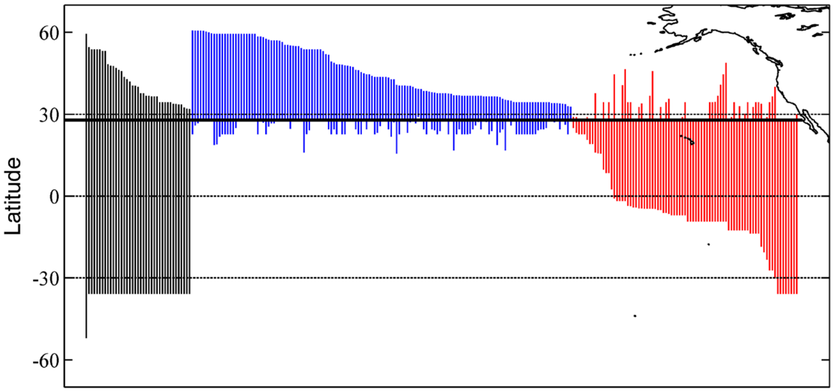

Figure 3. Distribution ranges (bars) in the eastern Pacific of 262 species included in Table 1. Black lines: species widely distributed in the EP surpassing the 30 degrees Latitude in both hemispheres. Blue lines: species with temperate affinity. Red lines: fishes with tropical-subtropical affinity. Black line: Latitude in where CEA archipelago is located.

3 species were present in both habitats). The intertidal fieldwork contributed with 24 species to the checklist.

Analyzing separately the species richness for each of the islands, Cedros had more than twice the number of taxa as San Benito (224 and 107, respectively) and four times that for Natividad Island (63 spp.). The differences are largely reduced when considering only the field surveys; in Cedros 78 species were seen or collected, 54 and 56 species at San Benito and Natividad, respectively.

The CEA represents the limit of geographical distribution for 104 species; 38% of the total species checklist. For 35 species the archipelago is the northern limit, and for 47 species it is the southernmost point of distribution (fig. 3). From the listing, we have range extensions for 19 species. For 9 species, this represents the northernmost documented record, and for 10 species the southernmost record (table 3).

According to the geographic distribution information of all the species, we found 14 distribution patterns; these included one or more biogeographic provinces (fig. 4). The distribution ranges of 95% of the species comprise two or more biogeographic provinces. The best-represented distribution in number of species was the Oregonian-San Diegan, with 46 species. The distribution pattern Aleutian-San Diegan was represented with 25 species.

The presence of 10 endemic species to the San Diegan province was recorded (fig. 4), including: the lined clingfish (*Gobiesox eugrammus*), the yellowchin sculpin (*Icelinus quadriseriatus*), the southern clingfish (*Rimicola dimorpha*), the Guadalupe blenny (*Starksia guadalupae*) the chocolate pipefish (*Syngnathus euchrous*), the tripefin poacher (*Xeneretmus ritteri*), the island kelpfish (*Alloclinus holderi*), the California moray (*Gymnothorax mordax*), the

TABLE 2

Systematic list of fishes of Cedros Archipelago, México, Northeastern Pacific. Classification according to Eschmeyer (2015). *Common name sensu Page et al. (2013); 1 = Fiel record, 2 = Museum recod, 3 = Literature; **Data from field surveys; ***BA = Biogeographic affinity: AL = Aleutian province, OR = Oregonian province, SD = San Diegan province, CZ = Cortez province, MX = Mexican province, PA = Panamic province, PE = Peruvian province, POI = Pacific Oceanic Islands province, CG = Circumglobal, CT = Circumtropical, NWP = Northwestern Pacific, EP = Eastern Pacific, AA = AmphiAmerican. sensu Love et al. (2005) and Robertson and Allen (2015).

CLASS	ORDER	FAMILY	Scientific name	Common name*	Cedros	San Benito	Natividad	Museum data	Habitat**	Notes	BA***
MYXINI											
	MYXINIFORMES										
		MYXINIDAE									
			Eptatretus deani (Evermann & Goldsborough 1907)	Black hagfish	2	2		LACM, SIO		Southern limit	AL-SD
			Eptatretus mcconnaugheyi (Wisner & McMillan 1990)	Shorthead hagfish	3	3				Southern limit	SD-CZ
			Eptatretus stoutii (Lockington 1878)	Pacific hagfish	2	2		LACM, SIO			OR-SD
CHONDRICHTHYES											
	HEXANCHIFORMES										
		HEXANCHIDAE									
			Notorynchus cepedianus (Péron 1807)	Broadnose sevengill shark			1		S		CG
	HETERODONTIFORMES										
		HETERODONTIDAE									
			Heterodontus francisci (Girard 1855)	Horn shark	1, 2	1	1	CICIMAR, LACM	S		OR-CZ
			Heterodontus mexicanus (Taylor & Castro-Aguirre 1972)	Mexican horn shark	1, 3	3	1		S		MX-PA
	LAMNIFORMES										
		LAMNIDAE									
			Isurus oxyrinchus (Rafinesque 1810)	Shortfin mako			1		S		CG
	CARCHARINIFORMES										
		SCYLIORHINIDAE									
			Cephaloscyllium ventriosum (Garman 1880)	Swell shark		2		SIO			OR-CH
		TRIAKIDAE									
			Galeorhinus galeus (Linnaeus 1758)	Tope		2		IGUNAM, SIO			CG
			Mustelus californicus (Gill 1864)	Gray smoothhound	2			CICIMAR			OR-CZ
			Mustelus lunulatus (Jordan & Gilbert 1882)	Sicklefin smoothhound		2		SIO			SD-CH
			Triakis semifasciata (Girard 1855)	Leopard shark		2		CICIMAR, SIO			OR-MX
		CARCHARHINIDAE									
			Carcharhinus brachyurus (Günther 1870)	Narrowtooth shark		2		IGUNAM, SIO			CG
		SPHYRNIDAE									
			Sphyrna zygaena (Linnaeus 1758)	Smooth hammerhead	3						CT
			Sphyrna sp.				1		S		
	SQUATINIFORMES										
		SQUATINIDAE									
			Squatina californica (Ayres 1859)	Pacific angelshark	1		1		S		EP

(continued)

TABLE 2 (Continued)

Systematic list of fishes of Cedros Archipelago, México, Northeastern Pacific. Classification according to Eschmeyer (2015). *Common name sensu Page et al. (2013); 1 = Fiel record, 2 = Museum recod, 3 = Literature; **Data from field surveys; ***BA = Biogeographic affinity: AL = Aleutian province, OR = Oregonian province, SD = San Diegan province, CZ = Cortez province, MX = Mexican province, PA = Panamic province, PE = Peruvian province, POI = Pacific Oceanic Islands province, CG = Circumglobal, CT = Circumtropical, NWP = Northwestern Pacific, EP = Eastern Pacific, AA = AmphiAmerican. sensu Love et al. (2005) and Robertson and Allen (2015).

CLASS	ORDER	FAMILY	Scientific name	Common name*	Cedros	San Benito	Natividad	Museum data	Habitat**	Notes	BA***
CHONDRICHTHYES (continued)											
	RAJIFORMES										
		RAJIDAE									
			Raja inornata (Jordan & Gilbert 1881)	California skate	2			CAS, LACM			AL-CZ
			Raja stellulata (Jordan & Gilbert 1880)	Starry skate	3					Southern limit	NEP
		RHINOBATIDAE									
			Rhinobatos productus (Ayres 1854)	Shovelnose guitarfish	2			LACM			OR-MX
			Zapteryx exasperata (Jordan & Gilbert 1880)	Banded guitarfish	1	1	1		S		SD-PA
	MYLIOBATIFORMES										
		MYLIOBATIDAE									
			Myliobatis californica (Gill 1865)	Bat ray	1				S		OR-MX-POI
		UROLOPHIDAE									
			Urobatis concentricus (Osburn & Nichols 1916)	Reef stingray	1, 3				S	Northern limit	CZ-MX
			Urobatis halleri (Cooper 1863)	Round stingray	1, 2		1	SIO	S		OR-PA
HOLOCEPHALI											
	CHIMAERIFORMES										
		CHIMAERIDAE									
			Hydrolagus colliei (Lay & Bennett 1839)	Spotted ratfish	2, 3			CICIMAR			AL-CZ
ACTINOPTERI											
	ANGUILLIFORMES										
		MURAENIDAE									
			Gymnothorax mordax (Ayres 1859)	California moray	1, 2	1, 2		UABC, LACM, SIO	I, S		SD
		CONGRIDAE									
			Gnathophis cinctus (Garman 1899)	Hardtail conger		2		SIO			SD-CH
		NEMICHTHYIDAE									
			Nemichthys scolopaceus (Richardson 1848)	Slender snipe eel	2			LACM			CT
		NETTASTOMATIDAE									
			Facciolella equatorialis (Gilbert 1891)	Dogface witch eel	2	2		SIO			SD-PA
	CLUPEIFORMES										
		CLUPEIDAE									
			Etrumeus teres (DeKay 1842)	Round herring	2, 3			CICIMAR, CMN, CAS			CG
			Sardinops sagax (Jenyns 1842)	Pacific sardine	1, 2, 3		1, 2		S		AL-CZ
		ENGRAULIDAE									
			Engraulis mordax (Girard 1854)	Northern anchovy	2			CICIMAR, LACM, SIO			AL-CZ

(continued)

TABLE 2 (Continued)

Systematic list of fishes of Cedros Archipelago, México, Northeastern Pacific. Classification according to Eschmeyer (2015). *Common name sensu Page et al. (2013); 1 = Fiel record, 2 = Museum recod, 3 = Literature; **Data from field surveys; ***BA = Biogeographic affinity: AL = Aleutian province, OR = Oregonian province, SD = San Diegan province, CZ = Cortez province, MX = Mexican province, PA = Panamic province, PE = Peruvian province, POI = Pacific Oceanic Islands province, CG = Circumglobal, CT = Circumtropical, NWP = Northwestern Pacific, EP = Eastern Pacific, AA = AmphiAmerican. sensu Love et al. (2005) and Robertson and Allen (2015).

CLASS	ORDER	FAMILY	Scientific name	Common name*	Cedros	San Benito	Natividad	Museum data	Habitat**	Notes	BA***
ACTINOPTERI (continued)											
	OSMERIFORMES										
		ARGENTINIDAE									
			Argentina sialis (Gilbert 1890)	Pacific argentine	2	2		CICIMAR, IBUNAM, LACM, SIO			OR-SD
		MICROSTOMATIDAE									
			Nansenia crassa (Lavenberg 1965)	Stout argentine	2			CICIMAR		Southern limit	OR-SD
		BATHYLAGIDAE									
			Bathylagoides wesethi (Bolin 1938)	Snubnose blacksmelt	2			CICIMAR			OR-SD
			Leuroglossus stilbius (Gilbert 1890)	California smoothtongue	2			CICIMAR			OR-PA
	STOMIIFORMES										
		GONOSTOMATIDAE									
			Cyclothone acclinidens (Garman 1899)	Benttooth bristlemouth	2			CICIMAR			CG
			Cyclothone signata (Garman 1899)	Showy bristlemouth	2			CICIMAR			EP
			Diplophos taenia (Günther 1873)	Pacific portholefish	2			CICIMAR			CG
		STERNOPTYCHIDAE									
			Argyropelecus sladeni (Regan 1908)	Sladen's hatchet fish	2			CICIMAR			CG
		PHOSICHTHYIDAE									
			Ichthyococcus irregularis (Rechnitzer & Böhlke 1958)	Bulldog lightfish	2			CICIMAR			NEP
			Vinciguerria lucetia (Garman 1899)	Panama lightfish	2			IBUNAM, CICIMAR			OR-CH
		STOMIIDAE									
			Idiacanthus antrostomus (Gilbert 1890)	Pacific blackdragon	2			CICIMAR			TEP
			Stomias atriventer (Garman 1899)	Blackbelly dragonfish	2			CICIMAR		Northern limit	SD-CH
	AULOPIFORMES										
		SCOPELARCHIDAE									
			Scopelarchus guentheri (Alcock 1896)	Staring pearleye	2			CICIMAR			CT
			Scopelarchoides nicholsi (Parr 1929)	Pearleye	3					Northern limit	SD-CH
		SYNODONTIDAE									
			Synodus lacertinus (Gilbert 1890)	Calico lizardfish	3						SD-CH-POI
			Synodus lucioceps (Ayres 1855)	California lizardfish	2	2		IBUNAM, CICIMAR, LACM, SIO		Southern limit	OR-CZ
		PARALEPIDIDAE									
			Arctozenus risso (Bonaparte 1840)	White barracudina	2			CICIMAR		Southern limit	CG
			Lestidiops ringens (Jordan & Gilbert 1880)	Slender barracudina	2			CICIMAR, LACM		Southern limit	OR-SD

(continued)

TABLE 2 (Continued)

Systematic list of fishes of Cedros Archipelago, México, Northeastern Pacific. Classification according to Eschmeyer (2015). *Common name sensu Page et al. (2013); 1 = Fiel record, 2 = Museum recod, 3 = Literature; **Data from field surveys; ***BA = Biogeographic affinity: AL = Aleutian province, OR = Oregonian province, SD = San Diegan province, CZ = Cortez province, MX = Mexican province, PA = Panamic province, PE = Peruvian province, POI = Pacific Oceanic Islands province, CG = Circumglobal, CT = Circumtropical, NWP = Northwestern Pacific, EP = Eastern Pacific, AA = AmphiAmerican. sensu Love et al. (2005) and Robertson and Allen (2015).

CLASS	ORDER	FAMILY	Scientific name	Common name*	Cedros	San Benito	Natividad	Museum data	Habitat**	Notes	BA***
ACTINOPTERI (continued)											
	MYCTOPHIFORMES										
		MYCTOPHIDAE									
			Ceratoscopelus townsendi (Eigenmann & Eigenmann 1889)	Dogtooth lampfish	2			CICIMAR			CG
			Diogenichthys atlanticus (Tåning 1928)	Longfin lanternfish	2			CICIMAR			CG
			Diogenichthys laternatus (Garman 1899)	Diogenes lanternfish	2			CICIMAR			SD-CH
			Electrona risso (Cocco 1829)	Electric lanternfish	2			CICIMAR			CG
			Gonichthys tenuiculus (Garman 1899)	Slendertail lanternfish	2			CICIMAR			SD-CH
			Hygophum atratum (Garman 1899)	Thickhead flashlightfish	2			CICIMAR			CZ
			Hygophum reinhardtii (Lütken 1892)	Reinhardt's lanternfish	2			CICIMAR			AA
			Lampadena urophaos (Paxton 1963)	Sunbeam lampfish	2, 3			CICIMAR			AA
			Loweina rara (Lütken 1892)	Laura's lanternfish	2			CICIMAR			CG
			Myctophum nitidulum (Garman 1899)	Pearly lanternfish	2			CICIMAR			CG
			Nannobrachium idostigma (Parr 1931)	Lanternfish	2			CICIMAR		Range extension North	TEP
			Nannobrachium ritteri (Gilbert 1915)	Broadfin lampfish	2			CICIMAR		Southern limit	NEP
			Notolychnus valdiviae (Brauer 1904)	Topside lampfish	2			CICIMAR			CT
			Protomyctophum crockeri (Bolin 1939)	California flashlightfish	2			CICIMAR			NP
			Symbolophorus californiensis (Eigenmann & Eigenmann 1889)	Bigfin lanternfish	2, 3			CICIMAR		Southern limit	NP
			Triphoturus mexicanus (Gilbert 1890)	Mexican lampfish	2			CICIMAR			AL-MX
	LAMPRIFORMES										
		TRACHIPTERIDAE									
			Zu cristatus (Bonelli 1820)	Scalloped ribbonfish	2			SIO			CG
	GADIFORMES										
		MORIDAE									
			Physiculus rastrelliger (Gilbert 1890)	Hundred-fathom codling	2			SIO			OR-PA
		MERLUCCIIDAE									
			Merluccius productus (Ayres 1855)	Pacific hake	2			CICIMAR, SIO			AL-MX

(continued)

TABLE 2 (Continued)

Systematic list of fishes of Cedros Archipelago, México, Northeastern Pacific. Classification according to Eschmeyer (2015). *Common name sensu Page et al. (2013); 1 = Fiel record, 2 = Museum recod, 3 = Literature; **Data from field surveys; ***BA = Biogeographic affinity: AL = Aleutian province, OR = Oregonian province, SD = San Diegan province, CZ = Cortez province, MX = Mexican province, PA = Panamic province, PE = Peruvian province, POI = Pacific Oceanic Islands province, CG = Circumglobal, CT = Circumtropical, NWP = Northwestern Pacific, EP = Eastern Pacific, AA = AmphiAmerican. sensu Love et al. (2005) and Robertson and Allen (2015).

CLASS	ORDER	FAMILY	Scientific name	Common name*	Cedros	San Benito	Natividad	Museum data	Habitat**	Notes	BA***
ACTINOPTERI (continued)											
	OPHIDIIFORMES										
		OPHIDIIDAE									
			Chilara taylori (Girard 1858)	Spotted cusk-eel	2			LACM, SIO			OR-PA
			Lepophidium negropinna (Hildebrand & Barton 1949)	Specklefin cusk-eel	2			CICIMAR, SIO		Northern limit	TEP
			Lepophidium prorates (Jordan & Bollman 1890)	Prowspine cusk-eel	2			LACM		Range extension North	TEP
			Lepophidium stigmatistium (Gilbert 1890)	Mexican cusk-eel	3					Northern limit	SD-CZ
			Lepophidium sp.		2			LACM			
			Ophidion galeoides (Gilbert 1890)	Spotfin cusk-eel	3					Northern limit	SD-PA
			Ophidion scrippsae (Hubbs 1916)	Basketweave cusk-eel	2			CICIMAR, CAS, LACM, SIO			OR-SD
	BATRACHOIDIFORMES										
		BATRACHOIDIDAE									
			Porichthys myriaster (Hubbs & Schultz 1939)	Specklefin midshipman	2			CICIMAR, SIO			OR-PA
			Porichthys notatus (Girard 1854)	Plainfin midshipman	2			CAS, IBUNAM, LACM, SIO			OR-SD
	GOBIESOCIFORMES										
		GOBIESOCIDAE									
			Gobiesox eugrammus (Briggs 1955)	Lined clingfish		2		SIO		Southern limit	SD
			Gobiesox rhessodon (Smith 1881)	California clingfish	1, 2	1, 2	1	UABC, LACM, SIO	I		OR-SD
			Rimicola dimorpha (Briggs 1955)	Southern clingfish		2		SIO		Southern limit	SD
			Rimicola eigenmanni (Gilbert 1890)	Slender clingfish	1, 2			UABC, LACM	I		SD
	ATHERINIFORMES										
		ATHERINIDAE									
			Leuresthes tenuis (Ayres 1860)	California grunion	1, 2			UABC, SIO	I, S		OR-SD
		ATHERINOPSIDAE									
			Atherinops affinis (Ayres 1860)	Topsmelt	1, 2	1, 2	1	UABC, CAS, LACM, SIO	I, S		AL-CZ
			Atherinopsis californiensis (Girard 1854)	Jacksmelt	1, 2	2		UABC, CAS, LACM, SIO	I		OR-CZ

(continued)

TABLE 2 (Continued)

Systematic list of fishes of Cedros Archipelago, México, Northeastern Pacific. Classification according to Eschmeyer (2015). *Common name sensu Page et al. (2013); 1 = Fiel record, 2 = Museum recod, 3 = Literature; **Data from field surveys; ***BA = Biogeographic affinity: AL = Aleutian province, OR = Oregonian province, SD = San Diegan province, CZ = Cortez province, MX = Mexican province, PA = Panamic province, PE = Peruvian province, POI = Pacific Oceanic Islands province, CG = Circumglobal, CT = Circumtropical, NWP = Northwestern Pacific, EP = Eastern Pacific, AA = AmphiAmerican. sensu Love et al. (2005) and Robertson and Allen (2015).

CLASS	ORDER	FAMILY	Scientific name	Common name*	Cedros	San Benito	Natividad	Museum data	Habitat**	Notes	BA***
ACTINOPTERI (continued)											
	BELONIFORMES										
		SCOMBERESOCIDAE									
			Cololabis saira (Brevoort 1856)	Pacific saury	2	2		CICIMAR, CAS, LACM, SIO			NP
		BELONIDAE									
			Platybelone argalus (Lesueur 1821)	Keeltail needlefish		2		SIO		Range extension North	CT
			Strongylura exilis (Girard 1854)	California needlefish	2, 3			LACM, SIO			OR-CH
			Tylosurus crocodilus (Péron & Lesueur 1821)	Hound needlefish	1, 2		1	UABCS	S	Northern limit	CG
		HEMIRAMPHIDAE									
			Euleptorhamphus viridis (van Hasselt 1823)	Ribbon halfbeak	2	2		SIO			TR
			Hemiramphus saltator (Gilbert & Starks 1904)	Longfin halfbeak	2			LACM		Range extension North	TEP
		EXOCOETIDAE									
			Cheilopogon heterurus (Rafinesque 1810)	Blotchwing flyingfish	2		2	CICIMAR, SIO			CT
			Cheilopogon pinnatibarbatus (Bennett 1831)	Smallhead flyingfish	2	2	2	CAS, LACM, SIO			OR-CZ
			Cypselurus sp.		2			LACM			
	STEPHANOBERYCIFORMES										
		MELAMPHAIDAE									
			Melamphaes lugubris (Gilbert 1890)	Highsnout melamphid	2			CICIMAR		Southern limit	NEP
	BERYCIFORMES										
		HOLOCENTRIDAE									
			Myripristis leiognathus (Valenciennes 1846)	Panamic soldierfish	1, 2			SIO	S	Northern limit	TEP
	SYNGNATHIFORMES										
		CENTRISCIDAE									
			Macroramphosus gracilis (Lowe 1839)	Slender snipefish		2		IBUNAM, CICIMAR, LACM, SIO			CG
		SYNGNATHIDAE									
			Syngnathus euchrous (Fritzsche 1980)	Chocolate pipefish	2			CAS, SIO		Southern limit	SD
			Syngnathus exilis (Osburn & Nichols 1916)	Barcheek pipefish	2, 3	2		CAS, SIO		Southern limit	OR-SD

(continued)

TABLE 2 (Continued)

Systematic list of fishes of Cedros Archipelago, México, Northeastern Pacific. Classification according to Eschmeyer (2015). *Common name sensu Page et al. (2013); 1 = Fiel record, 2 = Museum recod, 3 = Literature; **Data from field surveys; ***BA = Biogeographic affinity: AL = Aleutian province, OR = Oregonian province, SD = San Diegan province, CZ = Cortez province, MX = Mexican province, PA = Panamic province, PE = Peruvian province, POI = Pacific Oceanic Islands province, CG = Circumglobal, CT = Circumtropical, NWP = Northwestern Pacific, EP = Eastern Pacific, AA = AmphiAmerican. sensu Love et al. (2005) and Robertson and Allen (2015).

CLASS	ORDER	FAMILY	Scientific name	Common name*	Cedros	San Benito	Natividad	Museum data	Habitat**	Notes	BA***
ACTINOPTERI (continued)											
	SCORPAENIFORMES										
		SEBASTIDAE									
			Sebastes atrovirens (Jordan & Gilbert 1880)	Kelp rockfish	1, 2	1, 2		LACM, SIO	S	Southern limit	OR-SD
			Sebastes auriculatus (Girard 1854)	Brown rockfish	1	1			S		NEP
			Sebastes aurora (Gilbert 1890)	Aurora rockfish	3					Southern limit	NEP
			Sebastes carnatus (Jordan & Gilbert 1880)	Gopher rockfish			2	LACM			OR-SD
			Sebastes caurinus (Richardson 1844)	Copper rockfish		1, 2, 3		LACM	S	Southern limit	NEP
			Sebastes chrysomelas (Jordan & Gilbert 1881)	Black-and-yellow rockfish			2	LACM			OR-SD
			Sebastes diploproa (Gilbert 1890)	Splitnose rockfish	2, 3			SIO		Southern limit	NEP
			Sebastes elongatus (Ayres 1859)	Greenstriped rockfish	1, 3				S	Southern limit	NEP
			Sebastes flavidus (Ayres 1862)	Yellowtail rockfish	1				S	Range extension South	AL-SD
			Sebastes hopkinsi (Cramer 1895)	Squarespot rockfish	1	1			S	Range extension South	OR-SD
			Sebastes lentiginosus (Chen 1971)	Freckled rockfish	2			LACM		Southern limit	OR-SD
			Sebastes macdonaldi (Eigenmann & Beeson 1893)	Mexican rockfish	2			CICIMAR, LACM			SD-CZ
			Sebastes melanostomus (Eigenmann & Eigenmann 1890)	Blackgill rockfish	3					Southern limit	OR-SD
			Sebastes miniatus (Jordan & Gilbert 1880)	Vermilion rockfish		1, 2, 3		LACM	S	Southern limit	AL-SD
			Sebastes paucispinis (Ayres 1854)	Bocaccio rockfish	2			SIO		Range extension South	NEP
			Sebastes rosaceus (Girard 1854)	Rosy rockfish	2			SIO		Southern limit	OR-SD
			Sebastes saxicola (Gilbert 1890)	Stripetail rockfish	2			SIO			NEP
			Sebastes semicinctus (Gilbert 1897)	Halfbanded rockfish	2			SIO		Range extension South	OR-SD
			Sebastes serranoides (Eigenmann & Eigenmann 1890)	Olive rockfish		1, 2, 3		SIO	S	Southern limit	OR-SD
			Sebastes serriceps (Jordan & Gilbert 1880)	Treefish	1, 2, 3			LACM	S	Southern limit	OR-SD
			Sebastes sp.	Rockfish	1	1			S		
			Sebastes umbrosus (Jordan & Gilbert 1882)	Honeycomb rockfish		2		LACM		Southern limit	OR-SD

(continued)

TABLE 2 (Continued)

Systematic list of fishes of Cedros Archipelago, México, Northeastern Pacific. Classification according to Eschmeyer (2015). *Common name sensu Page et al. (2013); 1 = Fiel record, 2 = Museum recod, 3 = Literature; **Data from field surveys; ***BA = Biogeographic affinity: AL = Aleutian province, OR = Oregonian province, SD = San Diegan province, CZ = Cortez province, MX = Mexican province, PA = Panamic province, PE = Peruvian province, POI = Pacific Oceanic Islands province, CG = Circumglobal, CT = Circumtropical, NWP = Northwestern Pacific, EP = Eastern Pacific, AA = AmphiAmerican. sensu Love et al. (2005) and Robertson and Allen (2015).

CLASS	ORDER	FAMILY	Scientific name	Common name*	Cedros	San Benito	Natividad	Museum data	Habitat**	Notes	BA***
ACTINOPTERI (continued)											
	SCORPAENIFORMES (continued)										
		SCORPAENIDAE									
			Pontinus vaughani (Barnhart & Hubbs 1946)	Spotback scorpionfish	1, 2			SIO	S	Range extension North	CZ-POI
			Scorpaena guttata (Girard 1854)	California scorpionfish	1, 2			UABC, CICIMAR, LACM, SIO	I, S		SD-CZ
			Scorpaenodes xyris (Jordan & Gilbert 1882)	Rainbow scorpionfish	2	2		LACM, SIO			SD-PA-POI
		EPINEPHELIDAE									
			Mycteroperca rosacea (Streets 1877)	Leopard grouper			1		S		SD-MX
		TRIGLIDAE									
			Prionotus ruscarius (Gilbert & Starks 1904)	Rough searobin	2			CICIMAR		Range extension North	SD-CH
			Prionotus stephanophrys (Lockington 1881)	Lumptail searobin	2			CAS, LACM			OR-CH
	PERCIFORMES										
		POLYPRIONIDAE									
			Stereolepis gigas (Ayres 1859)	Giant seabass			1		S		SD-CZ
		SERRANIDAE									
			Alphestes immaculatus (Breder 1936)	Pacific mutton hamlet		1	1			Northern limit	TEP
			Epinephelus labriformis (Jenyns 1840)	Flag cabrilla	1, 3	1, 3			S		SD-PA-POI
			Paralabrax auroguttatus (Walford 1936)	Goldspotted sand bass	1, 2, 3			LACM	S	Northern limit	CZ
			Paralabrax clathratus (Girard 1854)	Kelp bass	1, 2	1, 2	1, 2	CICIMAR, LACM, SIO	S		OR-SD
			Paralabrax maculatofasciatus (Steindachner 1868)	Spotted sand bass	2			CICIMAR			OR-CZ
			Paralabrax nebulifer (Girard 1854)	Barred sand bass	1, 2	1, 2	1	CICIMAR, LACM, SIO	S		OR-MX
			Paranthias colonus (Valenciennes 1846)	Pacific creolefish		2	1	LACM	S	Northern limit	TEP
			Pronotogrammus multifasciatus (Gill 1863)	Threadfin bass	2			CICIMAR			SD-PA-POI
			Serranus psittacinus (Valenciennes 1846)	Barred serrano	1, 3				S	Northern limit	TEP

(continued)

TABLE 2 (Continued)

Systematic list of fishes of Cedros Archipelago, México, Northeastern Pacific. Classification according to Eschmeyer (2015). *Common name sensu Page et al. (2013); 1 = Fiel record, 2 = Museum recod, 3 = Literature; **Data from field surveys; ***BA = Biogeographic affinity: AL = Aleutian province, OR = Oregonian province, SD = San Diegan province, CZ = Cortez province, MX = Mexican province, PA = Panamic province, PE = Peruvian province, POI = Pacific Oceanic Islands province, CG = Circumglobal, CT = Circumtropical, NWP = Northwestern Pacific, EP = Eastern Pacific, AA = AmphiAmerican. sensu Love et al. (2005) and Robertson and Allen (2015).

CLASS	ORDER	FAMILY	Scientific name	Common name*	Cedros	San Benito	Natividad	Museum data	Habitat**	Notes	BA***
ACTINOPTERI (continued)											
	PERCIFORMES (continued)										
		APOGONIDAE									
			Apogon atricaudus (Jordan & McGregor 1898)	Plain cardinalfish	2, 3			CICIMAR			SD-CZ
			Apogon guadalupensis (Osburn & Nichols 1916)	Guadalupe cardinalfish		2		LACM, SIO			SD-CZ
			Apogon pacificus (Herre 1935)	Pink cardinalfish		1, 2, 3		SIO	S		SD-CH-POI
			Apogon retrosella (Gill 1862)	Barspot cardinalfish	1, 2, 3	1, 2, 3	1	LACM, SIO	S	Northern limit	TEP
		MALACANTHIDAE									
			Caulolatilus princeps (Jenyns 1840)	Ocean whitefish	1, 2	1, 2	1, 2	LACM, SIO	S		EP
		CARANGIDAE									
			Caranx caballus (Günther 1868)	Green jack			1		S		SD-CH
			Chloroscombrus orqueta (Jordan & Gilbert 1883)	Pacific bumper	2			CICIMAR			SD-CH
			Decapterus muroadsi (Temminck & Schlegel 1844)	Amberstripe scad	2	2		LACM		Northern limit	TR
			Seriola lalandi (Valenciennes 1833)	Yellowtail jack	1, 2	1	1, 2	CICIMAR, LACM, SIO	S		CT
			Trachurus symmetricus (Ayres 1855)	Pacific jack mackerel	1	1, 2		CICIMAR, LACM, SIO	S		AL-CZ
			Uraspis secunda (Poey 1860)	Whitemouth jack		2		SIO			CG
		CORYPHAENIDAE									
			Coryphaena hippurus (Linnaeus 1758)	Dolphinfish	2		1	CICIMAR, SIO	S		CT
		CARISTIIDAE									
			Caristius macropus (Bellotti 1903)	Bigmouth manefish	3					Southern limit	NEP
		GERREIDAE									
			Eucinostomus dowii (Gill 1863)	Pacific spotfin mojarra		2		SIO			SD-CH
		HAEMULIDAE									
			Anisotremus davidsonii (Steindachner 1876)	Sargo	1, 2	1, 2	1	CICIMAR, LACM, SIO	S		SD-CZ
			Anisotremus interruptus (Gill 1862)	Burrito grunt	1				S	Northern limit	TEP
			Orthopristis reddingi (Jordan & Richardson 1895)	Bronzestriped grunt	2, 3			CAS		Northern limit	SD-MX
			Xenistius californiensis (Steindachner 1876)	Salema	1	1			S		OR-PA

(continued)

TABLE 2 (Continued)

Systematic list of fishes of Cedros Archipelago, México, Northeastern Pacific. Classification according to Eschmeyer (2015). *Common name sensu Page et al. (2013); 1 = Fiel record, 2 = Museum recod, 3 = Literature; **Data from field surveys; ***BA = Biogeographic affinity: AL = Aleutian province, OR = Oregonian province, SD = San Diegan province, CZ = Cortez province, MX = Mexican province, PA = Panamic province, PE = Peruvian province, POI = Pacific Oceanic Islands province, CG = Circumglobal, CT = Circumtropical, NWP = Northwestern Pacific, EP = Eastern Pacific, AA = AmphiAmerican. sensu Love et al. (2005) and Robertson and Allen (2015).

CLASS	ORDER	FAMILY	Scientific name	Common name*	Cedros	San Benito	Natividad	Museum data	Habitat**	Notes	BA***
ACTINOPTERI (continued)											
	PERCIFORMES (continued)										
		SPARIDAE									
			Calamus brachysomus (Lockington 1880)	Pacific porgy		2	1	SIO	S		SD-CH
		SCIAENIDAE									
			Cheilotrema saturnum (Girard 1858)	Black croaker		2		SIO			SD-CZ
			Genyonemus lineatus (Ayres 1855)	White croaker	2			SIO			OR-SD
			Larimus acclivis (Jordan & Bristol 1898)	Steeplined drum	3					Northern limit	TEP
			Pareques sp.	Croaker	1	1, 2			S		
			Seriphus politus (Ayres 1860)	Queenfish	2			SIO			OR-CZ
			Umbrina roncador (Jordan & Gilbert 1882)	Yellowfin croaker	2			SIO			SD-CZ
		KYPHOSIDAE									
			Girella nigricans (Ayres 1860)	Opaleye	1, 2	1, 2	1, 2	UABC, LACM, SIO	I, S		SD-CZ
			Kyphosus azurea (Jenkins & Evermann 1889)	Zebraperch	1, 2		1, 2	UABC, CICIMAR	I, S		OR-CZ
			Medialuna californiensis (Steindachner 1876)	Halfmoon	1, 2	1, 2	1, 2	IBUNAM, CICIMAR, LACM, SIO	S		AL-CZ
		CHAETODONTIDAE									
			Chaetodon humeralis (Günther 1860)	Threebanded butterflyfish		2		SIO		Northern limit	SD-CH
			Johnrandallia nigrirostris (Gill 1862)	Barberfish	1, 3	3			S	Northern limit	TEP
			Prognathodes falcifer (Hubbs & Rechnitzer 1958)	Scythe butterflyfish	2	1, 2		LACM, SIO	S		SD-CZ
		MUGILIDAE									
			Mugil curema (Valenciennes 1836)	White mulet			1, 2	UABC	I		CT
		POMACANTHIDAE									
			Pomacanthus zonipectus (Gill 1862)	Cortez angelfish		2		SIO			TEP

(continued)

TABLE 2 (Continued)

Systematic list of fishes of Cedros Archipelago, México, Northeastern Pacific. Classification according to Eschmeyer (2015). *Common name sensu Page et al. (2013); 1 = Fiel record, 2 = Museum recod, 3 = Literature; **Data from field surveys; ***BA = Biogeographic affinity: AL = Aleutian province, OR = Oregonian province, SD = San Diegan province, CZ = Cortez province, MX = Mexican province, PA = Panamic province, PE = Peruvian province, POI = Pacific Oceanic Islands province, CG = Circumglobal, CT = Circumtropical, NWP = Northwestern Pacific, EP = Eastern Pacific, AA = AmphiAmerican. sensu Love et al. (2005) and Robertson and Allen (2015).

CLASS	ORDER	FAMILY	Scientific name	Common name*	Cedros	San Benito	Natividad	Museum data	Habitat**	Notes	BA***
ACTINOPTERI (continued)											
	PERCIFORMES (continued)										
		EMBIOTOCIDAE									
			Brachyistius frenatus (Gill 1862)	Kelp surfperch	1, 2	1, 2	1	SIO	S	Southern limit	AL-SD
			Embiotoca jacksoni (Agassiz 1853)	Black perch	1, 2	1, 2	1, 2	CICIMAR, SIO	S		OR-SD
			Embiotoca sp.		2			SIO			
			Hyperprosopon argenteum (Gibbons 1854)	Walleye surfperch	2			SIO		Southern limit	OR-SD
			Micrometrus minimus (Gibbons 1854)	Dwarf perch	2			SIO		Southern limit	OR-SD
			Phanerodon atripes (Jordan & Gilbert 1880)	Sharpnose seaperch	1	1, 2		SIO	S	Southern limit	OR-SD
			Phanerodon furcatus (Girard 1854)	White seaperch	1	1			S	Range extension South	AL-SD
			Rhacochilus toxotes (Agassiz 1854)	Rubberlip seaperch	1, 2	1, 2		LACM, SIO	S	Southern limit	OR-SD
			Rhacochilus vacca (Girard 1855)	Pile perch	2		1	LACM	S	Range extension South	NEP
			Zalembius rosaceus (Jordan & Gilbert 1880)	Pink seaperch	2			CAS, LACM, SIO		Range extension South	OR-CZ
		POMACENTRIDAE									
			Abudefduf troschelii (Gill 1862)	Panamic sergeant major	1, 2	1	1	UABC	I, S	Northern limit	SD-CH-POI
			Azurina hirundo (Jordan & McGregor 1898)	Swallow damselfish		2, 3		KU, SIO			SD-CZ
			Chromis alta (Greenfield & Woods 1980)	Silverstripe chromis	1, 2	1, 2		KU, SIO	S		SD-CH-POI
			Chromis atrilobata (Gill 1862)	Scissortail chromis	1, 2	2		SIO	S	Northern limit	TEP
			Chromis punctipinnis (Cooper 1863)	Blacksmith	1, 2	1, 2	1, 2	CICIMAR, KU, LACM, SIO	S		OR-SD
			Hypsypops rubicundus (Girard 1854)	Garibaldi	1, 2	1, 2	1, 2	UABC, CICIMAR, LACM, SIO	I, S		SD-CZ
			Stegastes flavilatus (Gill 1862)	Beaubrummel	1, 3				S	Northern limit	TEP
			Stegastes leucorus (Gilbert 1892)	Whitetail damselfish		1, 2		SIO	S		CZ-MX
			Stegastes rectifraenum (Gill 1862)	Cortez damselfish		2		LACM, SIO			SD-MX

(continued)

TABLE 2 (Continued)

Systematic list of fishes of Cedros Archipelago, México, Northeastern Pacific. Classification according to Eschmeyer (2015). *Common name sensu Page et al. (2013); 1 = Fiel record, 2 = Museum recod, 3 = Literature; **Data from field surveys; ***BA = Biogeographic affinity: AL = Aleutian province, OR = Oregonian province, SD = San Diegan province, CZ = Cortez province, MX = Mexican province, PA = Panamic province, PE = Peruvian province, POI = Pacific Oceanic Islands province, CG = Circumglobal, CT = Circumtropical, NWP = Northwestern Pacific, EP = Eastern Pacific, AA = AmphiAmerican. sensu Love et al. (2005) and Robertson and Allen (2015).

CLASS	ORDER	FAMILY	Scientific name	Common name*	Cedros	San Benito	Natividad	Museum data	Habitat**	Notes	BA***
ACTINOPTERI (continued)											
	PERCIFORMES (continued)										
		LABRIDAE									
			Bodianus diplotaenia (Gill 1862)	Mexican hogfish	1, 2, 3	2		LACM	S	Northern limit	SD-CH-POI
			Halichoeres dispilus (Günther 1864)	Chameleon wrasse	1	1, 2		SIO	S	Northern limit	TEP
			Halichoeres melanotis (Gilbert 1890)	Golden wrasse	3	1, 3			S	Northern limit	TEP
			Halichoeres notospilus (Günther 1864)	Banded wrasse	1, 2		1	UABC	I, S	Range extension North	TEP
			Halichoeres semicinctus (Ayres 1859)	Rock wrasse	1, 2	1, 2	1, 2	UABC, CICIMAR, CAS, LACM, SIO	I, S		SD-CZ
			Oxyjulis californica (Günther 1861)	Señorita	1	1, 2	1	SIO	S		OR-SD
			Semicossyphus pulcher (Ayres 1854)	California sheephead	1, 2	1, 2	1, 2	LACM, SIO	S		OR-CZ
			Thalassoma lucasanum (Gill 1862)	Cortez rainbow wrasse	1	1			S	Northern limit	TEP
		SCARIDAE									
			Nicholsina denticulata (Evermann & Radcliffe 1917)	Loosetooth parrotfish	1, 3	1, 3			S		SD-PA-POI
		ZOARCIDAE									
			Lyconema barbatum (Gilbert 1896)	Bearded eelpout	2	2		SIO		Southern limit	OR-SD
		CHIASMODONTIDAE									
			Chiasmodon niger (Johnson 1864)	Black swallower	2			CICIMAR		Range extension South	CG
		URANOSCOPIDAE									
			Kathetostoma averruncus (Jordan & Bollman 1890)	Smooth stargazer	2	2		UF, LACM, SIO			SD-CH
		TRIPTERYGIIDAE									
			Enneanectes carminalis (Jordan & Gilbert 1882)	Carmine triplefin		1, 2		LACM	S	Northern limit	TEP
			Enneanectes reticulatus (Allen & Robertson 1991)	Flag triplefin		2		SIO		Northern limit	CZ

(continued)

TABLE 2 (Continued)

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CLASS	ORDER	FAMILY	Scientific name	Common name*	Cedros	San Benito	Natividad	Museum data	Habitat**	Notes	BA***
ACTINOPTERI (continued)											
	PERCIFORMES (continued)										
		LABRISOMIDAE									
			Alloclinus holderi (Lauderbach 1907)	Island kelpfish	1, 2	1, 2	1	UABC, LACM, SIO	S		SD
			Labrisomus multiporosus (Hubbs 1953)	Porehead blenny	1, 2		1, 2	UABC	I	Northern limit	TEP
			Labrisomus sp.	Blenny		2		SIO			
			Labrisomus xanti (Gill 1860)	Largemouth blenny	1, 2		1	UABC, LACM	I	Northern limit	TEP
			Paraclinus integripinnis (Smith 1880)	Reef finspot	1, 2	1, 2	2	UABC, LACM, SIO	I		OR-SD
			Starksia guadalupae (Rosenblatt & Taylor 1971)	Guadalupe blenny		2		LACM			SD
		CLINIDAE									
			Gibbonsia elegans (Cooper 1864)	Spotted kelpfish	1, 2	1, 2	1, 2	UABC, LACM, SIO	I		OR-SD
			Gibbonsia montereyensis (Hubbs 1927)	Crevice kelpfish	1, 2	1, 2	1, 2	UABC, SIO	I	Range extension South	AL-SD
			Heterostichus rostratus (Girard 1854)	Giant kelpfish	1, 2	1, 2	1, 2	UABC, CAS, LACM, SIO	I, S		OR-SD
		CHAENOPSIDAE									
			Neoclinus blanchardi (Girard 1858)	Sarcastic fringehead	2, 3			LACM		Southern limit	OR-SD
		DACTYLOSCOPIDAE									
			Gillellus semicinctus (Gilbert 1890)	Halfbanded stargazer	2			SIO		Northern limit	TEP
		BLENNIIDAE									
			Hypsoblennius gilberti (Jordan 1882)	Rockpool blenny	1, 2		1, 2	UABC	I		SD
			Hypsoblennius jenkinsi (Jordan & Evermann 1896)	Mussel blenny	1, 2	1, 2		UABC, SIO	I		SD-CZ
			Hypsoblennius gentilis	Bay blenny	1		1		I		SD-CZ
			Ophioblennius steindachneri (Jordan & Evermann 1898)	Panamic fanged blenny	1, 2		1, 2	UABC	I, S		TEP
			Plagiotremus azaleus (Jordan & Bollman 1890)	Sabertooth blenny	1, 3				S		SD-PA-POI
		CALLIONYMIDAE									
			Synchiropus atrilabiatus (Garman 1899)	Blacklip dragonet	3						SD-CH-POI
		ELEOTRIDAE									
			Eleotris picta (Kner 1863)	Spotted sleeper	2			CICIMAR		Range extension North	TEP

(continued)

TABLE 2 (Continued)

Systematic list of fishes of Cedros Archipelago, México, Northeastern Pacific. Classification according to Eschmeyer (2015). *Common name sensu Page et al. (2013); 1 = Fiel record, 2 = Museum recod, 3 = Literature; **Data from field surveys; ***BA = Biogeographic affinity: AL = Aleutian province, OR = Oregonian province, SD = San Diegan province, CZ = Cortez province, MX = Mexican province, PA = Panamic province, PE = Peruvian province, POI = Pacific Oceanic Islands province, CG = Circumglobal, CT = Circumtropical, NWP = Northwestern Pacific, EP = Eastern Pacific, AA = AmphiAmerican. sensu Love et al. (2005) and Robertson and Allen (2015).

CLASS	ORDER	FAMILY	Scientific name	Common name*	Cedros	San Benito	Natividad	Museum data	Habitat**	Notes	BA***
ACTINOPTERI (continued)											
	PERCIFORMES (continued)										
		GOBIIDAE									
			Acanthogobius flavimanus (Temminck & Schlegel 1845)	Yellowfin goby	3					Range extension South	NWP
			Bathygobius ramosus (Ginsburg 1947)	Panamic frillfin	1, 2		1	UABC	I	Range extension North	TEP
			Lepidogobius lepidus (Girard 1858)	Bay goby	3					Southern limit	EP
			Lythrypnus dalli (Gilbert 1890)	Bluebanded goby	1, 2	1, 2	1	CICIMAR, LACM, SIO	S		SD-PA-POI
			Lythrypnus zebra (Gilbert 1890)	Zebra goby	2	1, 2	2	LACM, SIO	S		SD-CZ
			Rhinogobiops nicholsii (Bean 1882)	Blackeye goby	1, 2, 3	1	1	LACM	S	Southern limit	AL-SD
		LUVARIDAE									
			Luvarus imperialis (Rafinesque 1810)	Louvar	2			SIO			CG
		SPHYRAENIDAE									
			Sphyraena argentea (Girard 1854)	Pacific barracuda	2		1	CICIMAR, SIO	S		NEP
			Sphyraena lucasana (Gill 1863)	Cortez barracuda	1, 2, 3			UABCS	S	Northern limit	CZ-MX
		TRICHIURIDAE									
			Lepidopus fitchi (Rosenblatt & Wilson 1987)	Pacific scabbardfish	2			CICIMAR, LACM			OR-CH
		SCOMBRIDAE									
			Sarda chiliensis (Cuvier 1832)	Pacific bonito	2		2	SIO			AL-PA
			Scomber japonicus (Houttuyn 1782)	Pacific chub mackerel	2			CICIMAR, SIO			TR
		STROMATEIDAE									
			Peprilus simillimus (Ayres 1860)	Pacific pompano	3						OR-CZ
	COTTIFORMES										
		HEXAGRAMMIDAE									
			Ophiodon elongatus (Girard 1854)	Lingcod			1		S	Range extension South	AL-SD
			Zaniolepis frenata (Eigenmann & Eigenmann 1889)	Shortspine combfish	2	2		LACM, SIO			OR-CZ
			Zaniolepis latipinnis (Girard 1858)	Longspine combfish	2			LACM, SIO			OR-SD

(continued)

TABLE 2 (Continued)

Systematic list of fishes of Cedros Archipelago, México, Northeastern Pacific. Classification according to Eschmeyer (2015). *Common name sensu Page et al. (2013); 1 = Fiel record, 2 = Museum recod, 3 = Literature; **Data from field surveys; ***BA = Biogeographic affinity: AL = Aleutian province, OR = Oregonian province, SD = San Diegan province, CZ = Cortez province, MX = Mexican province, PA = Panamic province, PE = Peruvian province, POI = Pacific Oceanic Islands province, CG = Circumglobal, CT = Circumtropical, NWP = Northwestern Pacific, EP = Eastern Pacific, AA = AmphiAmerican. sensu Love et al. (2005) and Robertson and Allen (2015).

CLASS	ORDER	FAMILY	Scientific name	Common name*	Cedros	San Benito	Natividad	Museum data	Habitat**	Notes	BA***
ACTINOPTERI (continued)											
	COTTIFORMES (continued)										
		COTTIDAE									
			Chitonotus pugetensis (Steindachner 1876)	Soughback sculpin	2	2		LACM			NEP
			Clinocottus analis (Girard 1858)	Woolly sculpin	1, 2	1, 2	1, 2	UABC, LACM, SIO	I		OR-SD
			Icelinus cavifrons (Gilbert 1890)	Pit-head sculpin	2			LACM		Southern limit	OR-SD
			Icelinus fimbriatus (Gilbert 1890)	Fringed sculpin	3					Range extension South	OR-SD
			Icelinus quadriseriatus (Lockington 1880)	Yellowchin sculpin	2, 3			CAS, LACM, SIO			OR-SD
			Icelinus tenuis (Gilbert 1890)	Spotfin sculpin		2, 3		LACM		Southern limit	NEP
			Ruscarius creaseri	Roughcheek sculpin	2			SIO		Southern limit	OR-SD
			Scorpaenichthys marmoratus (Ayres 1854)	Cabezon	1, 2	2	1	UABC, LACM, SIO	I, S		AL-SD
		ANOPLOPOMATIDAE									
			Anoplopoma fimbria (Pallas 1814)	Sablefish		2, 3		LACM		Southern limit	NEP
		AGONIDAE									
			Agonopsis sterletus (Gilbert 1898)	Southern spearnose poacher	2			LACM, SIO		Southern limit	OR-CZ
			Odontopyxis trispinosa (Lockington 1880)	Pygmy poacher	2			LACM		Southern limit	NEP
			Xeneretmus ritteri (Gilbert 1915)	Stripefin poacher	3					Southern limit	SD
	PLEURONECTIFORMES										
		PARALICHTHYIDAE									
			Citharichthys fragilis (Gilbert 1890)	Gulf sanddab	2			CAS, SIO			SD-CZ
			Citharichthys sordidus (Girard 1854)	Pacific sanddab	2			CICIMAR, LACM, SIO			AL-CZ
			Citharichthys sp.		2			LACM			
			Citharichthys stigmaeus (Jordan & Gilbert 1882)	Speckled sanddab	2	2		CICIMAR, LACM, SIO			AL-CZ
			Citharichthys xanthostigma (Gilbert 1890)	Longfin sanddab	2	2		CICIMAR, SEMAR, CAS, LACM, SIO			SD-PA
			Etropus crossotus (Jordan & Gilbert 1882)	Fringed flounder	2			CICIMAR		Northern limit	AA
			Hippoglossina stomata (Eigenmann & Eigenmann 1890)	Bigmouth sole	2			CICIMAR, LACM			OR-CZ
			Paralichthys californicus (Ayres 1859)	California halibut	1, 2			IBUNAM, CICIMAR	S		OR-SD
			Xystreurys liolepis (Jordan & Gilbert 1880)	Fantail sole	2			LACM, SIO			OR-CZ

(continued)

TABLE 2 (Continued)

Systematic list of fishes of Cedros Archipelago, México, Northeastern Pacific. Classification according to Eschmeyer (2015). *Common name sensu Page et al. (2013); 1 = Fiel record, 2 = Museum recod, 3 = Literature; **Data from field surveys; ***BA = Biogeographic affinity: AL = Aleutian province, OR = Oregonian province, SD = San Diegan province, CZ = Cortez province, MX = Mexican province, PA = Panamic province, PE = Peruvian province, POI = Pacific Oceanic Islands province, CG = Circumglobal, CT = Circumtropical, NWP = Northwestern Pacific, EP = Eastern Pacific, AA = AmphiAmerican. sensu Love et al. (2005) and Robertson and Allen (2015).

CLASS	ORDER	FAMILY	Scientific name	Common name*	Cedros	San Benito	Natividad	Museum data	Habitat**	Notes	BA***
ACTINOPTERI (continued)											
	PLEURONECTIFORMES (continued)										
		BOTHIDAE									
			Monolene asaedai (Clark 1936)	Dark flounder	3					Range extension North	CZ-PA
		PLEURONECTIDAE									
			Glyptocephalus zachirus (Lockington 1879)	Rex sole	3					Southern limit	NEP
			Lyopsetta exilis (Jordan & Gilbert 1880)	Slender sole	2	2		CICIMAR, SIO			AL-SD
			Parophrys vetulus (Girard 1854)	English sole	2			SIO		Southern limit	NEP
			Pleuronichthys coenosus (Girard 1854)	C-O sole			2	LACM		Southern limit	AL-SD
			Pleuronichthys decurrens (Jordan & Gilbert 1881)	Curlfin sole	2			CAS		Southern limit	AL-SD
			Pleuronichthys ritteri (Starks & Morris 1907)	Spotted turbot	2			LACM			OR-SD
			Pleuronichthys verticalis (Jordan & Gilbert 1880)	Hornyhead turbot	2		2	CICIMAR, LACM, SIO			OR-CZ
		CYNOGLOSSIDAE									
			Symphurus atricaudus (Jordan & Gilbert 1880)	California tonguefish	2			CICIMAR, CAS, LACM, SIO			OR-PA
	TETRAODONTIFORMES										
		BALISTIDAE									
			Sufflamen verres (Gilbert & Starks 1904)	Orangeside triggerfish	1, 3				S	Northern limit	TEP
		TETRAODONTIDAE									
			Sphoeroides lobatus (Steindachner 1870)	Longnose puffer			1		S		SD-CH
		DIODONTIDAE									
			Diodon holocanthus (Linnaeus 1758)	Balloonfish	2			CICIMAR			CT

TABLE 3

Fish species that present range extension in their distribution in Cedros Archipelago. Reference corresponds to the most updated geographic distribution reference for these species. *Represents field records in this study.

Scientific Name	Reference	Extension to:	Northern End	Southern End
*Bathygobius ramosus**	Robertson and Allen, 2015	North	24.55 N	06.11 S
Eleotris picta	Love et al. 2005	North	23.05 N	09.25 S
*Halichoeres notospilus**	Robertson and Allen, 2015	North	26.13 N	06.93 S
Hemiramphus saltator	Love et al. 2005	North	26.01 N	09.25 S
Lepophidium prorates	Love et al. 2005	North	27.01 N	05.10 S
Monolene asaedai	Love et al. 2005	North	24.51 N	08.50 N
Nannobrachium idostigma	Love et al. 2005	North	27.20 N	35.75 S
Platybelone argalus	Love et al. 2005	North	26.10 N	35.75 S
Prionotus ruscarius	Love et al. 2005	North	26.00 N	35.75 S
Acanthogobius flavimanus	Love et al. 2005	South	52.10 N	32.68 N
Chiasmodon niger	Love et al. 2005	South	47.33 N	32.43 N
*Gibbonsia montereyensis**	Love et al. 2005	South	53.75 N	29.05 N
Icelinus fimbriatus	Love et al. 2005	South	53.50 N	32.71 N
*Ophiodon elongatus**	Love et al. 2005	South	55.00 N	29.61 N
*Phanerodon furcatus**	Love et al. 2005	South	40.60 N	29.60 N
*Rhacochilus vacca**	Love et al. 2005	South	53.75 N	29.03 N
Sebastes flavidus	Love et al. 2005	South	59.50 N	30.49 N
*Sebastes hopkinsi**	Love et al. 2005	South	43.75 N	29.03 N
Sebastes paucispinis	Love et al. 2005	South	59.50 N	29.08 N

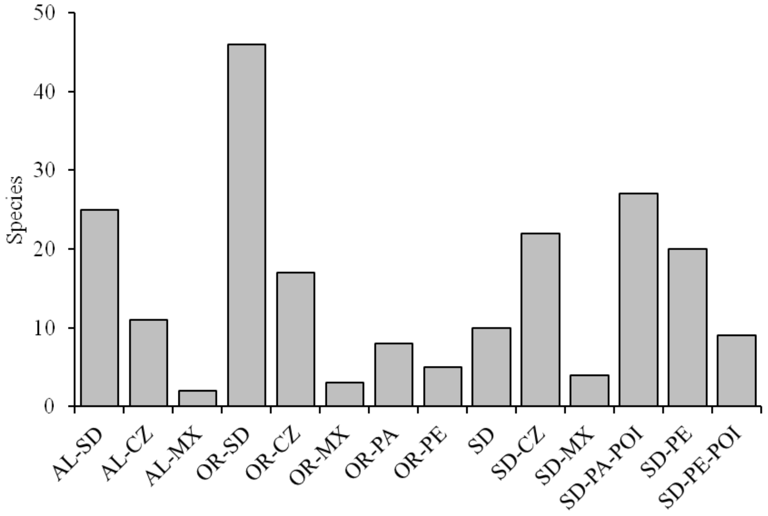

Figure 4. Distribution patterns of fish species of the Cedros Archipelago. (AL = Aleutian province, OR = Oregonian province, SD = San Diegan province, CZ = Cortez province, MX = Mexican province, PA = Panamic Province, PE = Peruvian province, POI = Pacific Oceanic Islands province)

rockpool blenny (*Hypsoblennius gilberti*), and the slender clingfish (*Rimicola eigenmanni*). Of these, the last four species were recorded in the field surveys at the CEA.

DISCUSSION

A comprehensive systematic checklist of the CEA, with a total of 269 species, is presented here. The biogeographic relationships of the fish assemblages from the CEA showed a separation from its counterparts in northern Baja California and California. Most of the fish community at the CEA (50%) has a temperate affinity (warm-temperate and cold-temperate) and the CEA represents the distribution limit for 106 species (40% of the species reported). The distribution range extension for 19 species is documented.

Based on these results, the archipelago has high species richness, 50% of the known species for the entire San Diegan province (Miller and Lea 1976; Horn et al. 2006) and 15% of those in the Cortez province (Hastings et al. 2010; Palacios-Salgado et al. 2012), are reported in this small insular territory. The CEA might be richer than coastal lagoons and bays on the Baja California Peninsula (Danemann and De la Cruz-Agüero 1993; De la Cruz-Agüero et al. 1994, 1996; Rosales-Casián

1996; Galván-Magaña et al. 2000) and even comparable with larger islands in the Gulf of California (155–190 spp.: Del Moral et al. 2013) and with those islands in the Tropical Eastern Pacific (203–363 spp.: Robertson and Cramer 2009; Erisman et al. 2011).

The species richness found in the CEA is the result of a blend of species consisting of 3 large groups with patterns of geographical distribution: 1) temperate species (warm and cold temperate) with limited intrusion into subtropical waters (51% of the species), 2) tropical species with limited intrusion into warm-temperate waters, and 3) tropical species with extended incursion into temperate waters of the Eastern Pacific (eurythermal species).

Field records showed greater species richness in Cedros (78 species), followed by Natividad and San Benito Islands, with 56 and 54 species, respectively. Although sampling effort is an important factor in species record accumulation, the sampled area for Cedros, Natividad, and San Benito is equivalent in number of transects, but not for sampling sites. The proximity between islands could assume a similarity in the fish assemblage, however the area of the islands may be an important factor. The perimeter of the island is an indicator of habitat availability and therefore increasing potential to provide shelter for more species (Planes et al. 2012). This relationship could not be obvious on islands with similar perimeters, however, the perimeter of Cedros is 6-fold higher than Natividad and 8-fold higher than San Benito.

The resulting nMDS (based on subtidal field surveys from eleven North-Eastern Pacific islands) shows the qualitative differences in fish composition along the CEA and the Southern California Bight islands. This analysis does not show the similarity pattern between San Benito and some of the Channel Islands (California) found by Pondella et al. (2005). A group of 24 species have the largest dissimilarities contribution (78%) between sites; most of them have a tropical affinity (e.g., *Abudefduf troschelii*, *Apogon retrosella*, *Caulolatilus princeps*, *Halichoeres semicinctus*, and *Zapterix exasperata*). The overall differences in the species richness between our field records and previous studies in San Benito (i.e., Pondella et al. 2005) may be related to the inclusion of diverse habitats in the field surveys (i.e., tidepools, and soft bottom), but also by the new records of a these tropical affinity species to the assemblage. Furthermore, transitional regions may be strongly influenced by seasonality, where environmental conditions can be dominant for one of the two converging regions (Horn et al. 2006), therefore inducing a shift in the presence of fish assemblages.

Comparisons to other islands and coastal rocky ecosystems highlight the importance of the CEA in terms of connectivity between warm-temperate and tropical regions. Nevertheless, conservation and management mechanisms such as Marine Protected Areas, Marine Reserves, or Marine Refuges have not yet been implemented in this region to date, excluding a small Marine Reserve at Natividad Island implemented by local fishermen 2006 (Micheli et al. 2012).

The fact that the CEA represents the distribution limit of 106 species (40% of the species reported) is evidence of the biogeographic transition zone. It has been extensively documented that the biogeographic boundaries work diffusely and that their boundaries are movable in response to climatic factors (Hubbs 1960).

This study represents the southernmost distribution extension for 10 species, and the northernmost distribution extension for 9 species. These findings may be explained by the scarcity of field studies in the region, but nevertheless, previous studies (Quast 1968; Mearns 1988; Lea and Rosenblatt 2000; Pondella et al. 2005; Palacios-Salgado and Ramirez-Valdez 2011) have noted a trend of tropical species being recorded farther north of their previously recognized distribution, especially crossing Bahía Magdalena, a geographic feature traditionally recognized as a biogeographical barrier. These extensions of distribution range may represent an indicator of the warming trend observed in this biogeographic province (Pondella et al. 2005).

In addition to the range extensions documented in this study, the record of tropical affinity species that have been reported in San Diego or even farther north are included. However, most of these records have been associated with El Niño events (Mearns 1988; Lea and Rosenblatt 2000). As some of the species were abundant and recurrent at the CEA, the record of these species in the CEA would represent their northernmost stable populations.

It is important to highlight the presence of some species in the archipelago that were absent in previous studies in the peninsula (Danemann and De la Cruz-Agüero 1993; Ruiz-Campos et al. 2010). This is the case for *Thalassoma lucasanum*, *Ophioblennius steindachneri*, *Chromis atrilobata*, and *Bodianus diplotaenia*, which were recorded farther north in Guadalupe Island (Reyes-Bonilla et al. 2010). The presence of fish species in islands and their absence on the mainland has been explained before by structural habitat differences rather than oceanographic differences (Ebeling et al. 1980), and this pattern can be important to consider when seeking to set priority among conservation areas. It also highlights the record in the Mexican coast for the Yellowfin goby (*Acanthogobius flavimanus*), a native species from the Northwestern Pacific that has been reported on the coast of California (Workman and Merz 2007).

To our knowledge, the presence of endemic species has not been recognized for the CEA. The record of *Gibbonsia norae* as an endemic species of Guadalupe Island

and San Benito (Hubbs 1960; Reyes-Bonilla et al. 2010) is now accepted as a semi-isolated population of *G. montereyensis* (Stepien and Rosenblatt 1991). Even though the proximity to the mainland may partly explain this absence of endemism, it is also known that limited endemism exists in the fish fauna of the west coast of the Baja California peninsula (Hubbs 1960).

This study demonstrates the importance of complementing recent underwater surveys with historical and museum records to prepare baseline information potentially useful for the conservation and management of fish communities. The CEA plays a key role on the connectivity in the biogeographic transition zone on the Pacific coast of the Baja California Peninsula.

SUMMARY

We documented the presence of 269 fish species in the Cedros Archipelago, and 105 species were recorded during field surveys. The observed species richness at the CEA may be the result of the confluence of three biogeographic provinces in the Pacific coast of Baja California peninsula, in addition to the proximity of the archipelago to the mainland coast and past terrestrial connection with the peninsula. Although habitat heterogeneity is an important factor in this ecosystem, our biogeographical analyses allowed us to identify the representation of 14 distribution patterns in the fish assemblage.

The biogeographic transition has a significant impact on the composition of fish communities is this region. That is evident when half of the species have temperate affinity and the rest is composed of species of tropical affinity and wide distribution. In addition, the implication as a biogeographic frontier is when the archipelago represents the distribution limit for 40% of registered species. Finally, the biogeographic analysis showed the low similarity between this island and its northern counterparts, marking the beginning of the transition to a subtropical region.

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REFERENCES

Aguilar-Rosas, L. E., S. Min Boo, F. Correa-Sandoval, A. Ramírez-Valdez, I. Giffard-Mena, and C.V. Aguilar-Rosas. 2011. First record of *Dictyopteris prolifera* (Dictyotales: Phaeophyceae) on the Eastern Pacific coast. Marine Biodiversity Records 4:1–5.

Aguirre-Munoz, A., D. A. Croll, C. J. Donlan, R. W. Henry III, M. A. Hermosillo, G. R. Howald, et al. 2008. High-impact conservation: Invasive mammal eradications from the islands of western Mexico. *Ambio*, 37, 101–107.

Briggs, J. C. 1955. A monograph of the clingfishes (Order Xenopterygii). *Stanford Ichthyol Bull*, 6, 1–224.

Briggs, J. C. 1974. *Marine Zoogeography*. McGraw-Hill, New York. 475 pp.

Busby-Spera, C. J. 1988. Evolution of a Middle Jurassic back-arc basin, Cedros Island, Baja California: Evidence from a marine volcaniclastic apron: Geological Society of America Bulletin, v. 100(2): 218–233.

Carpizo-Ituarte, E., A. Ramírez-Valdez, F. Correa-Sandoval, L. Aguilar-Rosas, I. Giffard-Mena, R. Escobar-Fernandez, and G. Montano-Moctezuma. 2012. Assessing a marine biogeographic transition zone: biogeographic patterns of the tidepools fishes of Isla de Cedros, Mexico. *In:* Hortal, J., K. Faller, K. Feeley, R. Field, et al. 2012. Conference program and abstracts. International Biogeography Society 6th Biennial Meeting 9–13 January 2013, Miami, Florida, USA. Frontiers of Biogeography, 4(5).

Castro-Aguirre, J. L., and H. Espinosa-Pérez. 1996. Catálogo sistemático de las rayas y especies afines de México (Chondrichthyes: Elasmobranchii: Rajiformes: Batoideiomorpha). México: Instituto de Biología, Universidad Nacional Autónoma de México, Listados Faunísticos de México 8:75.

Clarke, K. R., and R. N. Gorley. 2006. Primer v6. User manual/tutorial. Primer-E Ltd. Plymouth. 190 pp.

Danemann, G. D., and J. De la Cruz-Agüero. 1993. Ictiofauna de la Laguna de San Ignacio, B.C.S., México. Ciencias Marinas 19: 333–341.

De la Cruz-Agüero, J., F. M. Galván, A. C. Abitia, J. R. Rodríguez, and F. J. Gutiérrez. 1994. Lista sistemática de los peces marinos de bahía Magdalena, Baja California Sur, México. Ciencias Marinas 20: 17–31.

De la Cruz-Agüero, J., M. Arellano-Martínez, and V. M. Cota-Gómez. 1996. Lista sistemática de los peces marinos de las Lagunas Ojo de Liebre y Guerrero Negro, B.C.S. y B.C., México. Ciencias Marinas 22: 111–128.

Del Moral-Flores, L. F., A. F. González-Acosta, H. Espinosa-Pérez, G. Ruiz-Campos, and J. L. Castro-Aguirre. 2013. Annotated checklist of the ichthyofauna from the islands of the Gulf of California, with comments on its zoogeographic affinities. Revista Mexicana de Biodiversidad 84: 184–214.

Des Lauriers, M. R. 2010. Island of Fogs: Archaeological and Ethnohistorical Investigations of Isla Cedros, Baja California. Salt Lake City: University of Utah Press.

Ebeling, A. W., R. J. Larson, and W. S. Alevizon. 1980. Habitat Groups and Island-Mainland Distribution of Kelp-bed Fishes off Santa Barbara, CA. In: Proceedings of the 2nd California Islands Multidisciplinary Symposium. 403–431.

Erisman, B. E, G. R. Galland, I. Mascareñas, J. Moxley, H. J. Walker, O. Aburto-Oropeza, P. A. Hastings, and E. Ezcurra. 2011. List of coastal fishes of Islas Marías archipelago, Mexico, with comments on taxonomic composition, biogeography, and abundance. Zootaxa 2985: 26–40.

Eschmeyer, W. N. (ed). Catalog of fishes: genera, species, references. (http://research.calacademy.org/research/ichthyology/catalog/fishcatmain.asp). Electronic version accessed 14 oct 2014. [This version was edited by Bill Eschmeyer.]

Espinosa-Pérez, H., J. L. Castro-Aguirre, and L. Huidobro-Campos. 2004. Listados faunísticos de México. IX. Catálogo sistemático de tiburones (Elasmobranchii: Selachimorpha). Universidad Nacional Autónoma de México, México.

Félix-Uraga, R., R. M. Alvarado-Castillo, and R. Carmona-Piña. 1996. The sardine fishery along the western coast of Baja California, 1981 to 1994. California Cooperative Oceanic Fisheries Investigations Reports 37: 188–192.

Fischer, W., F. Krupp., W. Schneider., C. Sommer., K. E. Carpenter., and V. H. Niem. 1995. Guia FAO para la identificación de especies para los fines de pesca. Pacífico Centro-Oriental. (Vol- II–III). FAO.

Hastings, P. A. 2000. Biogeography of the tropical eastern Pacific: distribution and phylogeny of chaenopsid fishes. *Zoological Journal of the Linnean Society* 128:319–335.

Hastings, P. A., L. T. Findley, A. M. Van der Heiden. 2010. Fishes of the Gulf of California. Pp: 96–118. In: Brusca R. (ed.). The Gulf of California. Biodiversity and Conservation. University Arizona Press. Tucson, AZ, USA.

Hickey, B. M. 1979. The California Current System-hypothesis and facts. Progress in Oceanography 8:191–279.

Hoese, F. D., and S. Reader. 2001. A preliminary review of the eastern Pacific species of *Elacatinus* (Perciformes: Gobiidae). Rev Biol Trop 49 (Supl. 1): 157–167.

Horn, M. H., L. G. Allen, and R. N. Lea. 2006. Biogeography. *In*: The ecology of marine fishes. California and adjacent waters, L. G. Allen, D. J. Pondella and M. H. Horn, eds. Berkeley: University of California Press. pp. 3–25.

Hubbs, C. L. 1953. Revision of the Eastern Pacific fishes of the clinid fish genus *Labrisomus. Zoologica* 38(3):113–136.

Hubbs, C. L. 1960. The marine vertebrates of the outer coast. Symposium The Biogeography of Baja California and adjacent seas. Systematic Zoology 9:134–147.

Huey, L. M. 1942. Two new wrens and a new jay from Lower California, Mexico. Transactions of the San Diego Society of Natural History. Vol IX (35):427–434.

Kessler, W. S. 2006. The circulation of the eastern tropical Pacific: A review, Progress in Oceanography, Volume 69, Issues 2–4, May–June 2006, Pages 181–217.

Kruskal, J. B., and M. Wish. 1978. Multidimensional scaling, Sage Publications, Beverly Hills. 487 pp.

Lea, R. N., and R. H. Rosenblatt. 2000. Observations on fishes associated with the 1997–98 El Niño off California. California Cooperative Oceanic Fisheries Investigations Reports. 41:117–129.

Littler, M. M. 1980. Overview of the rocky intertidal systems of southern California. Multidisciplinary symposium on the California Islands (ed. by D. M. Power), pp. 265–306. Santa Barbara Museum of Natural History, Santa Barbara, CA.

Love, M. S., C. W. Mecklenburg, T. A. Mecklenburg, and L. K. Thorsteinson. 2005. Resource inventory of marine and estuarine fishes of the west coast and Alaska: A checklist of north Pacific and Arctic ocean species from Baja California to the Alaska-Yukon Border. U.S. Department of the Interior, U.S. Geological Survey, Biological Resources Division, Washington. 276 pp.

Mearns, A. J. 1988. The "odd fish": unusual occurrences of marine life as indicators of changing ocean conditions. In Marine organisms as indicators, (D. F. Soule and G. S. Kleppel (eds.). Springer-Verlag, New York, pp. 137–176.

Mellink, E. 1993. Biological conservation of Isla de Cedros, Baja California, México: assessing multiple treats. *Biodiversity and Conservation*, 2:62–69.

Micheli, F., A. Saenz-Arroyo, A. Greenley, L. Vazquez, J. A. Espinoza-Montes, M. Rosseto, and G. A. De Leo. 2012. Evidence that Marine Reserves Enhance Resilience to Climatic Impacts. *PLoS ONE*, 7(7):e40832.

Miller, A. J., J. C. McWilliams, N. Schneider, J. S. Allen, J. A. Barth, R. C. Beardsley, F. P. Chavez, T. K. Chereskin, C. A. Edwards, R. L. Haney, K. A. Kelly, J. C. Kindle, L. N. Ly, J. R. Moisan, M. A. Noble, P. P. Niiler, L. Y. Oey, F. B. Schwing, R. K. Shearman, and M. S. Swenson. 1999. Observing and modeling the California Current System. *Eos Transactions, American Geophysical Union* 80:533–9.

Miller, J. D., and N. R. Lea. 1972. Guide to the coastal marine fishes of California. *Fish. Bull.* 157: 1–249.

Oberbauer, T. A.1985. Floristic Analysis of Vegetation Communities on Isla de Cedros, Baja California, Mexico. *Pest Control* 1:75–82.

Page, L. M., H. Espinosa-Pérez, L. T. Findley, C. R. Gilbert, R. N. Lea, N. E. Mandrak, and R. L. Mayden. 2013. Common and scientific names of fishes from the United States, Canada, and Mexico, 7th edn. Spec Publ Am Fish Soc No. 34, Bethesda, MD.

Palacios-Salgado, D. S., and A. Ramirez-Valdez. 2011. New Records of Demersal Fishes in the Northwest of Mexico. J. Fisheries and Aquatic Science. 6(1): 93–100.

Palacios-Salgado, D. S., L. A. Burnes-Romo, J. J. Tavera, and A. Ramírez-Valdez. 2012. Endemic fishes of the Cortez biogeographic province (Eastern Pacific Ocean). Acta Ichthyologica Et Piscatoria 42 (3): 153–164.

Planes, S., D. Lecchini, C. Mellin, J. C. Charton, M. Harmelin-Vivien, M. Kulbicki, G. Mou-Tham, and R. Galzin. 2012. Environmental determinants of coral reef fish diversity across several French Polynesian atolls. Comptes Rendus Biologie 335: 417–423.

Pondella, D. J. II, B. E. Gintert, J. R. Cobb, and L. G. Allen. 2005. Biogeography of the nearshore rocky-reef fishes at the southern and Baja California islands. Journal of Biogeography 32:187–201.

Quast, J. C. 1968. Fish fauna of the rocky inshore zone. Utilization of kelp-bed resources in southern California (ed. By W. J. North and C. L. Hubbs), pp. 35–55. California Department of Fish and Game, Fish Bulletin, 139, 1–264.

Quiñonez-Velázquez, C., R. Alvarado-Castillo, and R. Félix-Uraga. 2002. Relación entre el crecimiento individual y la abundancia de la población de la sardina del Pacífico *Sardinops caeruleus* (Pisces: Clupeidae) (Girard 1856) en Isla de Cedros, Baja California, México. Revista de Biología Marina y Oceanografía 37 (1): 1–8.

Reyes-Bonilla, H., A. Ayala-Bocos, S. González-Romero, I. Sánchez-Alcántara, M. Walther-Mendoza, Y. R. Bedolla-Guzmán, A. Ramírez-Valdez, L. E. Calderón-Aguilera, and N. C. Olivares-Bañuelos. 2010. Checklist and biogeography of fishes from Guadalupe Island, Western México. Cal Coop Ocean Fish Invest Rep 51:195–209.

Richards, D.V. 2000. The status of rocky intertidal communities in the Channel Islands National Park. Proceedings of the fifth California Islands symposium (ed. by D. R. Browne, K. L. Mitchell and H. W. Chaney), pp. 356–358. Santa Barbara Museum of Natural History, Santa Barbara, CA.

Robertson, D. R., and G. R. Allen. 2015. Shore fishes of the Tropical Eastern Pacific: an information system on line. Ver 1.0 (2015). Smithsonian Tropical Research Institute, Balboa, Panamá. www.neotropicalfishes. org/sftep Robertson et al. (2004).

Robertson, D. R., and K. L. Cramer. (2009) Shore fishes and biogeographic subdivisions of the tropical Eastern Pacific. Marine Ecology Progress Series, 380, 1–17.

Rodriguez Valencia, J. A., F. Caballero Alegria, and J. Castro Gonzalez. 2004. Tendencias de temporales (1989–99) en las poblaciones de Haliotis fulgens y H. corrugata (Gastropoda: Haliotidae) de Isla Cedros, Baja California, México. Ciencias Marinas 30:489–501.

Rosales-Casián, J. A. 1996. Ichthyofauna of Bahía de San Quintín, Baja California, México and its adjacent coast. Cienc. Marinas 22:443–458.

Ruiz-Campos, G., A. Ramírez-Valdez, S. González-Guzmán, J. L. Castro-Aguirre, A. F. González-Acosta, and J. De La Cruz-Agüero. 2010. Composition, density and biogeographical affinities of the rocky intertidal fishes on the western coast of the Baja California peninsula, Mexico. California Cooperative Oceanic Fisheries Investigations Reports Vol. 51: 210–220.

Stephens, J. S. 1963. A revised classification of the blennioid fishes of the American family Chaenopsidae. University of California Publications. Zoology 68:1–165.

Stephens, J. S., E. S. Hobson, and R. K. Johnson. 1966. Notes on distribution, behavior and morphological variation in some Chaenopsid fishes from the Tropical Eastern Pacific with descriptions of two new species, *Acanthemblemaria castroi* and *Coralliozetus springeri*. Copeia 3:424–438.

Stepien, C. A., and R. H. Rosenblatt. 1991. Patterns of gene flow and genetic divergence in the northeastern pacific clinidae teleostei blennioidei based on allozyme and morphological data. *Copeia*, 873–896.

Taylor, R. E., J. Southon, and M. R. Des Lauriers. 2007. Holocene marine reservoir time series ΔR values from Cedros Island, Baja California. Radiocarbon, Vol 49(2): 899–904.

Wiley, E. O., and D. Johnson. 2010. A teleost classification based on monophyletic groups. In: Nelson, J.S., H. P. Schultze, M. V. H. Wilson (eds). Origin and Phylogenetic Interrelationships of Teleosts. Pfeil, München, pp 123–182.

Workman, M. L., and J. E. Merz. 2007. Introduced yellowfin goby, Acanthogobius flavimanus: Diet and habitat use in the Lower Mokelumne River, California. San Francisco. Estuary and Watershed Science 5(1).

PHYTOPLANKTON SPECIES IN THE CALIFORNIA CURRENT SYSTEM OFF SOUTHERN CALIFORNIA: THE SPATIAL DIMENSIONS

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ABSTRACT

This paper examines 16 years of microscopic information about phytoplankton taxonomic composition and abundances from each of four regions in the CalCOFI area. The NE region is approximately the region of the Southern California Bight; the SE region is the lower edge of the bight; the Offshore is the westernmost region; and the Alley is the path between the NE and the Offshore through which the California Current meanders.

The NE region and the Alley consistently had the highest phytoplankton abundances, dominated by diatoms. These two areas were most similar with respect to abundance fluctuations and species composition. The Offshore had the lowest abundances, dominated by coccolithophores. The SE region was intermediate with respect to both abundance and composition.

Temporal patterns of abundance and composition differed among regions. An increase in phytoplankton abundance was centered in the Offshore region, but was not accompanied by a change in phytoplankton composition. The only detectable effect of the ENSO cycle on phytoplankton abundance was an increase in abundance during La Niña events in the Offshore. However, a cycle of Offshore species composition with a period of five to eight years did not appear to be related to ENSO. Seasonal cycles were strongest in the NE and Alley. In both these regions, high abundances in spring during the early years of this study decreased and the annual abundance maximum appeared to migrate to summer and fall. These shifts may have been driven by decreases in the abundances of the diatom phytoplankton in the spring or by an interaction between the present cruise schedule and a gradual delay in the spring bloom.

INTRODUCTION

The region of the California Current off southern California is one of the best studied ocean areas in the world. The California Cooperative Oceanic Fisheries Investigations (CalCOFI) has accumulated 65-year data sets of temperature, salinity, ichthyoplankton, and macrozooplankton and more than 30 years of data for nutrients and chlorophyll *a*. Based on these data, several temporal cycles have been defined and studied, including the seasonal cycle (Lynn and Simpson 1987; Legaard and Thomas 2006); the El Niño–Southern Oscillation (ENSO; Chelton et al. 1982; Bograd and Lynn 2001); and two decadal cycles, the Pacific Decadal Oscillation (Ebesmeyer et al. 1991; Roemmich and McGowan 1995a, b; Mantua et al. 1997); and the North Pacific Gyre Oscillation (Bond et al. 2003; Di Lorenzo et al. 2008). Information on these scales of variability provides a background against which to evaluate longer period changes.

Routine sampling for phytoplankton species on CalCOFI cruises began in 1990. Prior to this, most phytoplankton studies in the California Current that were conducted on a taxonomic level had been relatively short term and/or local studies, difficult to extrapolate to a scale comparable to that of the CalCOFI studies (Allen, 1936, 1941, 1945a,b; Sverdrup and Allen 1939; Balech 1960; Beers 1986; Matrai 1986; Busse et al. 2006).

Using the routine CalCOFI samples, Venrick (2012) examined the influence of temporal scales of variability upon the abundance and taxonomic composition of phytoplankton collected from the mixed layer on CalCOFI cruises between 1990 and 2009. Spatial variability was removed by combining all counts for each taxon into a single mean value for each cruise. In addition to seasonal cycles, this time span encompassed three El Niño events and two La Niña events. It also included a period near the year 2000 in which a shift in the signs of the Pacific Decadal Oscillation (PDO) and the North Pacific Gyre Oscillation (NPGO) may have occurred (Ebbesmeyer et al. 1991; Bond et al. 2003; Lavaniegos and Ohman 2003; DiLorenzo et al. 2008). The exact natures of the interdecadal climate events are still open to debate (Bjorkstedt et al. 2012). These three scales and their influences upon the regional hydrography, chemistry and biology are summarized in some detail in Venrick (2012).

During the 1990–2009 study, there was a slow increase in both chlorophyll *a* and phytoplankton abundance, accompanied by a decrease in the number of phytoplankton species per cruise. There was no evidence

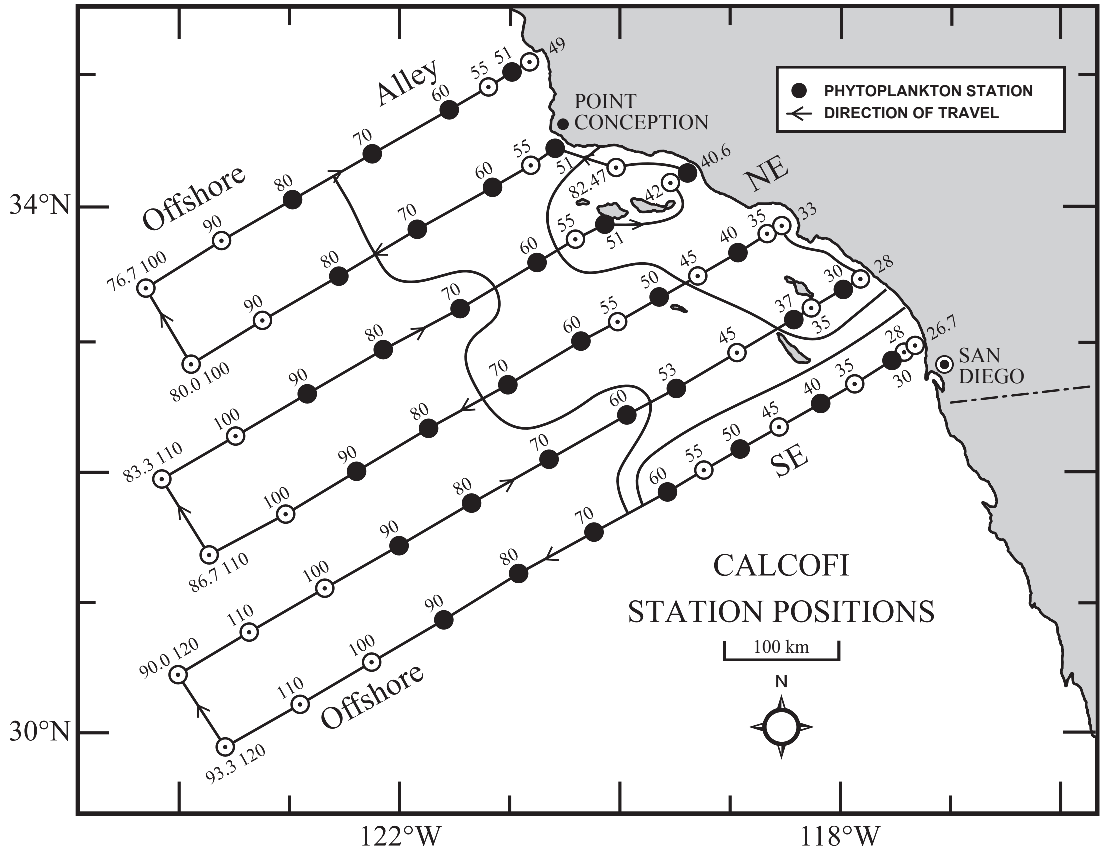

Figure 1. The basic CalCOFI station plan. Solid circles are stations from which phytoplankton samples were collected. Also indicated are the four environmental regions compared in this study.

for a major change in biomass or composition near the year 2000; however there was an unexplained increase in the temporal heterogeneity of phytoplankton composition after 2000.

During the 1990–2009 study, the response of phytoplankton abundance to ENSO events was similar to that of zooplankton, with reduced chlorophyll *a* and abundance during El Niño events and increased values during La Niña events. However, the relative magnitudes of changes were smaller than those of zooplankton. The effect of the ENSO cycle on phytoplankton abundance was not statistically significant.

During the 1990–2009 study, there was a clear seasonal cycle in both chlorophyll *a* and phytoplankton abundance. However, during the study period, the annual peak appeared to shift from spring to summer; this was accompanied by a change in composition of the peak, especially by a decrease in the abundance of hyalochaete species, a large subgroup of the diatom genus *Chaetoceros*. Venrick (2012) hypothesized that the shift reflected the change in nutrient source from wind-driven coastal upwelling in the spring to wind-stress-curl-driven upwelling in the summer (Rykaczewski and Checkley 2008).

A weakness of this first study is the lack of spatial resolution. The CalCOFI area is a dynamic, heterogeneous system and it is not known whether the temporal patterns revealed in Venrick (2012) reflect the entire region or whether they are merely a composite of several dissimilar, smaller-scale patterns. The present paper extends the observations of temporal scales to the spatial dimension, using the four regions defined by Hayward and Venrick (1998; fig. 1). The Northeast region (NE) is approximately the region of the Southern California Bight (SCB). The Southeast (SE) region often contains the southern, shoreward-flowing limb of the quasi-permanent Southern California Eddy, which entrains both California Current water and Offshore water, moving them toward the coast at the southern boundary of the SCB. The Offshore region is the easternmost Central Pacific, which is influenced by the California Current. The Alley is the region between the NE region and the Offshore through which the southward-flowing California Current meanders and generates eddies; where it approaches the coast, as at Point Conception, it may entrain locally upwelled water.

These four regions were initially defined on the basis of the similarity of temporal patterns of chlorophyll *a*

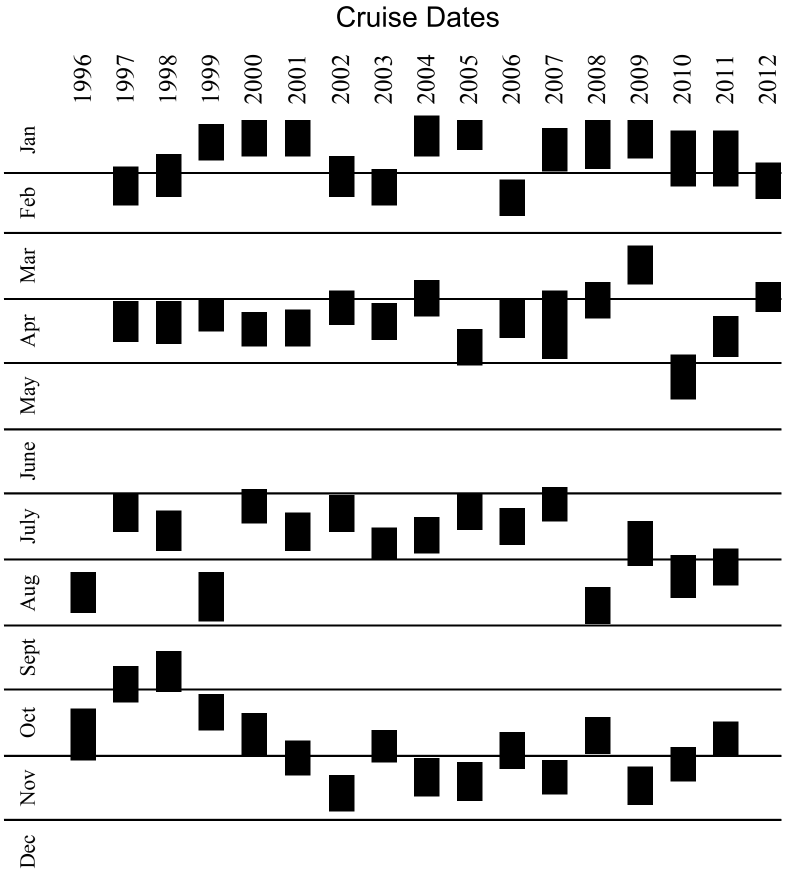

Figure 2. Cruise schedules, 1996–2012. Black bars indicate cruise dates.

at groups of stations between 1984 and 1996 (Hayward and Venrick 1998). Groups of stations with similar temporal patterns of chlorophyll were associated with similar physical forcing factors. Later, these groups of stations were shown to be characterized by different phytoplankton assemblages, with the exception of the Alley, which was characterized by the lack of a stable association (Venrick 1998a; Venrick 2009). The Alley appears to represent a meandering boundary between the NE and the Offshore. The phytoplankton assemblage in the Offshore, as defined here, has been shown to be more similar to that of the Central Pacific to the west than to that of the rest of the CalCOFI area (Venrick 1992, 2009).

The present study is based upon 16 years of quarterly data between summer 1996 and spring 2012 from each of the four regions; thus, there is a 13 year overlap with the previous study. The primary goal of this study is to add a spatial dimension to the temporal patterns and to examine on a regional basis the long-term increase in phytoplankton abundance, the phenological shift in the seasonal cycles, and compositional changes associated with both. In addition, these data may provide quantitative parameters of local phytoplankton that may be useful in future models of this region.

METHODS

CalCOFI Protocol

CalCOFI surveys have been conducted since 1949. Since 1984, cruises have occurred quarterly, and the basic sampling grid has consisted of 66 stations arranged in six lines spaced 40 nm apart (fig. 1). Within the quarterly framework, cruise dates and durations vary (fig. 2). In this study, seasons are defined as winter (Dec–Feb), spring (Mar–May), summer (June–Aug) and fall (Sept–Nov). A cruise is assigned to a season on the basis of its mid-date. Between 1996 and 2012, there were no cruises in June, or Dec, and only one in May.

Each station includes a large number of measurements and samples. These data and the methods by which they were acquired may be found on the CalCOFI website (http://www.calcofi.org/) and in individual data reports (http://www.calcofi.org/ccpublications/calcofi-data-reports.html).

Environmental Conditions

ENSO periods are defined as strong or moderate events lasting three months or longer based on the Oceanic Niño Index (ONI: http://ggweather.com/

TABLE 1
Summary of El Niño and La Niña dates, sampling cruises, and general characteristics in the CalCOFI area.

Equatorial Event	Dates in CalCOFI region	Cruises	Comments	References
1997–98 El Niño	June 1997 to July 1998	9707 9709 9802 9804 9807	Conditions relaxed somewhat during the spring; in 1998, zooplankton biomass the lowest on record; chlorophyll not noticeably reduced in field samples but remote imagery indicated a reduction in the extent of eutrophic waters.	Lynn et al. 1998; Hayward et al.1999; Hayward 2000; Kahru and Mitchell 2000; Bograd and Lynn 2001.
1998–00 La Niña	Nov 1998 to June 2000	9901 9904 9908 9910 0001 0004	Two La Niña pulses at the equator were not distinguishable in the CalCOFI area; record high chlorophyll values recorded during spring and summer 1999, subsequently returning to lower concentrations but generally continuing above the long-term mean; zooplankton biomass elevated throughout 1999, subsequently declining but remaining above low pre-1997 values.	Hayward et al. 1999; Bograd et al. 2000; Bograd and Lynn 2001; Durazo et al. 2001; Schwing et al. 2002; Venrick et al. 2003.
2002–03 El Niño	n.a.		A moderate equatorial El Niño did not significantly impact the CalCOFI area and is not considered in this study.	Venrick et al. 2003.
2007–08 La Niña	July 2007 to Feb 2009	0707 0711 0801 0804 0808 0810 0901	Cool conditions in the CalCOFI area appeared to precede this equatorial event by two months; most parameters did not respond strongly; satellite imagery indicated elevated chlorophylls, but these not apparent from the ship data.	McClatchie et al. 2008, 2009.
2009–10 El Niño	"Fall" 2009 to "Early" 2010	0911 1001	Strong impacts seen north of Pt. Conception; relatively weak in CalCOFI; SSH was elevated, but most physical and biological parameters near normal.	Bjorksted et al. 2010; Pacific Coast Ocean Observing System 2010.
2010–11 La Niña	July 2010 to Jan 2012	1008 1011 1101 1104 1108 1110	Strong impacts off Baja and inconsistently north of Pt. Conception; response in CalCOFI area mixed; SSH elevated and SST reduced but biological parameters near normal. Relaxation during summer 2011.	Bjorksted et al. 2011, 2012; Pacific Coast Ocean Observing System 2010 2011. Wells et al. 2013.

enso/oni.htm). The strength, timing, and influence in the CalCOFI area have been refined by local information (table 1).

Phytoplankton Sampling

Phytoplankton samples for this study were collected from summer 1996 through spring 2012. They were water samples collected from the second depth at 34 of the 66 standard stations, spaced approximately evenly across the grid (fig. 1). The CalCOFI protocol places the second sample within the mixed layer, whenever a mixed layer exists, generally between 5 and 15 meters. The samples were 30 ml water samples, preserved with 1% buffered formalin, and returned to the lab for enumeration. In the lab, equal aliquots from all samples from the same region were pooled into one sample, which was settled and counted under an inverted microscope. All larger cells were counted at 100X magnification; 17% of the sample was examined at 250X to enumerate the smaller cells. An attempt was made to count between 1,000 and 1,500 cells per sample. The volume of sample needed was determined by a relationship between chlorophyll *a* concentration and number of cells, modified by practical constraints such as volume of sample available, settling chamber size, and available time. During this study settled volumes varied from 1 to 100 ml. There were no consistent changes in volumes settled or in number of cells counted.

Taxonomic Considerations

The phytoplankton taxa in this study include all cells that could be identified to a specific taxon. This criterion includes most phytoplankton larger than 2–3 in diameter, but excludes picoplankton. The data set consists of abundances of 364 taxa in ten major taxonomic categories: diatoms, thecate dinoflagellates, athecate dinoflagellates (including heterotrophic species), coccolithophores, and silicoflagellates. In addition, there are nine species in five categories which are very rare and which have been combined into a single "miscellaneous" category. Most taxa were species or small groups of similar species, but for completeness, unidentified species were included, lumped into the lowest taxa possible. The genus *Pseudo-nitzschia* was subdivided into two categories according to

TABLE 2
Regional abundances. Differences among regions are assessed by the maginitude of the χ^2 large sample approximation for the Friendman 2-way ANOVA statistic, which removes temporal variability. Subtending bars indicate median differences according to a Nemenyi a posteriori procedure.

The critical value of χ^2 under the assumption of the null hypothesis at $p = 0.05$ is 7.82. Were the assumptions fulfilled, the result would be highly significant.

χ^2 (observed) = **86.3**

<table>
<tr><th></th><th colspan="4">Region</th></tr>
<tr><th></th><th>Alley</th><th>NE</th><th>SE</th><th>Offshore</th></tr>
<tr><td>abundance
(cells/ml)</td><td></td><td></td><td></td><td></td></tr>
<tr><td>median</td><td>243</td><td>210</td><td>95</td><td>57</td></tr>
<tr><td>mean</td><td>369</td><td>331</td><td>158</td><td>72</td></tr>
<tr><td></td><td colspan="2">▬</td><td>▬</td><td>▬</td></tr>
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whether cell width exceeded four microns. Both "slim *Pseudo-nitzschia*" and "robust *Pseudo-nitzschia*" are composites of several species, some overlapping. The athecate dinoflagellate species were more poorly resolved taxonomically than the species of the other major taxa, giving the "unidentified athecate" category a disproportionate weight in analyses of individual taxa. Consequently, athecate dinoflagellates have been retained only in the discussion of major taxa.

The absence of picoplankton data will produce a negative bias in the total number of cells, especially in the more oligotrophic regions. To the extent that picoplankton fluctuations are not coherent with fluctuations of other taxa, the results of this study will be biased toward larger taxa.

Statistical Procedures

Most statistical procedures in this study are nonparametric, which do not assume that the data are from a normal distribution, and which use the median as a measure of central tendency (Tate and Clelland 1957; Sprent 1993; Conover 1999). I present the mean as well as the median, because of its general familiarity. The difference between the median and the mean is an indication of the skew of the population distribution. Trend lines are least squares fits. As descriptive tools, neither the mean nor the least squares line assumes normality.

Procedures used include Spearman's nonparametric correlation (ρ), the Kruskal-Wallis one-way analysis of variance (ANOVA), and Friedmann's 2-way ANOVA. A significant ANOVA suggests that samples are not all from the same population. Following a significant result, a posteriori tests may indicate samples, or groups of samples that are likely to be from distinct populations (Nemenyi 1963; Sokal and Rohlf 1969). A posteriori results are indicated in tables by bars linking samples from the same population. Two nonoverlapping bars (table 2, Offshore and SE) indicate samples likely to be from two discrete populations; a bar under two or more samples (table 2, NE and Alley) indicates that discrete populations cannot be detected.

The study is focused on the strength of the relationships between the different regions. Correlation matrices are used where, under other circumstances, a single concordance test might be more appropriate.

Principal component analysis (PCA) was used to decompose the variability of the abundance data of the major taxa and to examine the importance of different scales. Input data were the log-transformed and normalized abundance data of four major taxa in each sample. To determine the acceptance criterion for the principal component, I ran 600 Monte Carlo simulations on the data, with the observed counts of the taxa associated randomly with samples (modified from Ledesma and Valero-Mora 2007). Resulting eigenvalues are more conservative than the commonly accepted value of 1.0.

With more than 350 taxa, examination of species composition and changes over time requires extreme reduction of data. I have used species correlation profiles, which plot the similarity of species composition of all pairs of samples as a function of their separation in time. Similarity was measured by Spearman's correlation (ρ) between rank orders of abundance. A correlation profile is analogous to a variogram through time using a measure of similarity rather than a measure of variance. Like a variogram, it detects temporal pattern. Unlike a variogram, peaks of a correlation profile represent greater similarity rather than greater variance (dissimilarity). To remove variability at the smallest scales, curves were smoothed with a 21 point running average. This represents an average interval of 26 days.

This study compares and contrasts characteristics of phytoplankton in four regions at three time scales. The resulting labyrinth of tests ("multiple testing") and statistical interdependencies negate the use of classical hypothesis testing. However, tabulated probability levels correct for sample size and give a yardstick for comparisons, even though the underlying assumptions have been violated. In the following study I present statistics and classical alpha errors (critical values) at $p = .05$ and indicate in bold, results that exceed critical values. The results, however, must be judged on the basis of the magnitude and consistency of the patterns over all analyses.

RESULTS

Phytoplankton Abundance

Regional patterns. Cruise-mean abundances were consistently higher in the Alley and NE, lower in the SE region and lowest in the Offshore (table 2, fig. 3).

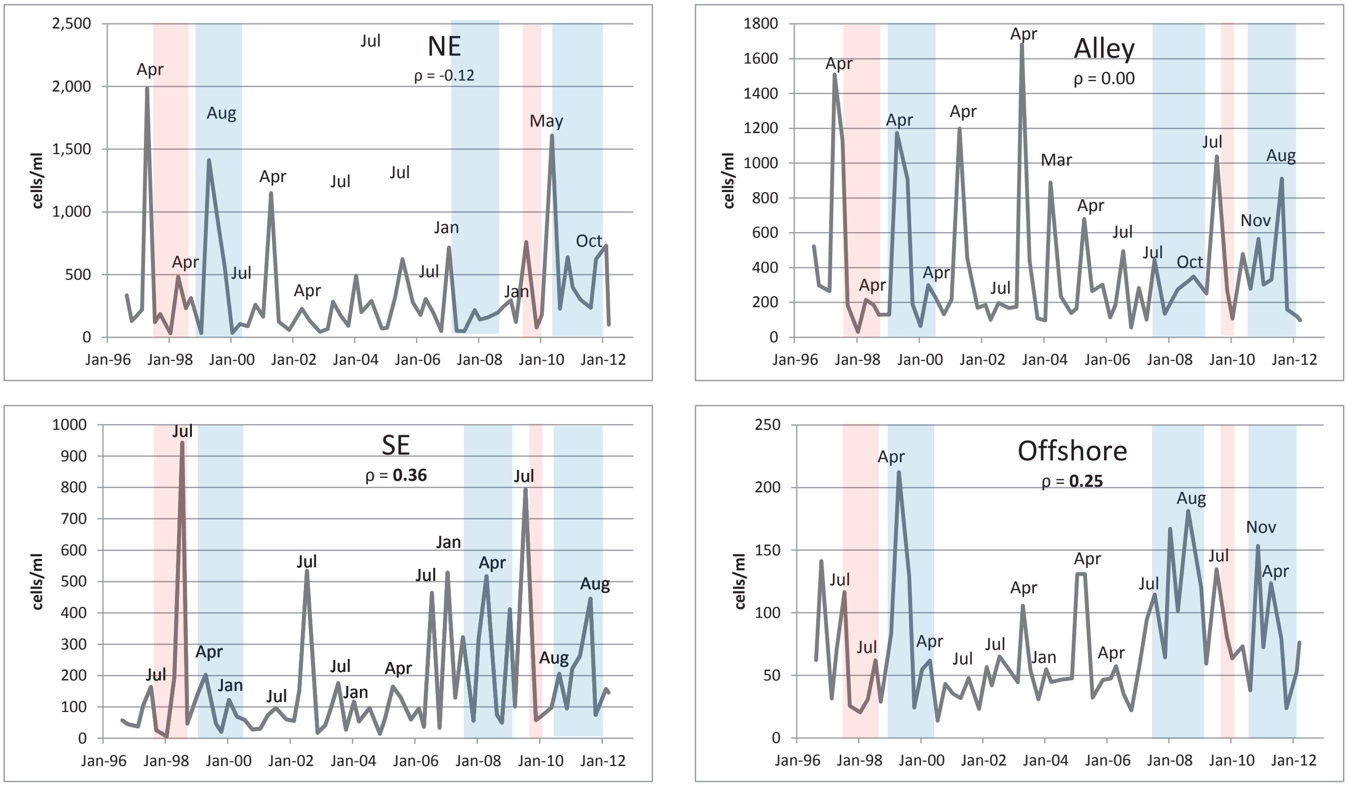

Figure 3. Temporal changes of phytoplankton abundance (excluding athecate dinoflagellates) in the four regions of the CalCOFI area. El Niño periods are shaded red; La Niña periods are shaded blue. Months of maximum annual abundance are indicated. Values of ρ indicate correlations of abundance and time (increase or decrease in abundance). The critical value of the statistic under the assumptions of the null hypothesis at p = 0.05 is 0.25. Were all assumptions fulfilled, the bold statistics would be significant.

TABLE 3

Pair-wise comparison of phytoplankton abundances. Values are Spearman's nonparametric correlation (ρ). Values above the diagonal are correlations across all samples; values below the diagonal have had the seasonal cycle removed.

Critical values of ρ under the assumptions of the null hypothesis at $p = 0.05$ are 0.25 ($n = 64$; above diagonal) and 0.52 ($n = 15$; below). Were assumptions fulfilled, bold correlations would be significant.

		Region				
		NE	Alley	SE	Offshore	
seasonal cycle removed	NE		**0.46**	–0.12	0.11	all data
	Alley	**0.60**		**0.32**	**0.44**	
	SE	–0.02	–0.35		**0.42**	
	Offshore	0.32	0.31	0.38		

Four of the six correlations between regions, over all data (table 3), were strongly positive, suggesting that abundance fluctuations in most regions were related. The only regions that appeared independent were the NE and SE regions and the NE and the Offshore. Most of the overall concordance among regions was driven by similar seasonal cycles. When the seasonal cycle was removed (table 3), most correlations decreased. Longer-period fluctuations remained correlated only in the NE and Alley.

Interannual changes. Phytoplankton abundances in both the SE region and the Offshore increased during the study period, in spite of one very high early value in each (fig. 3). In the Offshore, this peak occurred during the spring of the 1998-2000 La Niña, a period with record high chlorophyll *a* across most of the CalCOFI area (table 1). In the SE, however, the peak was earlier, more closely associated with the 1997–98 El Niño, and it appears to have been a more local phenomenon. Phytoplankton abundances in the two eutrophic regions were more stable during the study period.

ENSO effects. The ENSO signal was greatest in the Offshore (table 4). However, this was driven only by high abundances during La Niña conditions; reduction of abundances during El Niños was undetectable. Although the ENSO signal was weaker in other regions, they showed the expected pattern of abundances with abundances lower during El Niños and higher during La Niñas. An influence of ENSO cannot be disproved with these data, but the effects on phytoplankton abundance were relatively weak.

Seasonal patterns and phenological changes. Only the Alley and the SE region had consistent (detectable) seasonal cycles (table 5). In spite of differences in the

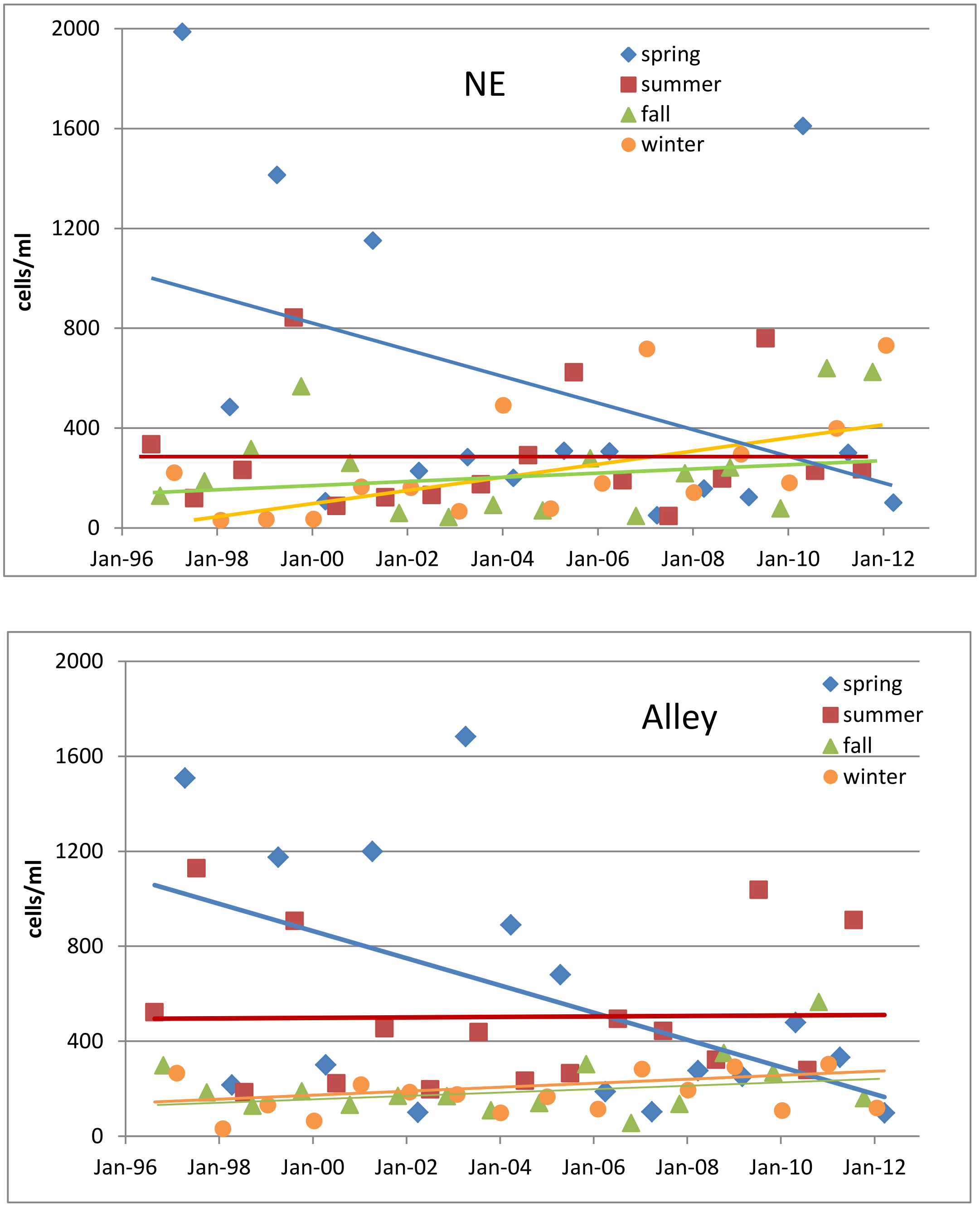

Figure 4. The long-term changes of annual peak abundance in the NE region and the Alley. Regression lines describe abundance trends within seasons.

amplitudes of the cycles, all four regions showed agreement in that higher abundances tended to occur in summer or spring and lower abundances in winter or fall.

During the study, the timing of the annual peak in the NE and Alley regions shifted toward later months (fig. 3). In the NE, before 2004, all annual peaks but one occurred in spring becoming irregular thereafter. In the Alley, before 2006, every peak except one occurred in the spring; after 2006 peaks occurred in summer and fall.

These shifts in the timing of the annual peaks resulted from interaction between a decrease in abundance in spring samples and changes in other seasons (fig. 4). In the NE, the spring decrease was accompanied by increases in fall and winter abundances. At the start of the study, spring abundances exceeded those of other

TABLE 4
Summary of the changes of the total number of cells in the three ENSO states. Changes are assessed by the magnitude of the Kruskal-Wallis 1-way ANOVA (H). Subtending bars indicate differences according to a Nemenyi a posteriori test.

The critical value of H under the assumptions of the null hypothesis at p = 0.05 is 5.99. Were assumptions fulfilled, the bold statistic would be significant.

Region	H (observed)	Abundance (cells/ml)	Enso State		
			La Niña	Neutral	El Niño
NE	1.62	median	235	196	181
		mean	354	346	187
			La Niña	Neutral	El Niño
Alley	2.75	median	301	220	195
		mean	366	375	303
			La Niña	Neutral	El Niño
SE	3.82	median	143	83	70
		mean	192	103	209
			La Niña	El Niño	Neutral
Offshore	**10.31**	median	102	62	50
		mean	103	57	58
			▬	▬	▬

TABLE 5
The seasonal variability of phytoplankton abundances. Changes are assessed by the magnitude of the χ^2 large sample approximation for the Friedman two-way ANOVA. Subtending bars indicate differences according to a Nemenyi a posteriori procedure.

The critical value of χ^2 under the assumptions of the null hypothesis at p = 0.05 is 7.8. Were assumptions fulfilled, the bold statistics would be significant.

Region	χ^2 (observed)	Abundance (cells/ml)	Season			
			Spring	Fall	Summer	Winter
NE	6.20	median	300	218	197	164
		mean	580	249	286	212
			Spring	Summer	Fall	Winter
Alley	**14.84**	median	439	332	175	168
		mean	625	501	204	175
			▬	▬		
					▬	▬
			Summer	Winter	Spring	Fall
SE	**24.2**	median	176	105	95	47
		mean	304	150	150	44
			▬	▬	▬	
				▬	▬	▬
			Spring	Summer	Winter	Fall
Offshore	6.92	median	71	62	56	43
		mean	83	77	69	55

TABLE 6
Summary of principal component analysis on major phytoplankton taxa. Input data are the abundances of each major taxa in each sample. Only the eigenvalue of the first component exceeds the critical value (estimated from Monte Carlo simulations).

Principal component	Eigenvalues	Cumulative %	Critical eigenvalues (p = 0.05)
PC1	**2.44**	**61.0**	1.17
PC2	0.714	78.9	1.02

Loadings of major taxa on principal component 1

Taxon	Loading
coccolithophores	0.53
athecate dinoflagellates	0.53
diatoms	0.46
thecate dinoflagellates	0.41

seasons and the annual maximum was stable. Decreasing spring abundances progressively fell into the range of abundances in other seasons, and the timing of the annual maximum became variable, no longer a predictable cycle. A similar interaction can be seen in the Alley. As declining spring abundances approached and overlapped those of summer, the regular spring peaks shifted to peaks in summer and occasionally autumn. In both regions, the abundance declines in spring were offset by increases during the other seasons, so the annual average remained stable.

Major Taxa

The most abundant major taxa were diatoms, thecate and athecate dinoflagellates, coccolithophores, and silicoflagellates; the first four taxa were present in at least one region on 63 or 64 of the 64 cruises. In addition there was a small category composed of nine infrequent species that belong to various other major groups.

The abundances of all major taxa were least in the Offshore region (fig. 5). Diatoms dominated the flora in the NE, Alley, and SE; coccolithophores dominated in the Offshore. This result changes very little when abundances are expressed as percentages of the total.

Principal component analysis (PCA) was used to examine the relative importance of spatial and temporal variability to the composition of major taxa. Descriptors are abundances of the four most frequent taxa: diatoms, thecate dinoflagellates, athecate dinoflagellates, and coccolithophores. A single meaningful component emerged, which explains 61% of the variability (table 6). The first principal component is highly correlated with chlorophyll *a* (Spearman's $\rho = 0.59$; critical value [0.05] = 0.12; data not shown) and may be viewed as an abundance axis. The most important attribute separating samples along component 1 is the regional abundance; this is followed by seasonal abundance and interannual abundance (table 7). The ENSO scale is relatively weakly expressed. Samples with high scores along this principal axis are summer samples from the Alley and NE regions. Among the highest

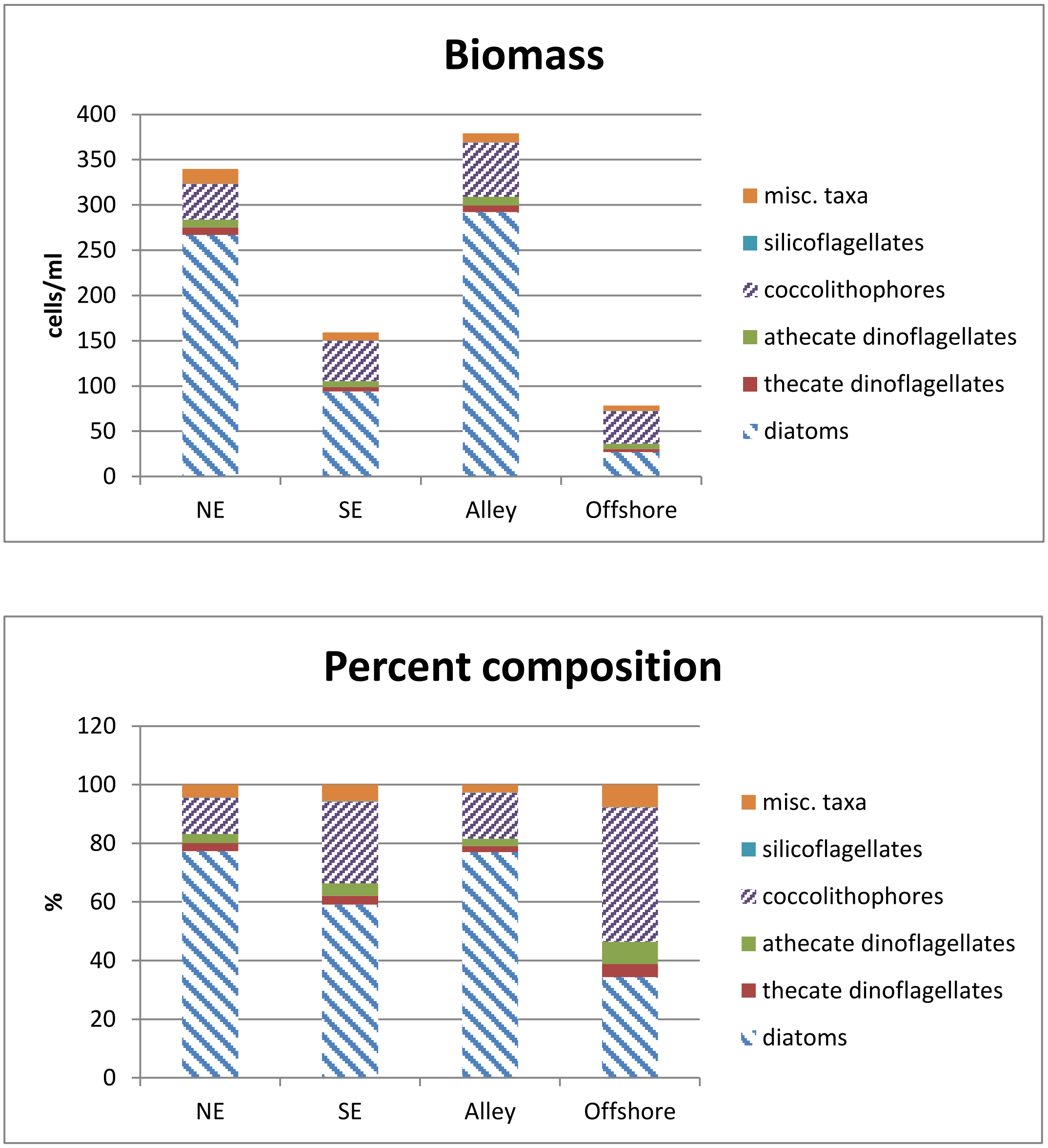

Figure 5. Regional composition of major taxonomic categories as means and percent composition.

25% of the scores, there are no samples from the Offshore. Samples with low scores along the axis are samples from the SE and Offshore regions.

All taxa have positive loadings on the first component, indicating that fluctuations of the four major taxa were correlated. This concordance is unexpected. Several characteristics of phytoplankton tend to sort along a eutrophic-oligotrophic axis, including taxonomic affiliation and cell size (Margalef 1978; Malone 1980; Goericke 2011), predicting a greater separation between, for instance, diatoms and dinoflagellates; or between small-celled groups, such as coccolithophores; and predominantly large-celled groups such as diatoms. Instead, the first component appears to express one large scale of variability that affects all taxa similarly through time and across the CalCOFI area.

Single Taxa

Over the entire study, there are 364 taxonomic categories. Athecate dinoflagellates were excluded from the following analysis because of their low taxonomic resolution, leaving 165 diatoms, 115 thecate dinoflagellates, 55 coccolithophores, three silicoflagellates, and nine species from five other taxonomic groups. Total numbers of species and abundances per cruise were inversely related, with more species found in the SE and Offshore regions (table 8a). Approximately half of the taxa (193) were found at least once in all four regions, while only

TABLE 7
Influence of four sources of variability in the scores of samples along principal component 1. Differences are assessed with the Kruskal-Wallis one-way ANOVA (H). Subtending bars indicate differences according to a Nemenyi a posteriori test.

Also shown is the critical value of H under the assumption of the null hypothesis at p = .05: c.v. (0.05). Were the assumptions fulfilled, the bold statistics would be significant.

Region
H = **52.7**; c.v. (0.05) = 7.81

	NE	Alley	SE	Offshore
median score	0.59	0.47	–0.45	–0.82
mean score	0.76	0.50	–0.50	–0.77

Season
H = **24.1**; c.v. (0.05) = 7.81

	Summer	Winter	Spring	Fall
median score	0.40	–0.05	–0.18	–0.71
mean score	0.93	–0.17	–0.19	–0.58

Years
H = **23.1**; c.v. (0.05) = 7.81

	2008–12	2004–08	1996–00	2000–04
median score	0.38	–0.13	–0.28	–0.77
mean score	0.52	0.06	–0.24	–0.34

ENSO State
H = **6.23**; c.v. (0.05) = 5.99

	Neutral	El Niño	La Niña
median score	–0.39	–0.06	0.16
mean score	–0.11	–0.10	0.25

TABLE 8
Overview of the phytoplankton parameters in the CalCOFI area.

a) General statistics: total numbers of species, mean numbers of species per cruise (n), the number of species unique to each region, and the changes of the number of species over time (ρ). The critical value of Spearman's ρ under the assumption of the null hypothesis at p = 0.05 is 0.25. Were the assumptions fulfilled, the bold correlation would be significant.

Number of species	NE Region	Alley	SE Region	Offshore
total	269	246	296	293
n	48	47	56	59
number unique	18	10	25	26
change over time (ρ)	–0.01	–0.10	–0.02	**–0.26**

b) Correlations between species compositions of different regions. Values are the mean correlations (ρ) between each pair of the 64 cruises. There are no critical values tabulated for mean statistics.

	Alley	SE	Offshore
NE	0.32	0.17	0.09
Alley		0.15	0.16
SE			0.25

79 were found in a single region. The highest numbers of species unique to a single region were found in the Offshore and SE regions (table 8a), which were the lower biomass regions (table 2). Comparisons of species composition between regions (table 8b) suggest the taxonomic compositions of the NE region and the Alley were similar, as were those of the SE region and the Offshore. Least similar were the compositions of the NE region and the Offshore. The top ten dominant species in all four regions consisted of 17 taxa (table 9); four taxa were dominant in all regions, but two of these, slim *Pseudo-nitzschia* spp. and hyalochaete species in the genus *Chaetoceros* are taxa with many similar species, and the dominant species may have changed among the regions.

Interannual patterns. A decline in the number of species per cruise was observed between 1990 and 2009 (Venrick 2012). This decline continued between 1996 and 2012 and was strongest in the Offshore (table 8a), coincident with the greater increase in abundance there (fig. 3). To look for interannual changes in taxonomic composition, the Offshore species composition, averaged over 2000 and 2001, was compared with the average of 2010 and 2011. The earlier period was used to minimize the influence of the preceding El Niño and La Niña events. Offshore phytoplankton abundance increased from a mean of 42.4 cells/ml to a mean of 87.2 cells/ml, while the number of species decreased from 173 to 155. As predicted by the principal component analysis (table 6), all major taxa increased in abundance. Relative to their abundances in 2000–01, diatoms, athecate dinoflagellates and the miscellaneous category increased by about 150%; thecate dinoflagellates by 85%; and coccolithophores by 60%. Eight of the ten dominant species were common to both periods. There were no major shifts in abundance other than the expected general increase. There is no evidence that a significant species change accompanied the interannual abundance increase.

Correlation profiles provide a means for detecting long-term changes and repeating patterns of species composition. The profile incorporates changes in species number, but is independent of total abundance. In all regions, the correlation profiles show a decrease in the similarity of species composition of sample pairs separated by longer time intervals, evidence for a slow evolution of species composition and/or dominance order (fig. 6).

Changes in species composition across the postulated interdecadal shift in 2000 were examined by partitioning the species correlation profiles into three sets: comparisons between samples before 2000, comparison between samples after 2000, and comparisons across the shift. A species shift would appear as a lower correlation between pairs of samples that span the shift.

TABLE 9

Dominant species in the regions of the CalCOFI area. Species are listed according to their median abundances.

NE region	median (cells/ml)	mean (cells/ml)	SE region	median (cells/ml)	mean (cells/ml)
slim *Pseudo-nitzschia* spp.	24.6	74.1	*Emiliania huxleyi*	16.2	24.9
Emiliania huxleyi	23.0	31.7	slim *Pseudo-nitzschia* spp.	5.0	32.6
Chaetoceros spp. (hyalochaetes)	15.4	42.2	unidentified coccolithophores	4.8	9.5
Chaetoceros radicans	12.0	19.2	*Fragilariopsis pseudonana*	4.4	7.4
Fragilariopsis pseudonana	11.0	17.3	*Chilomonas marina*	3.4	4.9
cf. *Nitzschia closterium*	6.4	17.4	cf. *Nitzschia closterium*	3.0	7.8
unidentified coccolithophores	5.6	13.2	*Gephyrocapsa* spp.	1.0	2.5
robust *Pseudo-nitzschia*	2.8	16.8	*Chaetoceros* spp. (hyalochaetes)	0.8	15.9
Chaetoceros socialis	0.3	18.2	*Mastogloia woodiana*	0.1	3.9
Chaetoceros debilis	0.1	42.3	*Phaeocystis pouchetti*	<<0.1	3.6
Alley	**median (cells/ml)**	**mean (cells/ml)**	**Offshore**	**median (cells/ml)**	**mean (cells/ml)**
Emiliania huxleyi	31.1	38.6	*Emiliania huxleyi*	12.7	19.0
slim *Pseudo-nitzschia* spp.	24.1	62.3	unidentified coccolithophores	5.3	8.8
Chaetoceros spp. (hyalochaetes)	15.8	46.4	*Chilomonas marina*	3.4	4.7
unidentified coccolithophores	10.9	14.1	slim *Pseudo-nitzschia* spp.	2.5	8.3
cf. *Nitzschia closterium*	5.5	11.2	cf. *Nitzschia closterium*	1.6	3.2
Chaetoceros debilis	5.2	42.9	*Fragilariopsis pseudonana*	1.2	2.1
robust *Pseudo-nitzschia*	4.5	16.2	*Umbilicosphaera hulburtiana*	0.7	1.4
Chaetoceros radicans	2.8	18.5	*Gephyrocapsa* spp.	0.6	2.1
Dactyliosolen fragilissima	1.2	12.4	*Chaetoceros* spp. (hyalochaetes)	0.2	2.4
Chaetoceros socialis	0.3	14.2	cf. *Phaeocystis* sp.	<<0.1	2.6

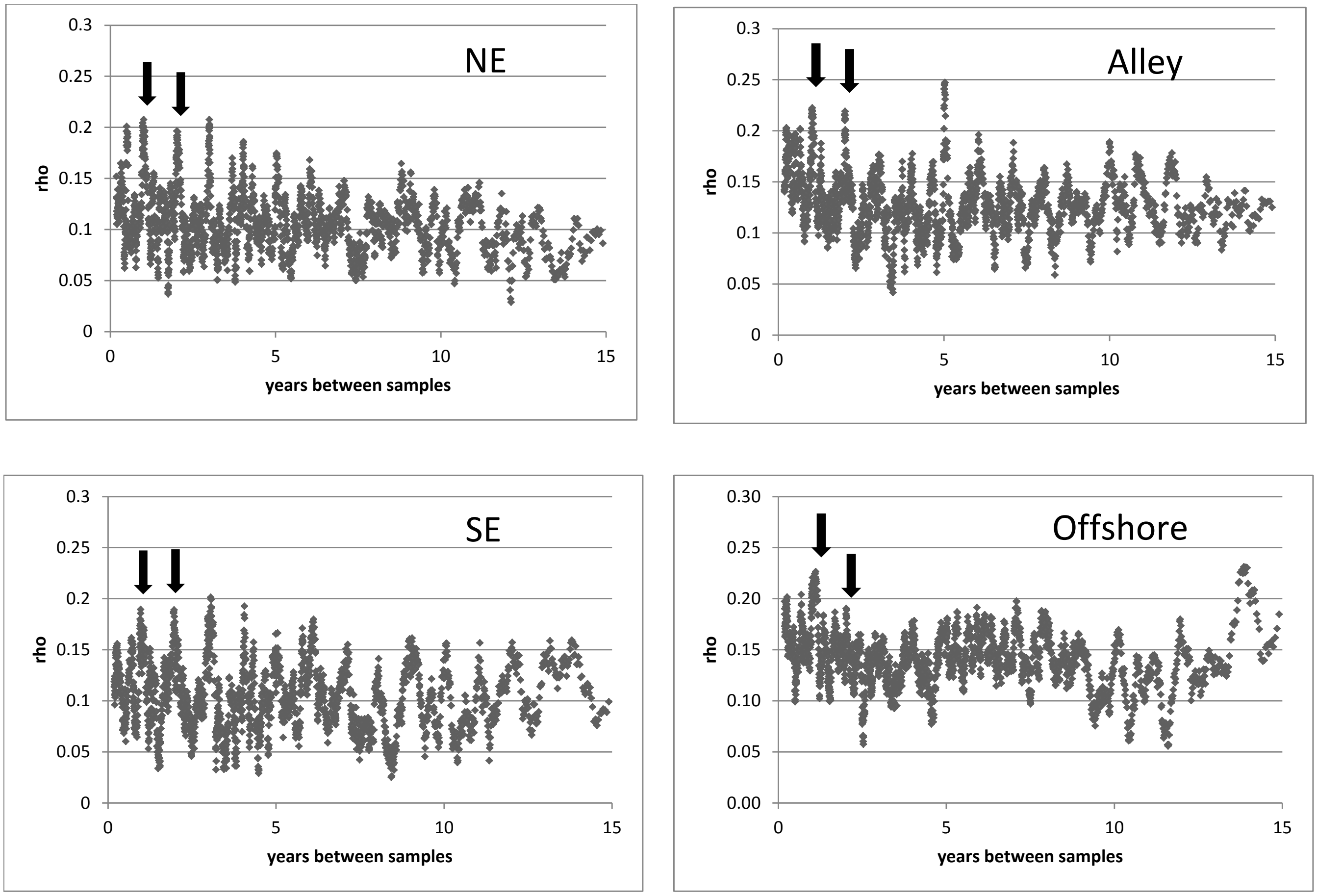

Figure 6. Correlation profiles for the four regions. Each plot is the correlation of rank order of abundance of species composition (ρ) between sample pairs as a function of their separation in time. Points are 21-point running means. Arrows indicate the first two annual peaks.

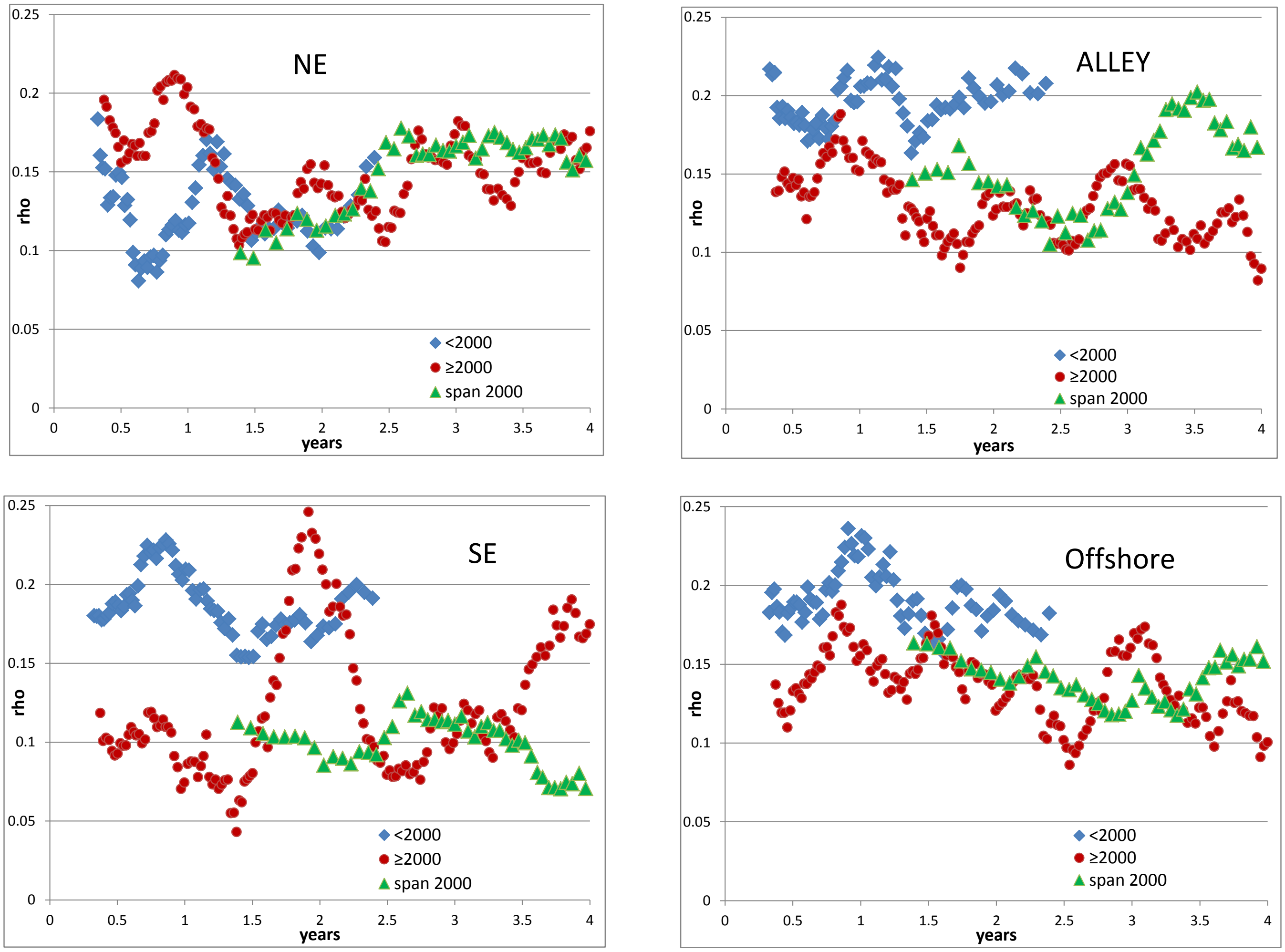

Figure 7. As for Figure 6 but data are divided into comparisons between sample pairs collected before 2000, comparisons between sample pairs collected during or after 2000, and comparisons between sample pairs one before 2000, one during or after 2000.

There is no evidence for a shift in composition within any of the regions near the year 2000 (fig. 7). An increase in heterogeneity after 2000 can be seen in the Offshore, the Alley, and in the SE region (where it is partially masked by a strong peak at a two-year interval). In contrast, the stability of species composition in the NE region was unchanged, apparently buffered from whatever changes occurred near the year 2000.

ENSO effects. The Offshore correlation profile (fig. 6) suggests a periodicity of species composition of about five to eight years. There appears to be a trough at 2.5–3.5 years, a broad peak between five and eight years, and a trough between 9.5–12.5 years, a periodicity of approximately 5 to 7 years. An echo of this pattern is apparent in the SE region. The periodicity of the ENSO cycle varies between three and seven years. However, there is no direct evidence that ENSO is the underlying driver. If the peaks represent pairs of samples from El Niño periods, or La Niña periods, this should be apparent from the makeup of the individual points. Instead, the highest 5% of the points defining the Offshore peak at five to eight years includes no sample pairs between two El Niño or two La Niña periods. Moreover, the points defining the trough at 2.5–3.5 years have more low correlations between two El Niño samples and two La Niña samples than low correlations between one of each. More data is needed to verify this pattern and determine causal mechanisms. At present, these data show no evidence for a shift in species composition directly related to the ENSO cycle.

Seasonal cycles and phenological shifts. All four correlation profiles show an annual peak indicative of a seasonal cycle of species composition (fig. 6). In all regions the magnitude of the annual peaks decreased over time and their regularity tended to erode. The cycle of species composition was most regular in the SE and least regular in the Offshore, consistent with the seasonal cycle of abundance (table 5).

TABLE 10

Composition of spring flora in 1997 and 1999 (the annual peak) and spring flora in 2011 and 2012 (not the annual peak). Also shown are the abundances of the *Chaetoceros* subgenus hyalochaete.

NE Region

	early spring (peak)					recent spring (not a peak)			
	1997	**1999**	**mean (cells/ml)**	**(%)**		**2011**	**2012**	**mean (cells/ml)**	**(%)**
major taxa					**major taxa**				
diatoms	1954	1282	1618	94.7	diatoms	144	38	91	42.7
(hyalochaete *Chaetoceros*)	(358)	(746)	(552)	(32.3)	(hyalochaete *Chaetoceros*)	(37)	(9)	(23)	(10.8)
coccolithophores	7	120	64	3.7	coccolithophores	104	50	77	36.2
thecate dinoflagellates	4	0	2	0.1	thecate dinoflagellates	40	7	24	11.3
athecate dinoflagellates	11	5	8	0.5	athecate dinoflagellates	9	17	12	5.6
other taxa	22	11	16	0.9	other taxa	13	5	9	4.2
all species	1997	1418	1708		all species	310	117	213	
dominant taxa					**dominant taxa**				
slim *Pseudo-nitzschia* spp.	1073	161	617	36.1	coccolithophorid spp.	46	28	37	17.3
Chaetoceros debilis	95	278	186	10.9	*Emiliania huxleyi*	50	19	34	16.0
Dactyliosolen fragilissimus	343	1	172	10.1	slim *Pseudo-nitzschia* spp.	63	5	34	16.0
Chaetoceros radicans	57	271	164	9.6	*Fragilariopsis pseudonana*	7	19	13	5.6
Chaetoceros spp. (hyalochaete)	95	121	108	6.3	athecate dinoflagellate spp	9	17	13	5.6
Skeletonema costatum	4	169	86	5.0	*Chaetoceros debilis*	19	2	10	5.0

Alley

	early spring (peak)					recent spring (not a peak)			
	1997	**1999**	**mean (cells/ml)**	**(%)**		**2011**	**2012**	**mean (cells/ml)**	**(%)**
major taxa					major taxa				
diatoms	1353	1097	1225	91.1	diatoms	276	36	156	70.9
(hyalochaete *Chaetoceros*)	(170)	(736)	(435)	(33.7)	(hyalochaete *Chaetoceros*)	(211)	(15)	(106)	(48.0)
coccolithophores	134	54	94	7.0	coccolithophores	34	60	47	21.3
thecate dinoflagellates	5	5	5	0.4	thecate dinoflagellates	5	3	4	1.8
athecate dinoflagellates	1	16	9	0.7	athecate dinoflagellates	1	13	7	3.1
other taxa	16	6	11	0.8	other taxa	11	1	6	2.7
all species	1509	1178	1343.5		all species	327	113	220	
dominant taxa					**dominant taxa**				
slim *Pseudo-nitzschia* spp.	521	133	327	24.3	*Chaetoceros debilis*	153	10	82	37.2
Dactyliosolen fragilissimus	538	1	270	20.1	*Emiliania huxleyi*	20	38	29	13.2
Chaetoceros debilis	52	284	168	12.0	*Chaetoceros* spp. (hyalochaete)	36	5	21	9.5
Chaetoceros radicans	35	209	122	0.0903	coccolithophorid spp.	13	19	16	7.2
Chaetoceros spp. (hyalochaete)	26	135	80	0.0598	slim *Pseudo-nitzschia* spp.	14	3	8	3.6
Emiliania huxleyi	112	44	78	0.0576	athecate dinoflagellate spp	13	19	7	7.4

Data from both the NE and the Alley suggest phenological shifts in abundance (figs. 3, 4). Between 1990 and 2009 (Venrick 2012), a long-term shift in the season of the annual peak abundance was accompanied by a shift in the dominant species, especially a decrease in the hyalochaete species of the genus *Chaetoceros*. To examine this within regions, the taxonomic composition of two early spring samples in the NE region and the Alley (1997 and 1999, skipping the depressed El Niño spring of 1998), were compared with the composition of the two most recent springs, 2011 and 2012. In both regions, the decrease in abundance was due to decreases in the abundances of diatom species (table 10), which underwent an 18-fold decrease in the NE and an 8-fold decrease in the Alley. In the NE, the diatom decrease was dominated by decrease of hyalochaete species. This was not the case in the Alley where hyalochaete *Chaetoceros* species decreased less than diatoms as a whole. The high variability between the two early spring samples and between the two recent spring samples may mask long-term changes in the other phytoplankton components. Because of the reduction in the diatom abundance, the compositions in recent years tended to shift toward a greater dominance of coccolithophorid taxa.

SUMMARY AND DISCUSSION

This study evolved from a study of the temporal variability of phytoplankton in the CalCOFI area (Venrick 2012), which covered the period 1990 to 2009 but lacked information about regional differences within that area. The present study between 1996 and 2012 includes the same stations but partitions the phytoplankton into four regions to address the question of regional heterogeneity and to examine temporal patterns within and across regions.

Spatial Patterns

On the largest scale, there is connectivity across the entire CalCOFI region that is seen in the positive correlations among regional phytoplankton abundances (table 3), in the positive loadings of all major taxa on the first axis of the PCA (table 6), in the high number of taxa abundant in all regions (table 9), and in the positive correlations of species composition between regions (table 8b).

The large-scale concordance indicated by these observations, however, tends to mask rather than negate regional differences. A principal component analysis, with the abundances of the major taxa as input variables, suggests that the spatial dimension was the strongest source of variability. Throughout this study, the NE region and the Alley have been more similar to each other and least similar to the Offshore. The NE region and the Alley were the most eutrophic regions, with highest abundances (table 2), fewest species (table 8a), and most similar species composition (table 8b). Both regions were dominated by diatoms (77%) with coccolithophores making up an additional 12%–16% (fig. 5). Neither region showed evidence for an increase in abundance over the study period (fig. 3). Neither region showed a response to the ENSO cycle (table 4). Initially, the two regions had clear seasonal cycles of abundance with high values in spring. Data from both regions indicate a progressive decline in the magnitude of the spring maximum and a deterioration of the regular cycle (figs. 3, 4).

The Offshore was the most oligotrophic region with the lowest abundances (table 2) and a high number of species (table 8a). There was an increase in abundance during the study (fig. 3), accompanied by a decrease in the number of species (table 8a). The Offshore was dominated by coccolithophores, which accounted for 46% of the total cells; diatoms accounted for an additional 34% (fig. 5). The Offshore was the only region with a detectable response to the ENSO cycle (table 4); this may reflect a relatively low level of local variability in the Offshore, making ENSO perturbations more easily detected, or it may indicate something fundamental about ENSO effects on phytoplankton in the CalCOFI area. The species correlation profile in the Offshore suggests a cycle of species composition with a period of five to eight years, which does not appear to be related to the ENSO cycle and remains unexplained. A seasonal cycle of abundance is not apparent (table 5), although there was some repetition of taxonomic composition on an annual scale (fig. 6).

The SE region was sometimes similar to the Offshore, and other times intermediate between the Offshore and the more eutrophic NE and Alley. The SE had the highest number of species (one more than the Offshore) but no evidence for a decrease in species number over time (table 8a). Abundances in the SE region were intermediate (table 2), and increased during the study (fig. 3). The SE had a clear seasonal signal (table 5), but there was no evidence for a phenological change. Like the NE and Alley it was dominated by diatoms and coccolithophores although the proportion of diatoms was lower (59%) and that of coccolithophores was higher (28%) (fig. 5).

These four regions were initially defined by temporal averages of cruise-derived parameters (Hayward and Venrick 1998). The geographical correspondence between the regional boundaries and the local currents suggest that the boundaries are strongly influenced, perhaps defined, by the currents. However, the currents are not static, and the use of mean regional boundaries has resulted in an unknown amount of hybridization of regional characteristics across boundaries. The differences that have emerged from this study are strong enough to be detected in spite of that hybridization. Ideally regions should be defined in real time not by long-term averages so that the regions would more accurately reflect in situ conditions.

Temporal Patterns

Two of the temporal patterns will not be discussed further: the five to eight year repetition of species composition in the Offshore (fig. 6), and the increase in variability of composition in all regions except the NE after the postulated interdecadal climate shift near the year 2000 (fig. 7). Explanations for these patterns are not immediately forthcoming, but should similar patterns in other parameters appear, the phytoplankton data can be revisited.

Two temporal patterns warrant further consideration: the long-term increase in the phytoplankton abundance seen in the SE region and the Offshore, and the changes in the timing of the annual peak seen in the Inshore region and the Alley.

Interannual changes. An increasing trend in average chlorophyll *a* concentration in the CalCOFI area has been recognized for more than a decade (Schwing et al. 2002; Goericke et al. 2005), and several physical mechanisms have been proposed to explain this increase, either in the CalCOFI area (Aksnes and Ohman 2009; Rykaczewski and Checkley 2008; Rykaczewski and Dunne 2010) or directly north, from where it is potentially linked by advection (Garcia-Reyes and Largier 2010; Bograd et al. 2015).

Regional differences in chlorophyll *a* trends in the CalCOFI area were identified in 2011 (Bjorkstedt et al. 2011). Shipboard chlorophyll *a* extractions, integrated through the water column, indicated an increase in chlorophyll *a* in the offshore stations and in the California Current, but a decrease in the nearshore stations. Although neither sampling scale nor spatial subdivisions are identical to those used here, those chlorophyll trends are consistent with the trends of phytoplankton abundance.

On the other hand, satellite observations have been pooled into a time series from late 1996 through 2011 (Kahru et al. 2012). In this case, the chlorophyll *a* increase was highest near the coast—the opposite of the abundance trends. Analysis of CalCOFI secchi disk depth estimates from 1969 to 2007 (Aksnes and Ohman 2009) showed a decrease in euphotic zone depth across the entire CalCOFI area, implying an increase in chlorophyll and phytoplankton abundance both inshore and offshore. A long-term increase in nearshore chlorophyll *a* has been documented off the end of the Scripps pier (Kim et al. 2009) and a diatom increase is implicated in the recent increase in export of biogenic silica in the Santa Barbara Channel (Krause et al. 2013). Thus, a long-term increase in phytoplankton has been documented from several perspectives, but there is little consensus about regional patterns or the geographical center of phytoplankton increase.

Phenological changes. On a coarse temporal scale, there were seasonal cycles of phytoplankton abundances in all regions except the Offshore. However, in the NE and Alley, the annual peaks, initially in spring, appeared to shift progressively later in the year (figs. 3, 4), apparently driven by a strong decrease in the diatom component of the spring flora (table 10), which greatly reduced the spring amplitude of the cycle. Venrick (2012) hypothesized a change in nutrient source from coastal wind-driven upwelling in the spring to wind-stress-curl-driven upwelling in the summer (Rykaczewski and Checkley 2008). Coastal upwelling is maximal during the spring in the NE region and the Alley. Wind-stress-curl-driven upwelling is centered further offshore and later in the year. Evidence for a shift in importance of the two mechanisms would be decreasing phytoplankton abundance in the spring in the NE region and the Alley and an increase in abundance in the Alley later in the year.

Results of this study are partially consistent with the original hypothesis. Spring abundances decreased in both the NE and Alley, but increases in summer abundances were small, if present at all (fig. 4). Thus the relative but not the absolute magnitudes of spring and summer abundances have changed in the direction predicted.

An alternate explanation for this phenological shift is an increasing mismatch between a rather static CalCOFI cruise schedule and a slowly shifting seasonal peak. During the study, 12 of the 16 spring cruises were centered in April, three in March, and only one in May (fig. 2). It is possible that the seasonal peaks in abundance have not diminished but have shifted a few weeks earlier or later in the season, outside the sampling window. In this case the phenological change may be due only to a shift in time and may not involve decreasing peak abundances.

Some evidence for this hypothesis comes from the NE region. The latest spring cruise (May 7, 2010) directly followed the earliest spring cruise (March 16, 2009; figs. 2, 3). In the NE region, the May abundance was the second-highest spring abundance (and fourth-highest annual abundance) in the entire series (fig. 3), while the March cruise had the fourth-lowest spring value. This is consistent with a spring peak delayed slightly beyond the usual cruise schedule. Not sampling a delayed abundance peak could cause the CalCOFI data to underestimate the mean annual phytoplankton abundance and might resolve the discrepancy between the long-term increase in chlorophyll *a* shown in satellite data and in ship-based data. However, the data from the Alley are less supportive. The May 2010 abundance in the Alley was higher than that of March 2009, but both values were near the middle of the data set and did not indicate a relationship between abundance and sampling date.

Predictions of the effects of climate change, suggest that spring productivity will move earlier, not later. Most evidence from the marine environment supports this. (Poloczanska et al. 2013; Edwards and Richardson 2004). However, based on direct examination of alongshore wind stress between 1967 and 2007, Bograd et al. (2009) estimated significant variability in both onset and duration of wind driven upwelling in the California Current large marine ecosystem (33°–48°N). A delay in upwelling was detected in the northern part of the area. Although a change was not detected in the vicinity of the NE region, a mechanism for a progressive delay in the seasonal cycle has been identified.

A shift in phenology, whether driven by a decrease of the spring abundance or a delay in peak date, has implications both for the subsequent responses of the zooplankton and fish as well as for our understanding of the physics and chemistry of the nutrient input into the euphotic layer and predictions of climate change. It is important that this ambiguity be resolved. If our sampling schedule has become uncoupled from the seasonal cycle, we risk misinterpreting the system entirely.

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The paper is dedicated to Jerry Fecht, who knows neither *Calanus* nor *Chaetoceros*, but who encourages and inspires nonetheless.

LITERATURE CITED

Aksnes, D. L., and M. D. Ohman 2009. Multi-decadal shoaling of the euphotic zone in the southern sector of the California Current System. Limnol. Oceanogr. 54: 1272–1281.

Allen, W. E. 1936. Occurrence of marine plankton diatoms in a ten-year series of daily catches in southern California. Amer. J. Bot. 23: 60–63.

Allen, W. E. 1941. Twenty years' statistical studies of marine plankton dinoflagellates of southern California. Amer. Midl. Nat. 26: 603–635.

Allen, W. E. 1945a. Seasonal occurrence of marine plankton diatoms off southern California in 1938. Bull. Scripps Institution of Oceanography, 5: 293–334.

Allen, W. E. 1945b. Vernal distribution of marine plankton diatoms offshore in southern California in 1940. Bull. Scripps Institution of Oceanography, 5: 335–369.

Anderson, C, R., D. A. Siegel, M. A. Brzezinski, and N. Guillocheau. 2008. Controls on temporal patterns in phytoplankton community structure in the Santa Barbara Channel, California. J. Geophys. Res. 113 C04038, doi: 10.1029/2007JC004321.

Balech. E. 1960. The changes in the phytoplankton population off the California Coast. CalCOFI Rep. 7: 127–132.

Beers, J. R. 1986. Organisms and the food web, in Plankton Dynamics of the Southern California Bight, R. W. Eppley, ed. Springer-Verlag: 84–175.

Bjorkstedt, E. P., R.Goericke, S. McClatchie, E. Weber, W. Watson, N. Lo, B. Peterson, B. Emmett, J. Peterson, R. Durazo, G. Gaxiola-Castro, F. Chavez, J. T. Pennington, C. A. Collins, J. Field, S. Ralston, K. Sakuma, F. Schwing, Y. Xue, W. Sydeman, S. A. Thompson, J. A. Santora, J. Largier, C. Halle, S. Morgan, Y. Kim, K. Merkens, J. Hildebrand, and L. Mungere. 2010. State of the California Current 2009–10: regional variation persists through transition from La Niña to El Niño (and back?). Calif. Coop. Oceanic Fish, Invest. Rep. 51: 39–69.

Bjorkstedt, E. P., R. Goericke, S. McClatchie, E. Weber, W. Watson, N. Lo, B. Peterson, B. Emmett, R. Brodeur, J. Peterson, M. Litz, J. Gomez-Valdez, G. Gaxiola-Castro, B. Lavaniegos, F. Chavez, C. A. Collins, J. Field, K. Sakuma, P. Warzybok, R. Bradley, J. Jahncke, S. Bograd, F. Schwing, G. S. Campbell, J. Hildebrand, W. Sydeman, S. Thompson, J. Largier, C. Halle, S. Kim, and J. Abell. 2011. State of the California Current 2010–2011: Regional Variable Responses to a Strong (But Fleeting?) La Niña. Calif. Coop. Oceanic Fish, Invest. Rep. 52: 36–68.

Bjorkstedt, E. P., R. Goericke, S. McClatchie, E, Weber, W. Watson, N. Lo, B. Peterson, R. Brodeur, T. Auth, J. Fisher, C. Morgan, J. Peterson, J. Largier, S. J. Bograd, R. Durazo, G. Gaxiola-Castro, B. Lavaniegos, F. P. Chavez, C. A. Collins, B. Hannah, J. Field, K. Sakuma, W. Satterthwaite, M. O'Farrell, S. Hayes, J. Harding, W. J. Sydeman, S. A. Thompson, P. Warzybok, R. Bradley, J. Jahncke, R. T. Golightly, S. R. Schneider, R. M. Suryan, A. J. Gladics, C. A. Horton, S. Kim, S. R. Melin, R. L. Delong, and J. Abell. 2012. State of the California Current 2011–12: Ecosystems Respond to Local Forcing as La Niña Wavers and Wanes. Calif. Coop. Oceanic Fish, Invest. Rep. 53: 41–76.

Bograd, S. J., T. L. Hayward, K. D. Hyrenbach, F. B. Schwing, P. M. Digiacomo, R. J. Lynn, W. J. Sydeman, C. S. Moore, R. Durazo, A. W. Mantyla, T. Baumgartner, and B. Lavaniegos. 2000. The State of the California Current, 1999–2000: forward to a new regime? Calif. Coop. Oceanic Fish, Invest. Rep. 41: 26–52.

Bograd, S. J., and R. J. Lynn. 2001. Physical-biological coupling in the California Current during the 1997–99 El Niño–La Niña cycle. Geophys. Res. Lett. 28: 275–278.

Bograd, S. J., I. Schroeder, N. Sakar, X. Qui, W. J. Sydeman, and F. B. Schwing. 2009. Phenology of coastal upwelling in the California Current. Geophys. Res. Lett. 36. L01602, doi: 10.1029/2008S=GL035933.

Bograd, S. J., M. Pozo Buil, E. Di Lorenzo, C. G. Castro, I. D. Schroeder, R. Goericke, C. R. Anderson, C. Benitez-Nelson, and F. A. Whitney. 2015. Changes in source waters to the Southern California Bight. Deep-Sea Res. II. 112:42–52.

Bond, N. A., J. E. Overland, M. Spillane, and P. Stabeno. 2003. Recent shifts in the state of the North Pacific. Geophys. Res. Lett. 30(23), 2183, doi:10.1029/2003GL018597.

Busse, L. B., E. L. Venrick, R. Antrobus, P. E. Miller, V. Vigilant, M. W. Silver, C. Mengelt, L. Mydlarz, and B. B. Prezelin. 2006. Domoic acid in phytoplankton and fish in San Diego, CA, USA. Harmful Algae. 5:91–101. 10.1016/j.hal.2005.06.005

Chelton , D. B., P. A. Bernal, and J. A. McGowan. 1982. Large-scale interannual physical and biological interaction in the California Current. J. Mar. Res. 40: 1095–1125.

Conover, W. J. 1999. Practical Nonparametric Statistics, 3rd ed. New York: John Wiley, 584 pp.

Di Lorenzo, E., N. Schneider, K. M. Cobb, P. J. S. Franks, K. Chhak, A. J. Miller, J. C. McWilliams, S. J. Bograd, H. Arango, E. Curchitser, T. M. Powell, and P. Rivière. 2008. North Pacific Gyre Oscillation links ocean climate and ecosystem change. Geophys. Res. Lett. , 35, L08607, doi: 10.1029/2007GL032838.

Durazo R., T. R. Baumgartner, S. J. Bograd, C. A. Collins, S. de la Campa, J. Garcia, G. Gaxiola-Castro, A. Huyer, K. D. Hyrenbach, D. Loya, R. J. Lynn, F. B. Schwing, R. L. Smith, W. J. Sydeman, and P. Wheeler. 2001. The state of the California Current, 2000–01: a third straight La Niña year. Calif. Coop. Oceanic Fish, Invest. Rep. 42: 29–60.

Ebbesmeyer, C. C., D. R. Cayan, D. R. McLain, F. H. Nichols, D. H. Peterson, and K. T. Redmond. 1991. 1976 step in the Pacific Climate: forty environmental changes between 1968–75 and 1977–84. In J. L. Betancourt and V. L. Tharp (Eds.), Proceedings of Seventh Annual Climate (PACLIM) Workshop, April 1990 (pp. 115–126). Calif. Dept. Water Research Interagency Ecological Studies Program Tech. Rept. 26.

Edwards, M., and A. J. Richardson. 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. Nature, 430: 881–883.

García-Reyes, M., and J. Largier. 2010. Observations of increased wind-driven coastal upwelling off central California. J. Geophys. Res. 115, C04011, doi:10.1029/2009JC005576.

Goericke, R., E. Venrick, A. Mantyla, S. J. Bograd, F. B. Schwing, A. Huyer, R. L. Smith, P. A. Wheeler, R. Hooff, W. T. Peterson, F. Chavez, C. Collins, B. Marinovic, N. Lo, G. Gaxiola-Castro, R. Durazo, K. D. Hyrenbach, and W. J. Sydeman. 2005. The State of the California Current, 2004–2005: Still Cool? Calif. Coop. Oceanic Fish, Invest. Rep. 46: 32–71.

Goericke, R. 2011. The size structure of marine phytoplankton—what are the rules? CalCOFI Rep. 52: 198–204.

Hayward, T. L. 2000. El Niño 1997–98 in the coastal waters of southern California: a timeline of events. Calif. Coop. Oceanic Fish, Invest. Rep. 41: 98–116.

Hayward, T. L., and E. L. Venrick. 1998. Nearsurface pattern in the California Current: coupling between physical and biological structure. Deep-Sea Res. II 45: 1617–1638.

Hayward, T. L., T. R. Baumgartner, D. M. Checkley, R. Durazo, G. Gaxiola-Castro, K. D. Hyrenbach, A. W. Mantyla, M. M. Mullin, T. Murphree, F. B. Schwing, P. E. Smith, and M. J. Tegner. 1999. The state of the California Current in 1998–99: transition to cool-water conditions. Calif. Coop. Oceanic Fish, Invest. Rep. 40: 29–62.

Kahru, M., R. M. Kudela, M. Manzano-Sarabia, and B. G. Mitchell. 2012. Trends in the surface chlorophyll of the California Current: Merging data from multiple ocean color satellites. Deep-Sea Res. II: 77–80: 8998.

Kim, H.-J., A. J. Miller, J. McGowan and M. L. Carter. 2009. Coastal phytoplankton blooms in the Southern California Bight. Progr. Oceanogr. 82: 137–147, doi.org/10.1016/j.pocean.2009.05.002.

Krause, J. W., M. A. Brzezinski, D. A. Siegel, and R. C. Thunell. 2013. Biogenic silica standing stock and export in the Santa Barbara Channel ecosystem. J. Geophys. Res: oceans, 118: 736–749, doi:10.1029/2012JC008070.

Lavaniegos, B. E., and M. D. Ohman. 2003. Long-tern changes in pelagic tunicates of the California Current. Deep-Sea Res. II 50: 2473–2498, doi: 10.1016/S0967-0645(03)00132-2.

Ledesma, R. D., and P. Valero-Mora. 2007. Determining the number of factors to retain in EFA: An easy-to-use computer program for carrying out Parallel Analysis. Practical Assessment Res. and Eval. 12(2). Available on line: http://pareonline.net/getvn.asp?v=12&n=2.

Legaard, K. R., A. C. Thomas. 2006. Spatial patterns in seasonal and interannual variability of chlorophyll and seas surface temperature in the California Current. J. Geophys. Res. 111: C06032, doi: 10.1029/2005JC003282.

Lynn, R. J., J. J. Simpson. 1987. The California Current System: the seasonal variability of its physical characteristics. J. Geophys. Res. 92: 12947–12966.

Lynn, R. J., T. Baumgartner, J. Garcia, C. A. Collins, T. L. Hayward, K. D. Hyrenbach, A. W. Mantyla, T. Murphree, A. Shankle, F. B. Schwing, K. M. Sakuma, and M. J. Tegner. 1998. The state of the California Current, 1997–98: transition to El Niño conditions. Calif. Coop. Oceanic Fish, Invest. Rep. 39, 25–49.

Malone, T. C. 1980. Algal size. Chapter 12. Pp 433–463 In The Physiological Ecology of Phytoplankton. I. Morris (ed.) Blackwell Scientific.

Mantua, N. J., S. R. Hare, Y. Zhang, J. M. Wallace, and R. C. Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. Bull. Amer. Meteorol. Soc. 78: 1069–1079.

Margaleff, R. 1978. Life-forms of phytoplankton as survival alternatives in an unstable environment. Oceanologica Acta 1(4): 493–509.

Matrai, P. 1986. The distribution of the dinoflagellate Ceratium in relation to environmental factors along 28N in the eastern North Pacific. J. Plankt. Res.8:105–118.

McClatchie, S., R. Goericke, A. J. Koslow, F. B. Schwing, S. J. Bograd, R. Charter, W. Watson, N. Lo, K. Hill, J. Gottschalk, M. L'Heureux, Y. Xue, W. T. Peterson, R. Emmett, C. Collins, G. Gaxiola-Castro, R. Durazo, M. Kahru, B. G. Mitchell, K. D. Hyrenbach, W. J. Sydeman, R. W. Bradley, P. Warzybok, and E. Bjorkstedt. 2008. The state of the California Current, spring 2007–08: La Niña conditions and their effects on the ecosystem. Calif. Coop. Oceanic Fish, Invest. Rep. 49, 39–76.

McClatchie, S., R. Goericke, F. B. Schwing, S. J. Bograd, W. T. Peterson, R. Emmett, R. Charter, W. Watson, N. Lo, K. Hill, C. Collins, M. Kahru, B. G. Mitchell, A. J. Koslow, J. Gomez-Valdes, B. E. Lavaniegos, G. Gaxiola-Castro, J. Gottschalk, M. L'Heureux, Y. Xue, M. Manzano-Sarabia, E. Bjorkstedt, S. Ralston, J, Field, L. Rogers-Bennett, L. Munger, G. Campbell, K. Merkens, D. Camacho, A. Havron, A. Douglas, and J. Hildebrand. 2009. The state of the California Current, 2008–09: cold conditions drive regional differences in coastal production. Calif. Coop. Oceanic Fish, Invest. Rep. 50: 43–68.

Nemenyi, P. 1963. Distribution-free multiple comparisons. Ph.D. Dissertation Princeton University. 127 pp.

Pacific Coast Ocean Observing System. 2012. PaCOOS Quarterly update of climatic and ecological conditions in the CA current LME. 2012. Annual Summary. [http://pacoos.org/QuarterlyUpdate_Climatic/2012_Annual_Summary.pdf].

Poloczanska, E. S., C. J. Brown, W. J. Sydeman, W. Kiesling, D. S. Schoeman, P. J. Moore, K. Brande, J. F. Bruno, L. B. Buckley, M. T. Burrows, C. M. Duarte, B. S. Halpern, J. Holding, C.V. Kappel, M. I. O'Connor, J. M. Pandolfi, C. Parmesan, F. Schwing, S. A. Thompson and A. J. Richardson. 2013. Global imprint of climate change on marine life. Nature Climate Change. 3: 919–925.

Roemmich, D., and J. McGowan. 1995a. Climatic warming and the decline of zooplankton in the California Current. Science 267: 1324–1326.

Roemmich, D., and J. McGowan. 1995b. Climatic warming and the decline of zooplankton in the California Current. Science 268: 352–353.

Rykaczewski, R. R., and D. M. Checkley. 2008. Influence of ocean winds on the pelagic ecosystem in upwelling regions. Proceed. Nat. Acad. Sci. 105: 1965–70, doi: 10.1073/pnas.0711777105.

Rykaczewski, R. R., and J. P. Dunne. 2010. Enhanced nutrient supply to the California Current Ecosystem with global warming and increased stratification in an earth system model. Geophys. Res. Lett. 37, L21606, doi:10.1029/2010GL045019.

Schwing, F. B., S. J. Bograd, C. A. Collins, G. Gaxiola-Castro, J. García, R. Goericke, J. Goméz-Valdéz, A., Huyer, K. D. Hyrenbach, P. M. Kosro, B. E. Lavaniegos, R. J., Lynn, A. W. Mantyla, M. D. Ohman, W. T. Peterson, R. L. Smith, W. J. Sydeman, E. Venrick, and P. A. Wheeler. 2002. The state of the California Current, 2001–02: will the California Current system keep its cool, or is El Niño looming? Calif. Coop. Oceanic Fish, Invest. Rep. 43, 31–68.

Sokal, R. R., and F. J. Rohlf. 1969. Biometry. W. H. Freeman and Co.

Sprent, P. 1993. Applied Nonparametric Statistical Methods, 2nd ed. London: Chapman and Hall. 342 pp.

Sverdrup, H. U., and W. E. Allen. 1939. Distribution of diatoms in relation to the character of water masses and currents off southern California in 1938. J. Mar. Res. 2:131–144.

Tate M. W., and R. C. Clelland. 1957. Nonparametric and Shortcut Statistics in the Social, Biological and Medical Sciences. Danville: Interstate Printers. 171 pp.

Venrick, E. L. 1992. Phytoplankton species structure in the central North Pacific: Is the edge like the center? J. Plankt. Res. 14: 665–680.

Venrick, E. L. 1998a. Spring in the California Current: the distribution of phytoplankton species, April 1993 and April 1995. Mar. Ecol. Progr. Ser. 167: 73–88.

Venrick, E. L. 1998b. The phytoplankton pf the Santa Barbara Basin: patterns of chlorophyll and species structure and their relationships with those of surrounding stations. CalCOFI Rep. 39: 124–131.

Venrick, E. L. 2000. Summer in the Ensenada Front: the distribution of phytoplankton species, July 1985 and September 1988. J. Plankt. Res. 22: 813–841.

Venrick, E. L., C. B. Lange, F. M. H. Reid, E. P. Dever, and A. Weinheimer. 2008. Temporal patterns of species composition of siliceous phytoplankton flux in the Santa Barbara Basin. J. Plankt. Res. 30: 283–297.

Venrick, E. L. 2009. Floral patterns in the California Current: The coastal-offshore boundary zone. J. Mar. Res. 67: 89–111.

Venrick, E. L. 2012. Phytoplankton in the California Current system off southern California: changes in a changing environment. Progr. Oceanogr. 104: 44–58.

Venrick, E. L., S. J. Bograd, D. Checkley, R. Durazo, G. Gaxiola-Castro, J. Hunter, A. Huyer, K. D. Hyrenbach, B. E. Lavaniegos, A. Mantyla, F. B. Schwing, R. L. Smith, W. J. Sydeman, and P. A. Wheeler. 2003. The state of the California Current, 2002–03: tropical and subarctic influences vie for dominance. Calif. Coop. Oceanic Fish, Invest. Rep. 44, 28–60.

Wells, B. K., I. D. Schroeder, J. A. Santora, E. L. Hazen, S. J. Bograd, E. P. Bjorkstedt, V. Loeb, S. McClatchie, E. D. Weber, W. Watson, A. R. Thompson, W. T. Peterson, R. D. Brodeur, J. Harding, J. Field, K. Sakuma, S. Hayes, N. Mantua, W. J. Sydeman, M. Losekoot, S. A. Thompson, J. L. Largier, S. Y. Kim, F. P. Chavez, C. Barchelo, P. Warzybok, R. Bradley, J. Jahncke, R. Goericke, G. S. Campbell, J. A. Hildebrand, S. R. Melin, R. I. Delong, J. Gomez-Valdez, B. Lavaniegos, G. Gaxiola-Castro, R. T. Golightly, S. R. Schneider, N. C. Lo, R. M. Suryan, A. J. Gladics, C. Horton, A. J. Fisher, C. Morgan, J. Peterson, E. A. Daly, T. D. Auth, and J. Abell. 2013. State of the California Current 2012–13: No Such Thing as an "Average" Year. Calif. Coop. Oceanic Fish, Invest. Rep. 54: 37–71.

Winn, C. D., L. Campbell, J. R. Christian, R. M. Letelier, D.V. Hebel, J. E. Dore, L. Fujieki, and D. M. Karl. 1995. Seasonal variability in the phytoplankton community of the North Pacific Subtropical Gyre. Global Biogeochemical Cycles 9: 605–620.

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BOOK:

Odum, E. P. 1959. Fundamentals of ecology. 2nd ed. Philadelphia: Saunders. 546 pp.

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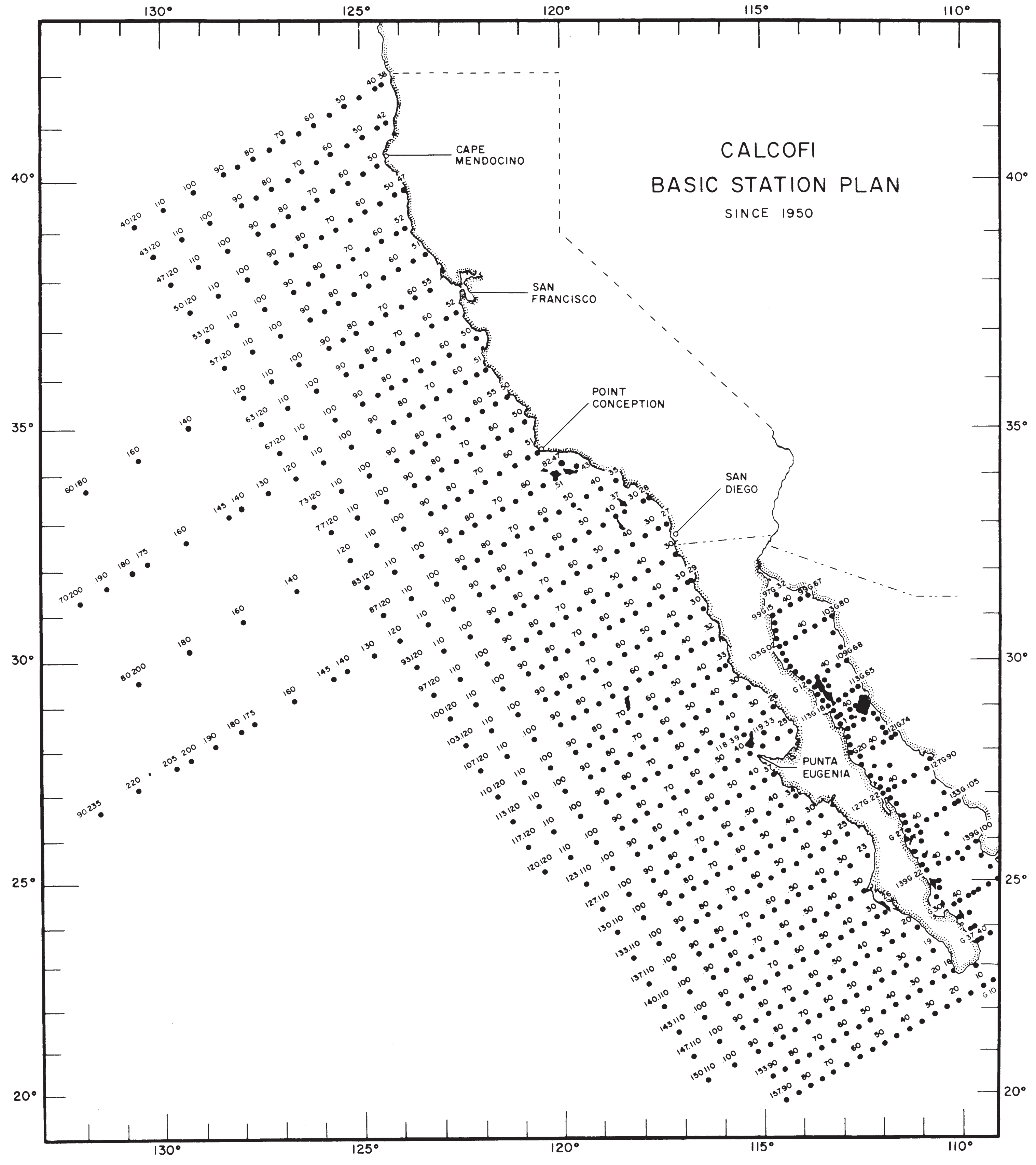

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