DIET ANALYSIS OF PACIFIC SARDINE (*SARDINOPS SAGAX*) OFF THE WEST COAST OF VANCOUVER ISLAND, BRITISH COLUMBIA FROM 1997 TO 2008

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ABSTRACT

Trawl surveys for Pacific sardine were conducted off the west coast of Vancouver Island (northern terminus of the California Current System) from 1997 to 2008. Stomachs of 1670 sardines were collected and analysed using standardized laboratory procedures. Sardines are opportunistic feeders with dominant groups in the diet reflecting abundance and availability of prey. Major prey groups included euphausiid (and eggs), copepods and diatoms; however a total of 11 other functional prey groups were identified. Dominant prey groups varied seasonally and interannually. Sardines fed throughout the day and night, with a peak feeding event after dusk.

INTRODUCTION

Pacific sardine (*Sardinops sagax*) off the west coast of North America have fluctuated in abundance for at least the last 1600 years (Baumgartner et al. 1992; McFarlane et al. 2002). Over the last century, sardines were a dominant species from Baja California to British Columbia during the 1930s, 1940s and 1950s, and again from the early 1990s to the present (Hill et al. 2008). Their fluctuations in abundance have been related to climate/ocean conditions (Kawasaki 1983; McFarlane et al. 2002; Chavez et al. 2003), however, the underlying mechanism is poorly understood. A number of authors have argued that physical factors are the main causal mechanisms (see Rykaczewski and Checkley 2008, McFarlane et al. 2002, and Barange et al. 2009 for a review of the studies). Alternatively, a number of authors have proposed links to larval and juvenile diet (Lasker 1975, 1981; Watanabe and Saito 1998; McFarlane and Beamish 2001; Logerwell and Smith 2001). Clearly both physical and biological factors play a role in regulating sardine abundance (McFarlane et al. 2002).

It is equally clear that sardines play an important role in the California Current System (CCS). They are omnivores, feeding on both phytoplankton and zooplankton (Lasker 1970; McFarlane et al. 2005; Emmett et al. 2005), and can consume vast amounts of both primary and secondary production (Lasker 1970). To better understand the role of sardines in the CCS and the dynamics of the stock itself, requires information on the diet of sardines along their entire range (McFarlane and Beamish 2001; Emmett et al. 2005).

In this paper we provide diet data for sardines captured off the west coast of Vancouver Island (the northern terminus of the CCS) from 1997 to 2008. We believe this information will be useful in understanding the role sardines play in the system.

METHODS

Sardine diet information was collected from randomly selected samples of approximately 50 fish during trawl surveys conducted off the west coast of Vancouver Island (WCVI) during June, July or August from 1997–2008 (with the exception of 2000 and 2007) aboard the R/V *W.E. Ricker* or F/V *Frosti* (2005). In addition, during 1998, 1999 and 2001 samples were collected before and after the summer period (June–August) to examine seasonal differences. In August 2005, samples were collected every 2 or 3 hours in 2 areas over 3 days to examine day/night differences in feeding. Samples (150 fish) were also collected in August 2005 from 2 commercial fishing trips in inlets off the WCVI aboard the seiners F/V *Kynoc* and F/V *Ocean Horizon*.

Preservation and Laboratory Methods

All stomachs collected from each set were pooled by set. Stomachs were excised and preserved in 3.7% buffered formalin. In the laboratory, contents of the cardiac stomach region were extracted with curved end forceps onto a petri dish. A total volume of stomach contents was visually estimated in cubic centimetres (cc) using a syringe marked at every 0.1 cc. An estimate indicating a proportion of a full stomach was expressed as a percentage; where 0% denoted an empty stomach, and 100% signified a completely full stomach. Degree of stomach contents digestion was also expressed as a percentage, where 0% denoted fresh contents and 100% indicated completely digested contents.

Under a dissecting microscope, probe and forceps were used to pull apart the stomach mass and identify individual food items. Items were identified to the lowest taxonomic group possible, then collated to a major prey group (e.g. euphausiid, diatom, copepod, etc.), and the contribution of each major group was expressed as a percent of the total stomach volume. Similarly, unidentifiable contents (categorized as digested matter) were expressed as a percent of the total stomach volume.

In 1997 and 1998, sardine scales were included as a prey item, and were considered a component of the overall stomach contents volume. Since 1999, the volume of sardine scales present in the stomach has been recorded separately from the stomach contents volume. In order to standardize all years, the total stomach volume from 1997 and 1998 samples was recalculated to exclude sardine scales.

Data Standardization

We have omitted stomachs analyzed using methodology inconsistent with the described laboratory methods, along with stomachs collected in spring or fall, empty stomachs, and stomachs containing 100% scales or 100% digested material.

Prey items which were present in trace amounts were converted to represent 1% of the total stomach content volume. To accommodate this change, the proportion of digested matter was adjusted accordingly. In rare cases where digested matter was not present, the reduction was applied to the most abundant prey item in that stomach.

Minor prey items were combined into a category named "Other." Prey items included in the "Other" prey item category had to respect two conditions: (1) the prey item was present in less than 5% of the stomachs in each year, and (2) the prey item was present in no more than two of all survey years. Summer months (June, July and August) exclusively, were used for the inter-annual comparisons.

Diet Analysis

The relative importance of each prey group was determined using the King and Beamish (2000) modification of the Index of Relative Importance (IRI) (Pinkas et al. 1971). Similar to the IRI, the modified index of relative importance (RI) describes the quantity of a particular prey item in each individual fish, how many fish eat that prey item, and how much that prey item contributes to the total volume of food consumed by all the fish. The equation for RI is as follows: RI = %FOx (%C+%V) where; %FO = percent frequency of occurrence, or percentage of stomachs containing at least one of the prey items, %C = percentage of contents importance, or the average percentage volume per stomach made up by the prey item, %V = total volume importance, or the percentage ratio of the total volume of the prey item consumed by all fish to the total volume of all prey consumed by all fish (excludes digested matter volume). The %RI ranges from 0, where a prey item is not consumed at all, to 20 000 where a prey item is exclusively consumed. The equation for %RI is as follows: %RI = RI/20 000 x 100.

In this report, the RI values are expressed as a percentage of the maximum attainable value of 20 000 (%RI), to allow for a simpler comparison between values. It is important to note that the %RI values are not cumulative for prey groups within a year, and that the %RI values for all prey items within a year may add up to be greater than 100.

Sardine diet overlap was estimated among all years, using the Morisita-Horn index of overlap (Horn 1966; in King and Beamish 2000) to compare among years:

$$O = 2\Sigma^{n}_{i}\, p_{ij}\, p_{ik} \,/\, \Sigma^{n}_{i}\, p^{2}_{ij} + \Sigma^{n}_{i}\, p^{2}_{ik}$$

Where O = Morisita-Horn index of overlap between year j and year k, n = total number of prey item groups. p_{ij} = proportion of prey item i consumed by sardines in year j. p_{ik} = proportion of prey item i consumed by sardines in year k.

The Morisita-Horn index of overlap was calculated separately based on total volume importance (%V: reflects an overall contribution) and index of relative importance (%RI: provides integrated expression of diet) as the measurements of proportion of prey items. The overlap index ranges from 0 (absolutely no overlap) to 1.0 (complete overlap) (Landingham et al. 1998; King and Beamish 2000). For the purposes of this study values greater than 0.6 were considered to reflect significant overlap.

We used %V since it reflects an overall contribution and is not influenced by small prey items unless they are consumed often and in large quantities. We used the %RI since it is a composite measurement that provides an integrated expression of diet.

RESULTS

A total of 2169 stomachs were examined from research cruises off the WCVI from 1997 to 2008 (tab. 1). Of these, 1670 were examined using standardized laboratory procedures of which, 1405 stomachs were examined using standardized laboratory procedures and contained identifiable prey items. All fish were adults measuring from 173mm to 290mm fork length (FL) and a modal size of 240mm (FL) for male and female groups.

Interannual Comparison

A total of 1849 stomachs were examined from sardines collected during summer months (June to August)

TABLE 1
Summary of stomach analysis for Pacific sardines (*Sardinops sagax*) captured off WCVI, 1997–2008.

Year/ Month	# of stomachs	# of stomachs analyzed by standard lab method	# of empty stomachs	# of stomachs with 100% digested matter or 100% scales	# of stomachs summarized for report	Total volume (cc)	Volume of digested matter (cc)	Volume of identifiable prey items (cc)	Average volume per stomach including digested matter (cc)	Average volume of identifiable prey items per stomach (cc)
1997										
June	549	67	0	52	15	40.02	38.26	1.76	0.60	0.03
July	22	5	0	5	0	4.26	4.26	0.00	0.85	0.00
August	53	53	0	38	15	40.19	35.54	4.65	0.76	0.09
October	15	15	0	14	0	6.90	6.82	0.08	0.46	0.01
1997 Total	**639**	**140**	**0**	**109**	**30**	**91.37**	**84.88**	**6.49**		
1998										
May	14	14	3	3	8	6.90	0.50	6.40	0.49	0.46
June	57	57	0	3	54	25.20	5.26	19.94	0.44	0.35
August	14	14	1	0	13	11.40	0.05	11.35	0.81	0.81
September	95	95	13	2	80	2.33	1.36	0.97	0.02	0.01
October	20	20	1	10	9	4.90	3.66	1.24	0.25	0.06
1998 Total	**200**	**200**	**18**	**18**	**164**	**50.73**	**10.83**	**39.90**		
1999										
March	30	30	0	0	30	13.50	8.89	4.61	0.45	0.15
July	80	80	0	0	80	16.51	4.69	11.82	0.21	0.15
August	45	45	0	0	45	5.80	3.61	2.19	0.13	0.05
1999 Total	**155**	**155**	**0**	**0**	**155**	**35.81**	**17.19**	**18.62**		
2000										
September	74	74	0	0	0	9.50	8.97	0.53	0.13	0.01
2000 Total	**74**	**74**	**0**	**0**	**0**	**9.50**	**8.97**	**0.53**		
2001										
July	38	38	0	0	38	4.80	4.45	0.35	0.13	0.01
August	22	22	0	0	22	3.70	3.45	0.25	0.17	0.01
October	50	50	0	2	48	5.70	5.00	0.70	0.12	0.01
2001 Total	**110**	**110**	**0**	**2**	**108**	**14.20**	**12.90**	**1.30**		
2002										
August	80	80	0	0	80	136.10	45.75	90.35	1.70	1.13
September	22	22	0	0	0	21.20	15.18	6.02	0.96	0.69
2002 Total	**102**	**102**	**0**	**0**	**80**	**157.30**	**60.93**	**96.37**		
2003										
August	20	20	0	0	20	4.00	1.38	2.62	0.20	0.13
2003 Total	**20**	**20**	**0**	**0**	**20**	**4.00**	**1.38**	**2.62**		
2004										
July	20	20	0	1	19	12.20	7.40	4.80	0.61	0.37
2004 Total	**20**	**20**	**0**	**1**	**19**	**12.20**	**7.40**	**4.80**		
2005										
August (coastal)	179	179	0	0	179	224.00	70.78	153.22	1.25	0.86
August (inlet)	150	150	0	0	150	199.83	86.81	113.02	1.33	0.75
2005 Total	**329**	**329**	**0**	**0**	**329**	**423.83**	**157.59**	**266.24**		
2006										
July	20	20	0	0	20	35.40	8.35	27.05	1.77	1.35
August	260	260	0	20	240	373.80	63.71	310.09	1.56	1.29
2006 Total	**280**	**280**	**0**	**20**	**260**	**409.20**	**72.06**	**337.14**		
2008										
August	240	240	0	0	240	451.60	85.97	365.64	1.88	1.52
2008 Total	**240**	**240**	**0**	**0**	**240**	**451.60**	**85.97**	**365.64**		
Overall total	**2169**	**1670**	**18**	**150**	**1405**	**1659.74**	**520.10**	**1139.65**		
Summer total	**1849**	**1350**	**1**	**119**	**1230**	**1588.81**	**469.72**	**1119.11**		

(tab. 1). Of these, 1350 were examined using standardized laboratory procedures and contained identifiable items. Average volume per stomach ranged from 0.13cc (Aug 1999, July 2001) to 1.88cc (Aug 2008). The average volume of identifiable prey items ranged from 0.01 cc (2001) to 1.52 cc (2008). A total of 14 functional groups of prey items were identified during summer months. In general, the majority of identifiable stomach contents consisted of euphausiids, copepods and diatoms (tab. 2, fig. 1). However, the relative contribution of prey items varied considerably (fig. 1) between years. For example, euphausiids were important in the diet of sardine in 1997, 2006 and 2008 (%RI of 21.63, 23.57 and 40.71 respectively), with importance influ-

TABLE 2
Pacific sardine (*Sardinops sagax*) diet composition by year 1997–2008. Data from summer months (June–August) only.

	Euphausiid	Copepod	Diatoms	Euphausiid eggs	Oikopleura	Eggs	Crab zoea	Cladoceran	Barnacle nauplii	Barnacle cyprids	Fish eggs	Cyclopoid	Amphipod	Other*
1997: 30 stomachs														
%FO	56.67	6.67	0.00	0.00	0.00	20.00	26.67	0.00	0.00	0.00	0.00	0.00	3.33	40.00
%V	55.30	1.55	0.00	0.00	0.00	16.25	5.80	0.00	0.00	0.00	0.00	0.00	0.22	20.87
%C	21.05	0.50	0.00	0.00	0.00	5.33	3.67	0.00	0.00	0.00	0.00	0.00	0.33	9.93
RI	4326.78	13.67	0.00	0.00	0.00	431.67	252.52	0.00	0.00	0.00	0.00	0.00	1.85	1232.11
%RI	21.63	0.07	0.00	0.00	0.00	2.16	1.26	0.00	0.00	0.00	0.00	0.00	0.01	6.16
1998: 67 stomachs														
%FO	23.88	17.91	74.63	74.63	0.00	0.00	0.00	0.00	7.46	1.49	1.49	1.49	11.94	19.40
%V	35.25	3.12	33.18	19.88	0.00	0.00	0.00	0.00	0.32	0.03	0.02	0.08	1.68	6.44
%C	18.21	1.06	36.41	21.02	0.00	0.00	0.00	0.00	0.32	0.03	0.01	0.08	1.04	4.19
RI	1276.55	74.83	5193.82	3052.76	0.00	0.00	0.00	0.00	4.74	0.09	0.05	0.24	32.57	206.30
%RI	6.38	0.37	25.97	15.26	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.16	1.03
1999: 125 stomachs														
%FO	1.61	96.77	46.77	66.13	37.90	8.06	10.48	3.23	10.48	0.81	8.06	10.48	3.23	3.23
%V	0.36	31.08	5.52	20.25	36.36	2.12	1.17	0.25	0.22	0.07	1.64	0.23	0.50	0.23
%C	0.09	17.37	2.41	13.45	16.77	0.94	0.35	0.18	0.14	0.04	0.52	0.18	0.22	0.14
RI	0.73	4688.98	371.13	2228.33	2013.80	24.65	15.87	1.38	3.75	0.09	17.40	4.25	2.31	1.20
%RI	0.00	23.44	1.86	11.14	10.07	0.12	0.08	0.01	0.02	0.00	0.09	0.02	0.01	0.01
2001: 60 stomachs														
%FO	8.33	95.00	71.67	16.67	8.33	1.67	3.33	10.00	6.67	0.00	0.00	10.00	6.67	1.67
%V	8.70	35.45	32.44	2.84	1.84	2.51	8.53	1.51	1.17	0.00	0.00	2.01	2.68	0.33
%C	0.52	2.23	2.02	0.17	0.15	0.08	0.85	0.10	0.07	0.00	0.00	0.17	0.13	0.02
RI	76.77	3580.06	2469.50	50.16	16.58	4.32	31.26	16.05	8.25	0.00	0.00	21.73	18.73	0.59
%RI	0.38	17.90	12.35	0.25	0.08	0.02	0.16	0.08	0.04	0.00	0.00	0.11	0.09	0.00
2002: 80 stomachs														
%FO	81.25	98.75	100.00	37.50	72.50	0.00	8.75	58.75	67.50	23.75	3.75	7.50	0.00	5.00
%V	15.24	23.38	45.32	2.35	7.51	0.00	0.17	2.31	1.50	0.43	1.57	0.13	0.00	0.08
%C	9.63	19.58	25.19	1.11	5.21	0.00	0.14	2.01	1.13	0.28	0.28	0.08	0.00	0.16
RI	2020.27	4241.88	7051.02	129.83	922.13	0.00	2.73	253.67	177.92	16.63	6.92	1.56	0.00	1.21
%RI	10.10	21.21	35.26	0.65	4.61	0.00	0.01	1.27	0.89	0.08	0.03	0.01	0.00	0.01
2003: 20 stomachs														
%FO	15.00	100.00	100.00	90.00	90.00	0.00	80.00	95.00	70.00	5.00	0.00	15.00	0.00	30.00
%V	0.36	28.99	26.70	2.04	17.35	0.00	15.06	6.90	1.11	0.08	0.00	0.27	0.00	1.30
%C	0.24	20.75	15.50	1.39	11.00	0.00	12.38	4.35	0.70	0.05	0.00	0.35	0.00	1.30
RI	9.00	4973.55	4219.72	308.51	2551.78	0.00	2195.19	1069.05	126.42	0.63	0.00	9.25	0.00	77.90
%RI	0.04	24.87	21.10	1.54	12.76	0.00	10.98	5.35	0.63	0.00	0.00	0.05	0.00	0.39
2004: 19 stomachs														
%FO	31.58	94.74	78.95	0.00	10.53	0.00	31.58	0.00	0.00	5.26	0.00	0.00	10.53	78.95
%V	6.31	22.07	5.29	0.00	0.31	0.00	12.08	0.00	0.00	0.21	0.00	0.00	0.42	53.52
%C	1.89	10.32	2.21	0.00	0.11	0.00	4.00	0.00	0.00	0.05	0.00	0.00	0.11	17.12
RI	259.09	3068.52	592.10	0.00	4.40	0.00	507.74	0.00	0.00	1.37	0.00	0.00	5.49	5576.46
%RI	1.30	15.34	2.96	0.00	0.02	0.00	2.54	0.00	0.00	0.01	0.00	0.00	0.03	27.88
2005 (Coastal): 179 stomachs														
%FO	26.26	100.00	98.88	26.26	0.00	0.00	2.23	19.55	6.70	6.15	0.00	1.12	2.23	7.26
%V	59.97	18.26	16.61	2.78	0.00	0.00	0.06	0.27	0.06	0.06	0.00	0.01	0.34	1.58
%C	16.10	16.49	16.04	3.24	0.00	0.00	0.09	0.57	0.07	0.06	0.00	0.01	0.07	0.46
RI	1997.53	3475.36	3228.46	157.94	0.00	0.00	0.34	16.36	0.86	0.73	0.00	0.02	0.90	14.86
%RI	9.99	17.38	16.14	0.79	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.00	0.00	0.07
2005 (Inlets): 150 stomachs														
%FO	6.00	98.67	83.33	54.67	4.00	0.00	0.67	30.67	48.00	30.00	0.00	20.00	4.00	18.00
%V	0.94	18.51	62.22	11.55	0.23	0.00	0.01	0.88	2.22	1.37	0.00	0.87	0.39	0.81
%C	0.15	14.93	17.57	6.86	0.06	0.00	0.01	0.47	0.82	0.38	0.00	0.31	0.38	0.42
RI	6.54	3299.73	6649.41	1006.78	1.14	0.00	0.01	41.42	145.97	52.32	0.00	23.77	3.07	22.19
%RI	0.03	16.50	33.25	5.03	0.01	0.00	0.00	0.21	0.73	0.26	0.00	0.12	0.02	0.11
2006: 260 stomachs														
%FO	72.31	98.85	95.77	51.92	21.54	0.00	3.08	43.85	21.92	2.69	4.62	54.62	3.85	16.15
%V	43.52	19.47	29.29	3.70	0.22	0.00	0.09	1.68	0.47	0.04	0.11	0.97	0.05	0.38
%C	21.66	17.18	22.62	1.95	0.34	0.00	0.03	1.32	0.29	0.03	0.05	0.79	0.04	0.38
RI	4713.48	3622.95	4972.06	293.25	11.91	0.00	0.38	131.80	16.67	0.19	0.71	96.47	0.35	12.17
%RI	23.57	18.11	24.86	1.47	0.06	0.00	0.00	0.66	0.08	0.00	0.00	0.48	0.00	0.06
2008: 240 stomachs														
%FO	87.08	99.17	66.25	22.50	25.83	0.00	2.92	11.67	2.50	0.83	2.08	10.00	3.75	25.83
%V	57.62	22.27	17.12	1.23	0.26	0.00	0.07	0.13	0.03	0.00	0.02	0.08	0.05	1.14
%C	35.87	13.24	17.74	1.27	0.51	0.00	0.07	0.17	0.04	0.01	0.02	0.13	0.11	0.79
RI	8141.03	3521.00	2309.43	56.29	19.82	0.00	0.39	3.46	0.16	0.01	0.08	2.02	0.58	50.05
%RI	40.71	17.60	11.55	0.28	0.10	0.00	0.00	0.02	0.00	0.00	0.00	0.01	0.00	0.25

*Other prey items include: 1997 (crab megalops, pteropod, juvenile shrimp, larval shrimp, juvenile octopus, juvenile crab) 1998 (fish larvae, crab megalops, gastropod, algae filaments) 1999 (shrimp zoea, ostracod, algae filaments) 2001 (chaetognath) 2002 (chaetognath, shrimp zoea) 2003 (shrimp remains, shrimp larvae, juvenile octopus) 2004 (crab megalops, pteropod, shrimp remains, shrimp larvae, juvenile octopus) 2005 (crab megalops, pteropod, shrimp remains, shrimp larvae, juvenile octopus, peleypoda, ectoprocta, mysid) 2006 (rotifers, cumacea, larval shrimp, ectoprocta, chaetognath, gastropod, fish larvae) 2008 (chaetognath, shrimp remains, pteropod, crab megalops, pelecypoda, larval polychete, ectoprocta).

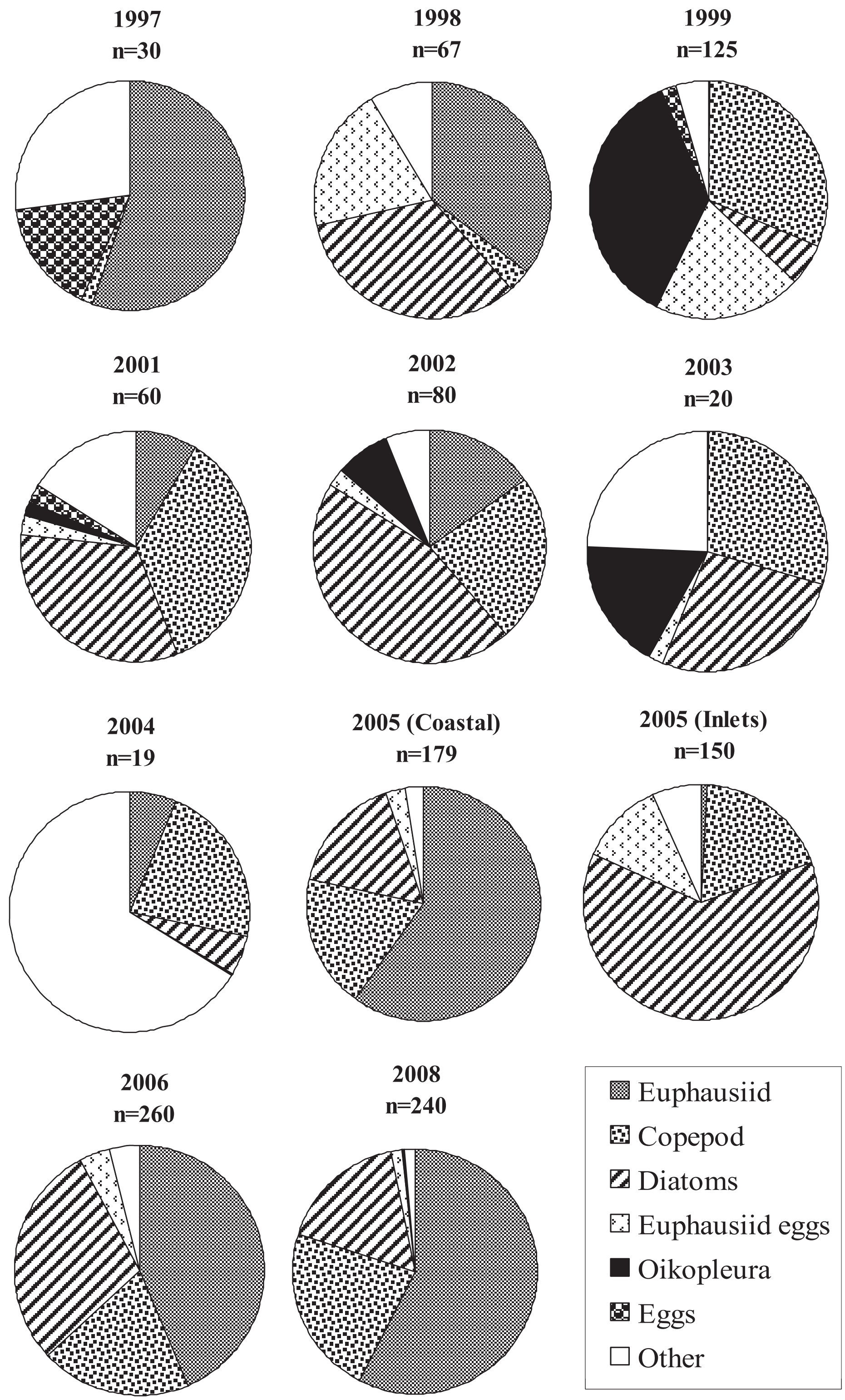

Figure 1. Major prey items of the Pacific sardine (*Sardinops sagax*) diet by percent volume (%V). Data from summer months (June–August) only. Other prey items may include: crab megalops, pteropod, juvenile shrimp, larval shrimp, shrimp zoea, juvenile octopus, juvenile crab, fish larvae, gastropod, algae filaments, ostracod, algae filaments, chaetognath, peleypoda, ectoprocta, mysid, rotifers, cumacea, chaetognath, shrimp, larval polychete.

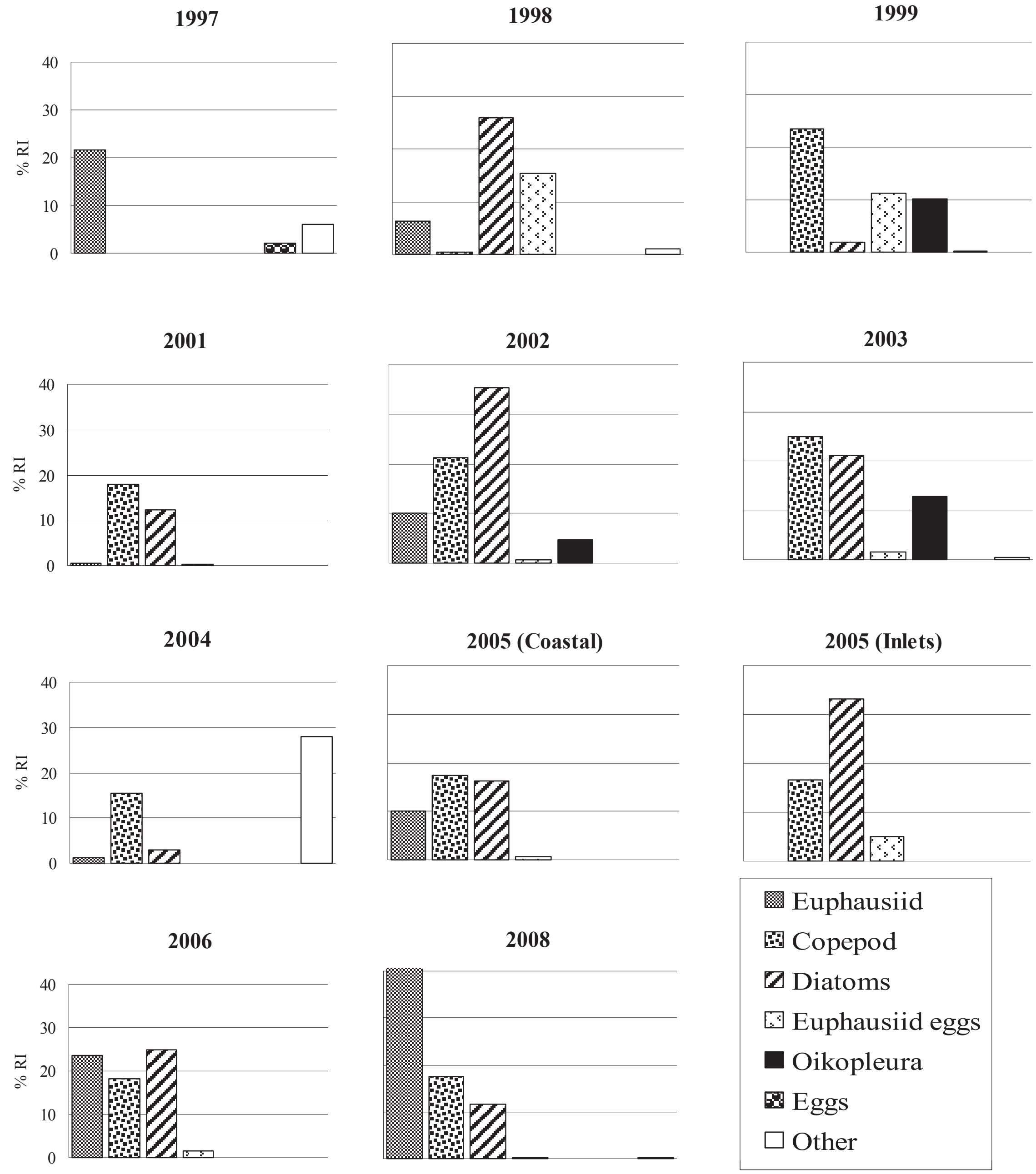

Figure 2. Major prey items of the Pacific sardine (*Sardinops sagax*) diet by total relative importance (%RI). Data from summer months (June–August) only. Other prey items may include: crab megalops, pteropod, juvenile shrimp, larval shrimp, shrimp zoea, juvenile octopus, juvenile crab, fish larvae, gastropod, algae filaments, ostracod, algae filaments, chaetognath, peleypoda, ectoprocta, mysid, rotifers, cumacea, chaetognath, shrimp, larval polychete.

enced mainly by %FO and %V (tab. 2, fig. 1), however it should be noted that night-time samples were included in the 2006 and 2008 data. Copepods were important components of diet in all years from 1999–2008 (but virtually absent in 1997 and 1998), with %RI ranging from 0.07 to 24.87 (tab. 2, fig. 2) again influenced mainly by %FO and %V. Diatoms were dominant in the diet in 1998, 2002, and 2006 (%RI of 25.97, 35.26, and 24.86 respectively), but were also important in 2001, 2003, 2005, and 2008 influenced by all measures (%FO, %V, %) (tab. 2, fig. 2). Interestingly, in 1999 and 2003, oikopleurids (larvaceans) were important components of the diet (%RI of 10.07 and 12.76, respectively) influenced by %V in 1999 and %FO in 2003. In the 2004 sample, the "Other" category dominated diet samples (%RI of 27.88), and was composed of 39.47% shrimp by volume.

Where identification to species within a prey cat-

TABLE 3
Taxonomic summary of prey items in the Pacific sardine (*Sardinops sagax*) by percent frequency of occurrence (%FO). Data from summer months (June–August) only.

Year	Group	Taxa	%FO
1998	Diatoms	*Coscinodiscus* sp.	45
	Copepods	*Calanus* sp.	4
		Pseudocalanus sp.	3
		Metridia sp.	1
		Epilabidocera longipedata	1
		Paracalanus parvus	1
	Euphausiids	*Euphausia pacifica*	22
		Thysanoessa spinifera	9
	Amphipods	*Parathemisto* sp.	12
1999	Diatoms	*Coscinodiscus* sp.	48
		Thalassiothrix sp.	3
		Rizosolenia sp.	2
		Dinoflagellates	1
	Copepods	*Acartia longiremis*	81
		Paracalanus parvus	31
		Pseudocalanus sp.	6
		Centropages abdominalis	6
		Metridia sp.	1
	Amphipods	*Parathemisto* sp.	2
		Calliopius sp.	1
	Cyclopoids	*Oithona* sp.	25
2001	Diatoms	*Coscinodiscus* sp.	72
	Copepods	*Acartia longiremis*	67
		Pseudocalanus sp.	17
		Centropages abdominalis	12
		Eucalanus bungii	8
		Paracalanus parvus	3
	Amphipods	*Parathemisto* sp.	7
	Cyclopoids	*Oithona* sp.	13
2002	Diatoms	*Thalassiosira* sp.	95
		Coscinodiscus sp.	75
		Skeletonema sp.	69
		Chaetocerus sp.	50
		Dinoflagellates	41
		Ditylum sp.	31
		Pseudo-nitzschia sp.	15
		Biddulphia sp.	5
		Thalassiothrix sp.	4
	Copepods	*Acartia longiremis*	84
		Paracalanus parvus	48
		Centropages abdominalis	28
		Pseudocalanus sp.	23
		Eucalanus bungii	3
		Metridia sp.	1
	Euphausiids	*Thysanoessa spinifera*	16
		Euphausia pacifica	3
	Cyclopoids	*Corycaeus anglicus*	9
		Oithona sp.	6
2003	Diatoms	*Dinoflagellates*	100
		Chaetocerus sp.	65
		Coscinodiscus sp.	55
		Thalassiosira sp.	45
		Skeletonema sp.	15
		Ditylum sp.	15
		Biddulphia sp.	5
	Copepods	*Paracalanus parvus*	60
		Pseudocalanus sp.	60
		Centropages abdominalis	40
		Acartia longiremis	35
	Cyclopoids	*Corycaeus anglicus*	5
	Crab zoea	*Porcellanidae*	80
		Brachyura	10
		Anomura	5
2004	Diatoms	*Dinoflagellates*	63
		Thalassiosira sp.	26
		Coscinodiscus sp.	21
		Skeletonema sp.	11
		Pseudo-nitzschia sp.	5
	Copepods	*Acartia longiremis*	74
		Centropages abdominalis	37
		Calanus sp.	21
		Eucalanus bungii	5
		Metridia sp.	5
	Amphipods	*Hyperiid*	5
		Themisto sp.	5
	Gastropods	*Limacina* sp.	5
	Crab zoea	*Anomura*	26
		Brachyura	11
		Cancridae	5
2005 (Coastal)	Diatoms	*Skeletonema* sp.	79
		Thalassiosira sp.	77
		Ditylum sp.	65
		Dinoflagellates	61
		Pleurosigma sp.	53
		Coscinodiscus sp.	25
		Chaetocerus sp.	11
		Pseudo-nitzschia sp.	7
		Thalassiothrix sp.	7
		Biddulphia sp.	1
	Copepods	*Acartia longiremis*	80
		Centropages abdominalis	39
		Paracalanus parvus	37
		Calanus sp.	21
		Metridia sp.	3
		Eucalanus bungii	2
		Pseudocalanus sp.	1
		Neocalanus cristatus	1
		Tortanus discaudatus	1
	Euphausiids	*Euphausia pacifica*	22
		Thysanoessa spinifera	21
	Amphipods	*Themisto* sp.	2
		Vibilia armata	2
	Cyclopoids	*Corycaeus anglicus*	1
	Gastropods	*Limacina* sp.	3
	Crab zoea	*Porcellanidae*	1
		Brachyura	1
		Cancridae	1
		Anomura	1
2005 (Inlets)	Diatoms	*Thalassiosira* sp.	74
		Skeletonema sp.	53
		Ditylum sp.	51
		Coscinodiscus sp.	41
		Pseudo-nitzschia sp.	33
		Thalassiothrix sp.	30
		Dinoflagellates	20
		Biddulphia sp.	17
	Copepods	*Acartia longiremis*	77
		Centropages abdominalis	22
		Pseudocalanus sp.	19
		Paracalanus parvus	10
		Calanus sp.	2
		Metridia sp.	1
		Eucalanus bungii	1
		Epilabidocera longipedata	1
	Amphipods	*Grammarid*	3
	Cyclopoids	*Corycaeus anglicus*	13
		Oithona sp.	5
	Crab zoea	*Brachyura*	1
2006	Diatoms	*Ditylum* sp.	94
		Thalassiosira sp.	90
		Skeletonema sp.	80
		Coscinodiscus sp.	68
		Thalassiothrix sp.	50
		Pseudo-nitzschia sp.	44

TABLE 3 (Continued)
Taxonomic summary of prey items in the Pacific sardine (*Sardinops sagax*) by percent frequency of occurrence (%FO). Data from summer months (June–August) only.

Year	Group	Taxa	%FO
		Dinoflagellates	43
		Chaetocerus sp.	27
		Pleurosigma sp.	17
		Biddulphia sp.	4
	Copepods	*Acartia longiremis*	89
		Paracalanus parvus	73
		Centropages abdominalis	47
		Calanus sp.	38
		Pseudocalanus sp.	37
		Metridia sp.	4
		Eucalanus bungii	3
		Tortanus discaudatus	2
	Euphausiids	*Thysanoessa spinifera*	28
		Euphausia pacifica	23
	Amphipods	*Hyperiid*	3
	Cyclopoids	*Oithona* sp.	50
		Corycaeus anglicus	4
		Oncaea borealis	1
2008	Diatoms	*Coscinodiscus* sp.	65
		Thalassiosira sp.	64
		Thalassiothrix sp.	50
		Chaetocerus sp.	46
		Dinoflagellates	48
		Skeletonema sp.	35
		Pseudo-nitzschia sp.	23
		Biddulphia sp.	6
		Ditylum sp.	2
	Copepods	*Calanus* sp.	54
		Acartia longiremis	50
		Pseudocalanus sp.	46
		Centropages abdominalis	18
		Paracalanus parvus	15
		Metridia sp.	13
		Eucalanus bungii	3
		Epilabidocera longipedata	2
		Neocalanus cristatus	1
	Euphausiids	*Euphausia pacifica*	37
		Thysanoessa spinifera	28
	Amphipods	*Hyperiid*	3
	Cyclopoids	*Oithona* sp.	8
		Corycaeus anglicus	1
	Gastropods	*Limacina helicina*	22

TABLE 4A
Morisita-Horn overlap indices using %RI of prey items of the Pacific sardine (*Sardinops sagax*) diet by year. Data from summer months (June–August) only. Values greater than 0.6 (bold) were considered to reflect significant overlap.

	1997	1998	1999	2001	2002	2003	2004	2005	2006
1998	0.20								
1999	0.00	0.26							
2001	0.02	0.47	**0.71**						
2002	0.19	**0.72**	0.47	**0.72**					
2003	0.02	0.50	**0.71**	**0.77**	**0.84**				
2004	0.26	0.12	0.4	0.42	0.31	0.4			
2005	0.37	**0.62**	**0.62**	**0.91**	**0.84**	**0.76**	0.39		
2006	0.51	**0.67**	0.43	**0.65**	**0.90**	**0.68**	0.30	**0.88**	
2008	**0.68**	0.37	0.30	0.37	**0.61**	0.39	0.23	**0.65**	**0.87**

TABLE 4B
Morisita-Horn overlap indices using %V of prey items of the Pacific sardine (*Sardinops sagax*) diet by year. Data from summer months (June–August) only. Values greater than 0.6 (bold) were considered to reflect significant overlap.

	1997	1998	1999	2001	2002	2003	2004	2005	2006
1998	**0.63**								
1999	0.04	0.25							
2001	0.20	0.59	0.55						
2002	0.26	**0.76**	0.46	**0.91**					
2003	0.06	0.42	**0.71**	**0.90**	**0.81**				
2004	0.43	0.26	0.24	0.37	0.26	0.36			
2005	**0.84**	**0.80**	0.21	0.51	0.59	0.32	0.25		
2006	**0.70**	**0.89**	0.29	**0.72**	**0.81**	0.53	0.26	**0.94**	
2008	**0.82**	**0.78**	0.25	0.56	**0.62**	0.36	0.26	**1.00**	**0.95**

egory was possible, euphausiids were composed of *Euphausia pacifica* and *Thysanoessa spinifera*; copepods were dominated by *Acartia longeremis*, *Centropages abdominalis*, *Paracalanus parvus, Calanus* sp. and *Pseudocalanus* sp. (tab. 3) and phytoplankton (ie. diatoms and dinoflagellates) were dominated by *Coscinodiscus* sp., *Thalassiosira* sp., *Chaetocerus* sp., *Ditylum* sp., *Skeletonema* sp., and dinoflagellates (tab. 3).

The amount of diet overlap based on %RI and %V, between years was substantial for most years examined (tab. 4a and 4b), with the exception of 1997 and 2004 when using %RI. Both these years were dominated by only one prey item (1997 euphausiids; 2004 "Other"). Based on a %V 1997 overlapped to a very high degree with 2005 to 2008, but showed less overlap with other years (ie. 1999, 2001, and 2003).

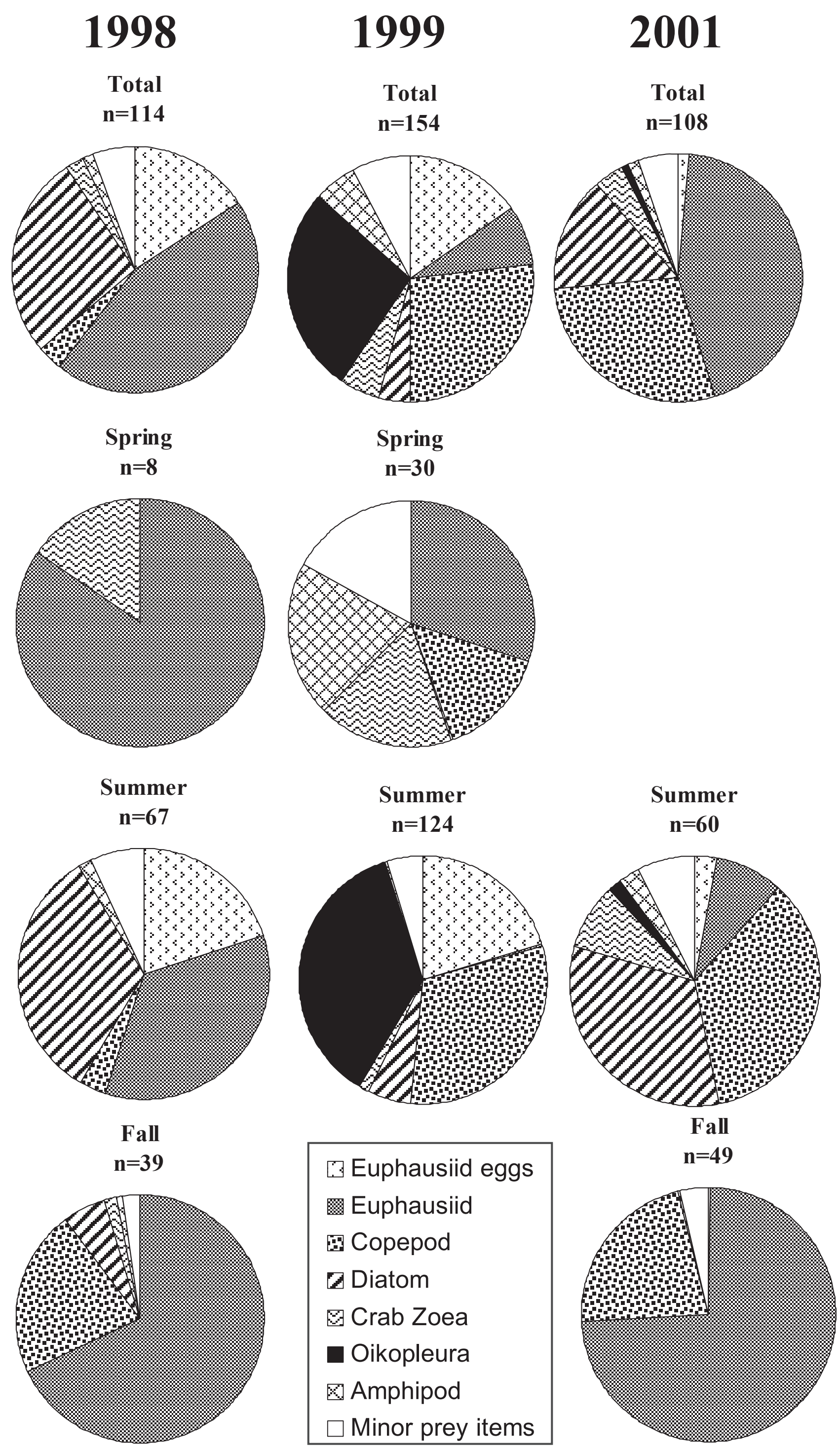

Figure 3. Seasonal summary of major prey items of the Pacific sardine (*Sardinops sagax*) diet by %V. Minor prey items include: cyclopoid, algae filaments, gastropods, barnacle cyprids and nauplii, fish eggs, crab megalops, shrimp zoea, unknown eggs, chaetognath, ostracod, cladoceran.

Seasonal Comparison

In 1998, samples were collected throughout the spring (May), summer (June, August) and fall (September, October). Euphausiids and crab zoea dominated (%V) in the spring, euphausiids, euphausiid eggs, and diatoms in the summer, and euphausiids and copepods in the fall (fig. 3).

For the three years (1998, 1999 and 2001), for which some seasonal diet information was available, prey items varied considerably between seasons and

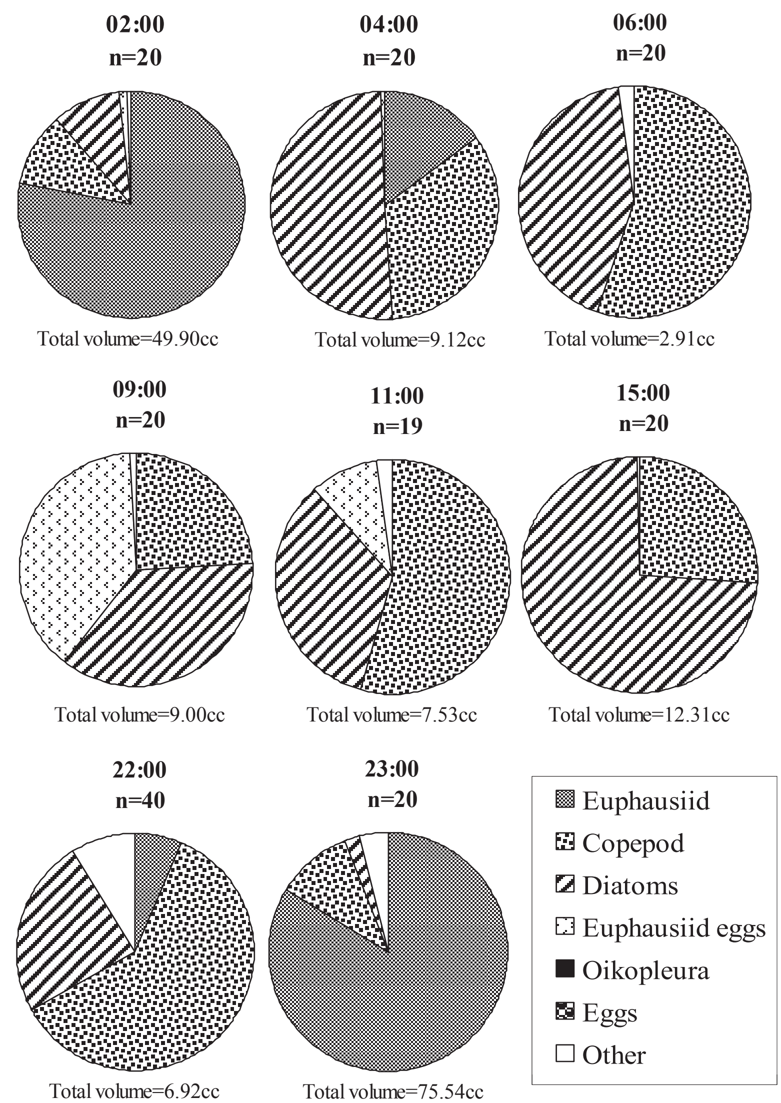

Figure 4. Hourly summary of major prey items of the Pacific sardine (*Sardinops sagax*) diet by %V during one period in 2005. Other prey items may include: crab megalops, pteropod, shrimp remains, shrimp larvae, juvenile octopus, peleypoda, ectoprocta, mysid. Average total volume (cc) of food eaten is shown in parenthesis. Average sunrise and sunset times during this period were 06:05 PDT and 20:51 PDT respectively.

years (fig. 3). In 1998, euphausiids (44.63%) were dominant in sardine diets in all seasons. As well, crab zoea (15.63%) were important in the spring; and diatoms (33.18%) and euphausiid eggs (19.88%) in summer. Copepods (21.54%) were present in late fall (fig. 3). Similarly, in 2001, euphausiids were an important prey item in summer (8.70%) and fall (73.97%), with diatoms again being important contributing 32.44% in summer. However, copepods also accounted for (35.45%) of the summer diet. During 1999, euphausiids (29.99%), crab zoea (17.68%), copepods (14.53%) and also amphipods were important in spring. Of note, however, oikopleurids (larvaceans) were a major food item in summer contributing 36.36%, followed by copepods (31.08%) and euphausiid eggs (20.25%) (fig. 3).

Day/Night Comparison

During August 2005, 179 stomachs were collected over two 24 hour periods conducted over three days. As contents were similar from sets at similar times the data was combined (fig. 4). Diatoms and copepods dominated (%V) in samples collected from just prior to sunrise (0400 hrs) until just after sunset (2200 hrs). Samples taken from 2200 hrs to 0400 hrs were dominated by euphausiids. Average volume of prey items (stomach fullness) ranged from 0.5 cc to 1.0 cc from 0400 hrs to 2200 hrs but increased dramatically to 2.9 cc to 4.3 cc from 2200 hrs to 0400 hrs (fig. 5).

Inlet/Coastal Comparison

Sardines collected in 2005 aboard commercial vessels in WCVI inlets fed primarily (%V) on diatoms (62.22%)

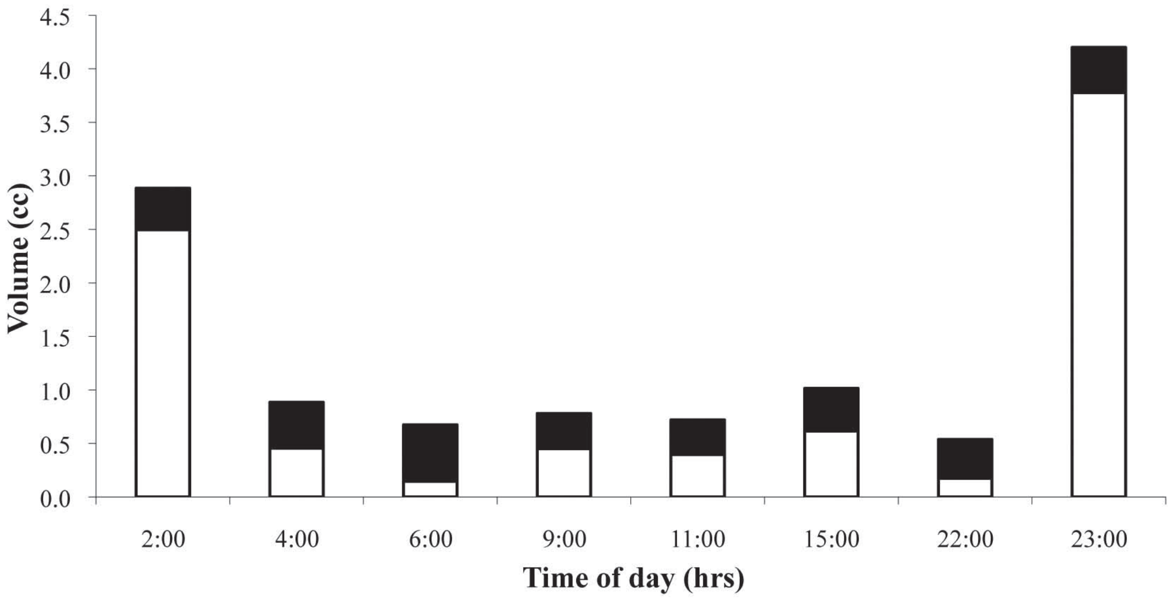

Figure 5. Hourly summary of average total stomach volume (open bar) and average volume of digested matter (dark bar) of the Pacific sardine (*Sardinops sagax*). Sample size of 20 stomachs for all hours with the exception of 11:00 and 22:00 where the sample sizes are 19 and 40 respectively. Average sunrise and sunset times during this period were 06:05 PDT and 20:51 PDT respectively.

composed mainly of *Thalassiosira* sp., *Skeletonema* sp. and *Ditylum* sp.; copepods (18.51%), mainly *A. longiremis* and *C. abdominalis*; and euphausiid eggs (11.55%). Sardines collected from coastal research sets at the same time fed mainly on euphausiids (59.97%), both *E. pacifica* and *T. spinifera*, and diatoms (16.61%) mainly *Skeletonema* sp., *Thalassiosira* sp., *Ditylum* sp., dinoflagellates, and *Pleurosigma* sp.; and copepods (18.26%) mainly *A. longiremis* (fig. 1). Although euphausiids dominated the diet of coastal samples by volume (fig. 1), %RI values show that they were slightly less important than copepods and diatoms (tab. 2, fig. 2).

DISCUSSION

In general, our study of sardine diets indicates sardines prey primarily on phytoplankton (diatoms), copepods and euphausiids (including euphausiid eggs), accounting for > 80% (by volume) of diet in most years. This confirms earlier preliminary work in this area (Hart and Wailes 1931; McFarlane et al. 2005), and is similar to previous studies in other areas of the northeast Pacific (Emmett et al. 2005) and Alaska (Wing et al. 2000). The relative contribution of primary prey items varied considerably seasonally and annually. For example, euphausiid were the most important prey item in 1997, 2005, 2006 and 2008 but were virtually absent in 1999, 2001, 2003 and 2004. In contrast, phytoplankton (mainly diatoms) were virtually absent in 1997, 1999 and 2004 but were the dominant prey item in 1998 and 2002 and important in sardine diet in all other years. Copepods were important in all years after 1999 but were rarely consumed in 1997 and 1998. Similarly, seasonal diet composition reflects the same changes in the relative contribution of dominant prey items. These seasonal and annual variations most likely reflect changes in availability and/or abundance of major prey groups illustrating the opportunistic feeding behaviour of sardines. Changes in the distribution and abundance of prey items have been linked to changes in ocean conditions (Peterson and Schwing 2003; King 2005; Mackas et al. 2009) indicating that sardine may be a key species for monitoring ocean productivity changes on annual and decadal scales.

Dominant prey groups found in sardine diet each year match groups identified by Mackas and Tsuda (1999) as major contributors to the zooplankton biomass throughout the oceanic subarctic Pacific, both locally and at a basin scale. Mackas et al. (2009) found most zooplankton taxa underwent large year–to-year variations in abundance during the study period off the WCVI. For example, the euphausiids *E. pacifica* and *T. spinifera* were low in abundance before 1987, increased in abundance in the late 1980s through the early 1990s, then levelled off or declined by the late 1990s (Mackas et al. 2009). In particular, *E. pacifica* was high in abundance in 1997 and 1998 and well below average or average from 1999 to 2003, followed by above average to average since. Our diet data indicate that *E. pacifica* and *T. spinifera* were important prey items in 1998 but declined in importance thereafter until 2004 when they dominated sardine diets once again.

Species assemblage shifts of copepods observed during our study period (Mackas et al. 2009) was only loosely correlated with prominent species present in sardine diets. This could be a reflection of the dominance of *A. longiremis*, *C. abdominalis* and *Pseudocalanus* sp. in the diet in all years since 1999, or a function of sample timing (seasonally and temporally).

We found no major shifts in the dominant phytoplankton species present in sardine diets over the study period with *Coscinodiscus* sp., *Thalassiosira* sp., *Skeletonema* sp. and *Ditylum* sp. dominating in all years. The lack of species identified in 1998 and 1999 is a refection of identification standards in the early years of our study and not an absence of phytoplankton in the diet.

We believe the overall seasonal and annual variation in major prey groups (but not major shifts in prey species within groups), coupled with the number of other prey groups which include unusual major contribution to sardine diet in some years (Oikopleurids in 1999 and 2003; shrimps in 2004) confirm the opportunistic feeding behaviour of sardines off Vancouver Island.

Given their opportunistic plankton feeding, it is not surprising that the diet comparison between years showed high or very high overlap for many years and low overlap for others. This is a reflection of the opportunistic nature of sardine predation and the variability in abundance (availability) of the major prey groups annually.

Analysis of stomach contents and fullness over two 24 hour periods in 2005 indicated sardines feed throughout the 24 hour period but had a peak in feeding activity after dusk (2200–0400 hrs). During this time, they preyed primarily on euphausiids. At all other times, they fed primarily on copepods and diatoms. This probably reflects movement of euphausiids upwards in the water column after dusk into the feeding regions of sardine.

Our study also indicated sardines showed inshore (inlets)/offshore differences in feeding, with phytoplankton (diatoms) and copepods dominating the inshore samples and offshore (coastal) sardines feeding more heavily on euphausiids, similar to feeding behavior reported by Emmett et al. (2005). This is a reflection of the abundance (availability) of these prey species in these areas, again indicating the opportunistic feeding behaviour of sardines.

The return or increase of large numbers of Pacific sardine (*Sardinops sagax*) to waters off California, Oregon, Washington and British Columbia, after an absence of almost 60 years, stimulated great interest in understanding the factors which influence both the numeric and geographic elements of sardine populations. Recent studies have shown that large-scale climate changes (regime shifts) can be associated with fluctuations in sardine abundance and distribution (McFarlane et al. 2002). Decadal scale changes in abundance and distribution of sardine populations in the North Pacific may be responding to these ecosystem changes in a fundamental, but as yet little understood, way. It is beyond the scope of this paper to specifically examine linkages between changes in ocean conditions and sardine dynamics. However, considering and answering the questions of natural variability in sardine stocks is key to understanding the underlying mechanisms of ecosystem change in the North Pacific.

One approach to examining the role of sardines in the CCS is to examine the feeding behaviour of sardine and their predators over the entire CCS and develop ecotrophic models which will allow us to test hypotheses regarding the expansion and contraction of this population. As mentioned, changes in distribution and abundance of plankton species have been linked to changes in oceanographic conditions (King 2005). Monitoring sardine diet may provide immediate feedback on changing ocean conditions, since sardines opportunistically prey on organisms directly impacted by these changes. We believe current studies along the west coast of North America from Canada to Mexico should be expanded to include detailed annual diet analysis with the goal of developing improved ecosystem assessments and management strategies.

ACKNOWLEDGMENTS

We greatly appreciate the expertise of Carol Cooper, who processed and identified all stomach contents, and the crews of the *W.E. Ricker* and F/V *Frosti* who ensured our research cruises ran smoothly. This study was supported, in part by the Canadian Pacific Sardine Association.

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