Food habits of the sandpaper skate, *Bathyraja kincaidii* (Garman, 1908) off central California: seasonal variation in diet linked to oceanographic conditions

Christopher S. Rinewalt · David A. Ebert · Gregor M. Cailliet

Abstract The stomachs of 130 sandpaper skates, *Bathyraja kincaidii* (Garman, 1908), were sampled from off central California to determine their diet composition. The overall diet was dominated by euphausiids, but shrimps, polychaetes and squids were also important secondary prey. A three-factor MANOVA demonstrated significant differences in the diet by sex, maturity status and oceanographic season using numeric and gravimetric measures of importance for the major prey categories. These three main factors explained more variation in diet than interactions between the factors, and season explained the most variance overall. A detailed analysis of the seasonal variation among the prey categories indicated that abundance changes in the most important prey, euphausiids, were coupled with seasonal changes in the importance of other prey. When upwelling occurred and productivity was great (Upwelling and Oceanic seasons), euphausiids were likely highly abundant in the study area and were the most important prey for *B. kincaidii*. As productivity declined (Davidson Current season), euphausiids appeared to decrease in abundance and *B. kincaidii* switched to secondary prey. At that time, gammarid amphipods and shrimps became the most important prey items and polychaetes, mysids and euphausiids were secondary.

Keywords Arhynchobatidae · MANOVA · Euphausiids · Gammarid amphipods

Introduction

The trophic ecology of a species, determined through diet analysis, gives an insight to its place in the food web, as well as that of its prey. This kind of study can also help to understand how a predator could influence its prey populations, and vice versa. Without this knowledge, problems could arise from changes to the food web when the abundance of one or more species is altered, such as those caused by overfishing.

Skates (Rajiformes) are common demersal fishes and the most speciose elasmobranch order, occurring in nearshore temperate environments and deep-water tropical and boreal regions (Compagno 1990). Skates are often taken as bycatch in important fisheries that target various gadoids, monkfish and shrimps, as well as in research trawls (Walmsley-Hart et al. 1999; Alonso et al. 2001; Brickle et al. 2003; Cedrola et al. 2005; Perez and Wahrlich 2005). Skates may also compete with commercial species by sharing

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the same food resources (Berestovskiy 1990; Pedersen 1995; Orlov 1998a; Dolgov 2005). Smale and Cowley (1992) concluded that because of their wide breadth of diet and their biomass, skates are likely to have a significant influence on the benthos. These varied trophic interactions suggest that thorough dietary studies are needed (Stevens et al. 2000).

The unique biological attributes of elasmobranchs (see current volume), coupled with a lack of species-specific fishery data and unregulated bycatch could lead to overfishing in certain skate species (Holden 1977; Jennings et al. 1998; Dulvy et al. 2000; Musick et al. 2000; Zorzi et al. 2001). The commercial catch of skates has increased dramatically along the Pacific coast of the United States during the past decade (Camhi 1999). Though skates have been fished commercially off California since 1916, only recently have the fishery landings grown by an order of magnitude (Zorzi et al. 2001). From 1995 to 2003, annual skate landings, undifferentiated by species, in California ranged from 2 to 10 times the landings for each of the years from 1981 to 1994, and were often greater than the combined landings of all other elasmobranch species (PacFin Database 2006). This increase in landings indicates that skates have become an important component of commercial fisheries in the eastern North Pacific (ENP), yet these are some of the least studied elasmobranchs.

The sandpaper skate, *Bathyraja kincaidii* (Garman, 1908), is a deep-water elasmobranch endemic to the ENP. This species occurs between 55 m and 1,372 m (most commonly between 200 m and 500 m) from the Gulf of Alaska to northern Baja California (Miller and Lea 1972; Ebert 2003). *Bathyraja kincaidii* is the smallest skate along the ENP, growing to 635 mm total length (TL) with a longevity of at least 18 years (Perez 2005). Little research has been conducted on its life history, yet it is frequently caught in trawls off central California. Wakefield (1984) examined stomach contents from two individuals off the coast of northern Oregon and found seven prey taxa, including shrimp in the genus *Crangon*, *Citharichthys sordidus*, a pinnotherid crab and the mysid *Acanthomysis nephrophthalma*. Ebert (2003) reported anecdotal information on the

diet of *B. kincaidii*, listing polychaetes, amphipods, crabs and shrimp. This study serves to increase the knowledge of an important aspect of the life history of *B. kincaidii* by identifying the prey items of this species and describing its place in the ENP food web. The diet of *B. kincaidii* is described and statistically tested for differences between sexes, maturities and among oceanographic seasons from central California.

Materials and methods

Bathyraja kincaidii were collected by approximately monthly trawl surveys along the central California coast from March 2002 to February 2005 by the National Marine Fisheries Service Santa Cruz Lab (Fig. 1). Specimens were collected from 24 hauls among four varying depth strata per cruise with average depths of 395 m (1), 285 m (2), 226 m (3) and 146 m (4). Skates were frozen onboard and later processed at which time the stomachs were removed. Stomach contents were sorted with a dissecting microscope and prey taxa were identified, counted and weighed to the nearest 0.001 g. Any prey item that did not register at least this was given a mass of 0.0005 g for use in calculations. Any material that was not identifiable to any taxonomic level was excluded. Prey taxa were grouped into nine higher taxonomic categories: polychaetes, cephalopods, small benthic crustaceans, shrimp-like crustaceans, crabs, unidentifiable crustaceans, teleosts, molluscs and echinoderms.

The importance of prey was described by their component indices: number, mass and frequency of occurrence. $\overline{\% N}$ is the mean percentage number of a given prey category (j) for the total number of all prey items, $\overline{\% M}$ is the mean percentage mass of a given prey category for the total mass of all prey items and %FO is the percentage frequency of occurrence of a given prey category from all stomachs. To estimate precision for %N and %M, each stomach was considered its own sample; the values reported here are the mean values on a stomach-by-stomach basis (Tirasin and Jørgensen 1999). Along with the component indices of importance,
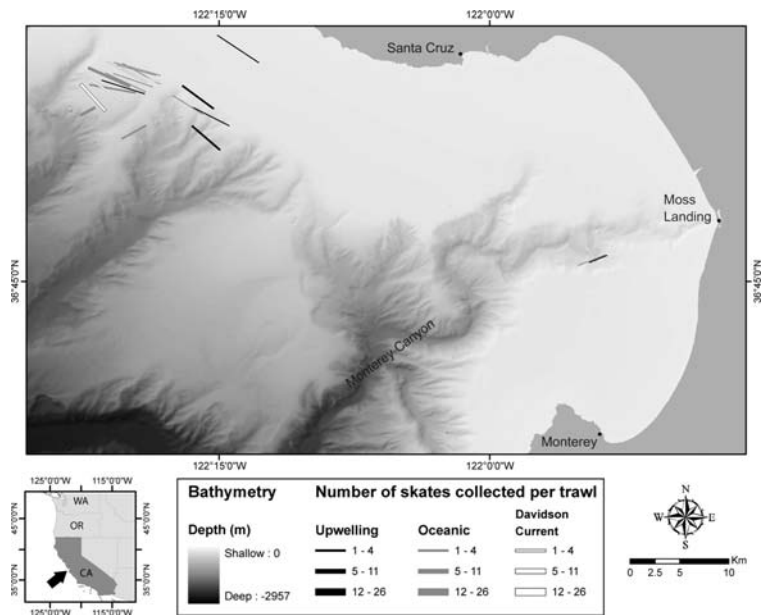
a mean Index of Relative Importance ($\overline{IRI}$) was used to describe the diet of this skate (Pinkas et al. 1971; Hyslop 1980). This index was modified to incorporate percentage mass instead of percentage volume:

$$\overline{IRI}_j = (\overline{\% \, N_j} + \overline{\% \, M_j}) * \% \, FO_j$$

Mean percentage IRI, $\overline{\% \, IRI}$, was further calculated to provide the easiest measure to visualize the importance of any given prey:

$$\overline{\% \, IRI}_j = \left(\overline{IRI}_j / \sum \overline{IRI}\right) * 100$$

A randomized prey curve was generated using 100 resamplings (Ferry and Cailliet 1996), which plots the cumulative number of stomachs analyzed against the cumulative number of prey taxa encountered. A leveling of the curve and a reduction in variance indicates that enough stomachs have been examined to describe the taxonomic richness of the diet. An examination of lower taxa was conducted for prey that composed >5% of $\overline{\% \, N}$, $\overline{\% \, M}$ or $\overline{\% \, IRI}$.

The monthly samples were divided into three defined oceanographic seasons that characterize the study area, as described by Skogsberg (1936), Skogsberg and Phelps (1946) and Bolin and Abbott (1963). The Upwelling Season (UPS) (March–July) is characterized by the upwelling of cold, nutrient-rich water which can move far offshore due to strong southbound winds. This is followed by the Oceanic Season (OCS) (August–November), when the winds and upwelling weaken. During this weakening, oceanic water from the California Current moves close to shore. The Davidson Current Season (DCS) (December–February) is characterized by the continued weakening of the California Current, the development of an inshore northward current, a negligible thermocline and warm upper waters.

A three factor MANOVA was used to test the null hypothesis that there were no differences in the diet between sexes, maturity stages (mature versus immature) and among the three oceanographic seasons (Somerton 1991; Paukert and Wittig 2002). Compound indices should not be used because they can conceal the information of individual measurements, so both number and mass of the major prey categories were used separately in the analysis (Tirasin and Jørgensen 1999). The proportion of each category (not be confused with the percentage used in diet description) was arcsine transformed (Zar 1999, Eq. 13.8) to more closely meet the assumptions of homoscedasticity and normality. These assumptions

were tested with Levene's Test (variance across groups for a single variable), Box's M test (covariance matrix across groups for all variables) and by examination of residual plots for each variable. Pillai's Trace was chosen as the reported test statistic as it is the most robust to violations of parametric assumptions (Olson 1974).

Six of the higher taxonomic categories (polychaetes, shrimp-like crustaceans, small benthic crustaceans, crabs, cephalopods and teleosts), accounting for the 12 variables (number and mass) were used in the statistical tests. Unidentifiable crustaceans and other taxa considered incidentally ingested (molluscs and echinoderms) were excluded as they contributed little to the diet. Additional randomized cumulative prey curves were created for each level of the three factors (e.g. immature females in the OCS, etc.) using these higher taxonomic categories.

A multivariate factor fit model using the three fixed factors (sex, maturity status and oceanographic season) was approximated from the univariate two factor fixed model provided by Graham and Edwards (2001). By describing how much of the observed variance is explained by these factors, the fit of these factors can often give more information about the model than their significance in the test itself. Because the data set was multivariate, the variance component for a single factor was calculated using the mean square and mean square error for each response variable as in the univariate model. These components were then averaged, with negative variances set to 0. The number of replicates per cell was not equal for this analysis, so the mean number of samples per cell was used for analysis. That averaged variance component for the factor was then used to calculate the magnitude of effects (ω^2), the percentage of the variance explained by that factor, which is analogous to the r^2 of regressions (Graham and Edwards 2001).

Results

In total, 138 *B. kincaidii* stomachs were collected, of which 8 (5.8%) were empty. The number of skates collected per trawl ranged from 1 to 26 individuals (mean 5.4 ± 6.5 SD) and ranged in

size from 327 mm to 585 mm TL (mean 482 ± 53 SD mm TL). Examined by season, 21 skates with stomach contents were collected during the UPS, 78 from the OCS and 31 in the DCS. However, the majority of samples came from 3 months, January (22%), October (17%) and November (41%). The depth distribution of the specimens was also clumped, with most collected from the two deepest hauls at average depths of 395 m (46%) and 285 m (31%). The randomized cumulative prey curve revealed that enough stomachs had been collected to describe species richness accurately, averaging only three unique new prey taxa from the final 50 stomachs (Fig. 2).

Bathyraja kincaidii were found to prey on a wide variety of invertebrates and teleosts. The mean number, mass and IRI (68.4, 40.4, and 69.5%, respectively) revealed that the diet of *B. kincaidii* was dominated by shrimp-like crustaceans (euphausiids, mysids and shrimps), which were found in >98% of the stomachs examined (Fig. 3 and Table 1). Polychaetes were the second most important prey and were more important by mass than number and $\overline{IRI}$, with a large frequency of occurrence (11.6 $\overline{\% N}$, 21 $\overline{\% M}$, 65.4 %FO and 13.8 $\overline{\% IRI}$). Like polychaetes, cephalopods (5.3 $\overline{\% N}$, 19 $\overline{\% M}$ and 8.4 $\overline{\% IRI}$) and teleosts (4.6 $\overline{\% N}$, 12.3 $\overline{\% M}$ and 5.4 $\overline{\% IRI}$) were both most important by mass and were consumed by approximately half of the skates examined. Small benthic crustaceans (8.3 $\overline{\% N}$, 5.8 $\overline{\% M}$, 28.8 %FO and 2.7 $\overline{\% IRI}$) were not very important overall, but were more important by number than both cephalopods and teleosts. The remaining four major categories, crabs, unidentifiable crustaceans, molluscs and echinoderms, composed 0.2, 0.03, 0.01 and <0.01 $\overline{\% IRI}$, respectively, of the diet.

A qualitative examination of the importance of lower taxa revealed each categories major prey (Table 1). In terms of shrimp-like crustaceans, unidentifiable euphausiids (34.7 $\overline{\% N}$, 13.8 $\overline{\% M}$ and 50.1 $\overline{\% IRI}$) was by far the most important taxon, *Thysanoessa spinifera* (5.5 $\overline{\% N}$ and 5.7 $\overline{\% IRI}$) was the major identifiable species, and unidentifiable shrimps (5.2 $\overline{\% N}$) were of secondary importance. Onuphid (6 $\overline{\% M}$ and 5.8 $\overline{\% IRI}$) and nephtyid (8.4 $\overline{\% M}$) worms were the most important polychaete prey. Although a

Fig. 2 Cumulative prey curve for all prey items collected from *Bathyraja kincaidii* stomach samples. Error bars represent the standard deviation of the plotted mean generated from 100 resamplings
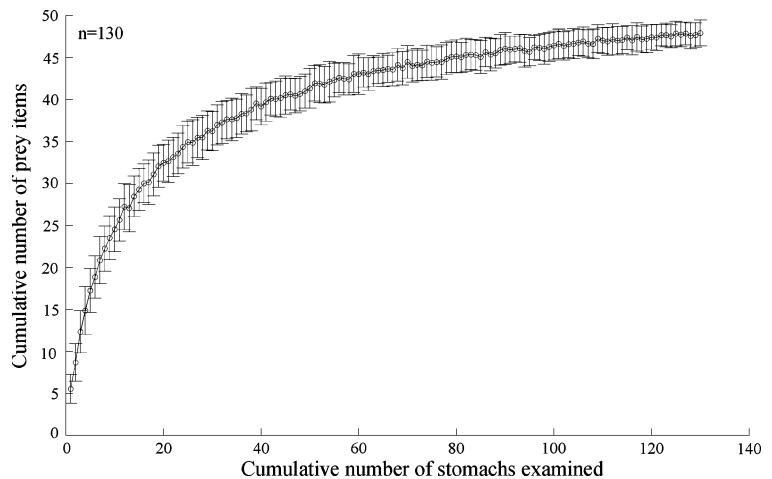
variety of cephalopod species were consumed, most of the remains were unidentifiable squids (7.5 $\overline{\% M}$ and 5.2 $\overline{\% IRI}$). Although not considered important, *Loligo opalescens* and *Octopus rubescens* comprised the largest percentage by mass of the identifiable cephalopods. Gammarid amphipods were also important (7.4 $\overline{\% N}$ and 6.5 $\overline{\% IRI}$) and ranked second by $\overline{\% IRI}$ and third by $\overline{\% N}$ in overall lower taxa importance. No species of teleost, crab, mollusc or echinoderm composed more than 5% of the diet by any of the three measures.

Analyses of the factorized random cumulative prey curves (Fig. 4) highlighted the low sample sizes of immature males and females in the UPS, so data from this season were excluded from the quantitative analysis, but were qualitatively com-

pared to the other seasons. The randomized curves indicated enough stomachs were sampled to describe the richness of the eight other predator groupings (Fig. 4).

The assumptions for parametric tests were found to have been violated in this data set. Tests of the assumptions revealed that neither data series was homoscedastic. Levene's test was significant for polychaetes ($p = 0.004$) and Box's M was also significant ($p < 0.01$) for the mass data. Testing of the numeric data revealed only teleosts were not significant by Levene's test ($p = 0.189$) and Box's M was again significant ($p < 0.01$). An examination of the residuals indicated that both data sets were distributed normally.

The proportional mass data indicated significant differences in the diet by sex ($p = 0.028$,

Fig. 3 Graphical representation of the component indices of importance for major prey categories in the diet of *Bathyraja kincaidii*. Numbers in parentheses indicate $\overline{\% IRI}$ and error bars represent the standard error for their respective measurement. Crabs, unidentified crustaceans, molluscs and echinoderms are not included because of their low importance
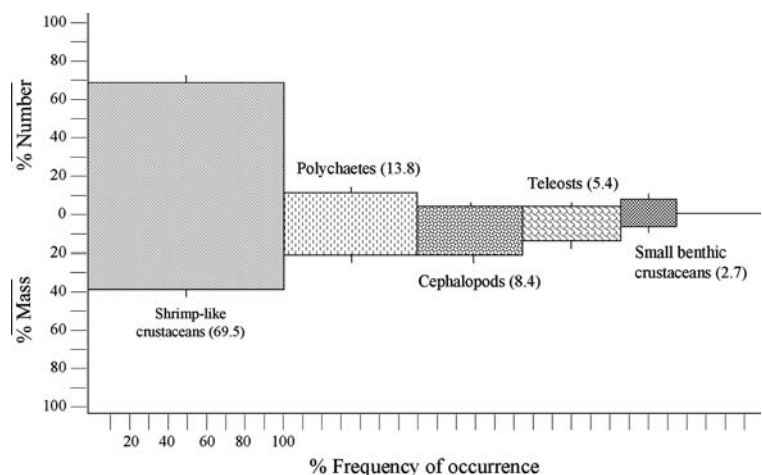
Table 1 The importance of prey items consumed by *Bathyraja kincaidii* at the major category (bold) and lowest identifiable taxa scales

Taxa	% N	% M	%FO	$\overline{IRI}$	% IRI
Polychaetes	**11.61**	**20.99**	**65.38**	**2,131.57**	**13.83**
Onuphidae	4.65	5.98	26.92	286.28	5.83
Nephtys sp.	1.16	8.35	16.92	160.96	3.28
Polychaete A	1.22	0.86	10.77	22.48	0.46
Opheliidae	3.57	3.36	12.31	85.33	1.74
Polychaetes (unid)	1.01	2.43	20.00	68.71	1.40
Cephalopods	**5.34**	**18.97**	**53.08**	**1,290.18**	**8.37**
Octopus rubescens	0.98	3.94	16.15	79.47	1.62
Octopoda (unid)	0.02	0.04	0.77	0.05	0.00
Abraliopsis felis	0.42	0.77	3.85	4.58	0.09
Gonatus sp.	0.15	0.61	1.54	1.16	0.02
Loligo opalescens	0.65	4.66	6.92	36.70	0.75
Squids (unid)	1.93	7.50	26.92	253.93	5.17
Cephalopods (unid)	1.19	1.46	5.38	14.26	0.29
Small benthic crustaceans	**8.27**	**5.79**	**29.23**	**411.08**	**2.67**
Gammarid amphipods	7.39	4.20	27.69	320.99	6.54
Paraphronima sp.	0.19	0.06	0.77	0.19	0.00
Rocinela angustata	0.34	0.73	3.85	4.13	0.08
Isopods (unid)	0.35	0.80	1.54	1.76	0.04
Shrimp-like crustaceans	**68.44**	**40.41**	**98.46**	**10,717.33**	**69.52**
Euphausia pacifica	0.86	0.65	6.92	10.44	0.21
Thysanoessa raschi	0.04	0.01	0.77	0.04	0.00
Thysanoessa spinifera	5.49	4.02	29.23	278.14	5.67
Euphausiidae (unid)	34.65	13.76	50.77	2,458.01	50.09
Boreomysis californica	0.25	0.18	0.77	0.33	0.01
Holmsiella anomala	0.56	0.29	3.85	3.28	0.07
Mysidae (unid)	1.37	1.50	6.15	17.64	0.36
Euphausiid/mysid mix	2.22	1.40	4.62	16.71	0.34
Euphausiid/mysid/shrimp mix	1.17	0.84	2.31	4.64	0.09
Euphausiid/shrimp mix	9.54	5.39	17.69	264.11	5.38
Shrimp/Mysid mix	0.65	1.07	3.08	5.32	0.11
Neocrangon communis	0.39	0.90	3.85	4.96	0.10
Crangonidae (unid)	0.72	0.60	6.15	8.12	0.17
Heptacarpus sp.	0.38	0.40	0.77	0.60	0.01
Spirontocaris holmesi	0.21	0.33	3.08	1.65	0.03
Spirontocaris sica	1.18	1.42	3.85	9.99	0.20
Spirontocaris sp.	0.75	0.70	2.31	3.35	0.07
Hippolytidae (unid)	0.12	0.06	0.77	0.14	0.00
Pasiphaea pacifica	0.77	0.60	6.92	9.44	0.19
Sergestes similis	1.87	2.45	8.46	36.56	0.75
Shrimps (unid)	5.24	3.84	20.00	181.52	3.70
Crabs	**0.92**	**1.13**	**12.31**	**25.27**	**0.16**
Majoidea (unid)	0.18	0.24	1.54	0.65	0.01
Brachyuran (unid)	0.03	0.04	0.77	0.05	0.00
Crabs (unid)	0.47	0.56	9.23	9.50	0.19
Pagurus tanneri	0.23	0.23	0.77	0.35	0.01
Paguridae (unid)	0.02	0.05	0.77	0.06	0.00
Unidentifiable crustaceans	**0.57**	**0.09**	**6.15**	**4.08**	**0.03**
Unidentifiable crustaceans	0.57	0.09	6.15	4.08	0.08
Teleosts	**4.64**	**12.34**	**49.23**	**835.76**	**5.42**
Diaphus theta	0.31	0.26	2.31	1.32	0.03
Diaphus sp.	0.27	1.30	2.31	3.62	0.07
Stenobrachius leucopsarus	1.33	4.34	8.46	47.95	0.98
Myctophidae (unid)	0.19	0.54	4.62	3.36	0.07

Table 1 continued

Taxa	% N	% M	%FO	$\overline{IRI}$	% IRI
Pleuronectidae (unid)	0.05	0.30	1.54	0.54	0.01
Sebastes sp.	0.50	1.55	8.46	17.33	0.35
Teleosts (unid)	1.99	4.05	26.92	162.68	3.31
Molluscs	**0.19**	**0.21**	**4.51**	**1.84**	**0.01**
Bivalve (unid)	0.01	0.00	0.75	0.01	0.00
Amphissa bicolor	0.07	0.20	1.50	0.40	0.01
Astyris gausapata	0.04	0.00	0.75	0.03	0.00
Gastropods (unid)	0.07	0.01	1.50	0.13	0.00
Echinoderms	**0.03**	**0.01**	**0.75**	**0.03**	**0.00**
Strongylocentrotus sp.	0.03	0.01	0.75	0.03	0.00

df = 6, 96), maturity ($p < 0.01$, df = 6, 96) and season ($p < 0.01$, df = 6, 96) with a significant interaction of maturity–season ($p = 0.014$, df = 6, 96). Pairwise comparisons revealed that males consumed a significantly larger proportion of shrimp-like crustaceans, small benthic crustaceans and crabs than females. Immature skates were found to have consumed more small benthic crustaceans and crabs than mature individuals. Greater proportions of small benthic crustaceans and crabs were consumed during the DCS than in the OCS. Though there was a significant maturity–season interaction, no prey category had significant interactions when examined by univariate tests (Fig. 5a). Most likely it was the combination of all prey categories that caused the interaction. Additionally there were significant sex–maturity interactions for the three crustacean prey categories ($p < 0.03$ for each) even though overall that interaction was not significant ($p = 0.13$, df = 6, 96) (Fig. 5b). In all cases (and for teleost prey, $p = 0.051$ for this interaction), immature males and females consumed nearly equal proportions of each category but mature males consumed significantly more of each than mature females.

Qualitatively, it appeared that there was no large difference in consumption by mass of certain prey during the UPS compared to the other two seasons. Predation on polychaetes was nearly equal among all three seasons, as was that of teleosts and cephalopods; the proportion ingested of the latter two categories during the UPS was less than the other seasons, but with a larger variance. However, shrimp-like crustaceans were consumed in a greater proportion during the UPS than the other two seasons. Consumption of small benthic crustaceans and crabs in the UPS was greater than that during the OCS; for the former prey category this was less than the proportion ingested in the DCS, while for the latter the UPS and DCS were similar.

Testing of the numeric data revealed significant differences in the diet by maturity ($p < 0.01$, df = 6, 96) and season ($p < 0.01$, df = 6, 96) with significant sex–season ($p = 0.037$, df = 6, 96) and maturity–season ($p < 0.01$, df = 6, 96) interactions. Shrimp-like crustaceans and teleosts were consumed in a greater proportion by mature skates, whereas immature individuals consumed more polychaetes and small benthic crustaceans. Between seasons, shrimp-like crustaceans were consumed more in the OCS, whereas polychaetes, teleosts, small benthic crustaceans and crabs were consumed in greater proportions in the DCS. The sex–season interaction was driven by shrimp-like crustaceans and polychaetes (Fig. 6a). Both sexes decreased their consumption of shrimp-like crustaceans from the OCS to DCS, but females displayed a greater decrease, having the greater consumption of the two sexes in OCS, but the lesser of the two in the DCS. Female skates greatly increased consumption of polychaetes from OCS to DCS, while males decreased slightly. The maturity–season interaction was caused by teleosts, small benthic crustaceans and cephalopods (Fig. 6b). Mature skates greatly increased their consumption of teleosts from the OCS to DCS, whereas immature skates increased only slightly. Predation on small
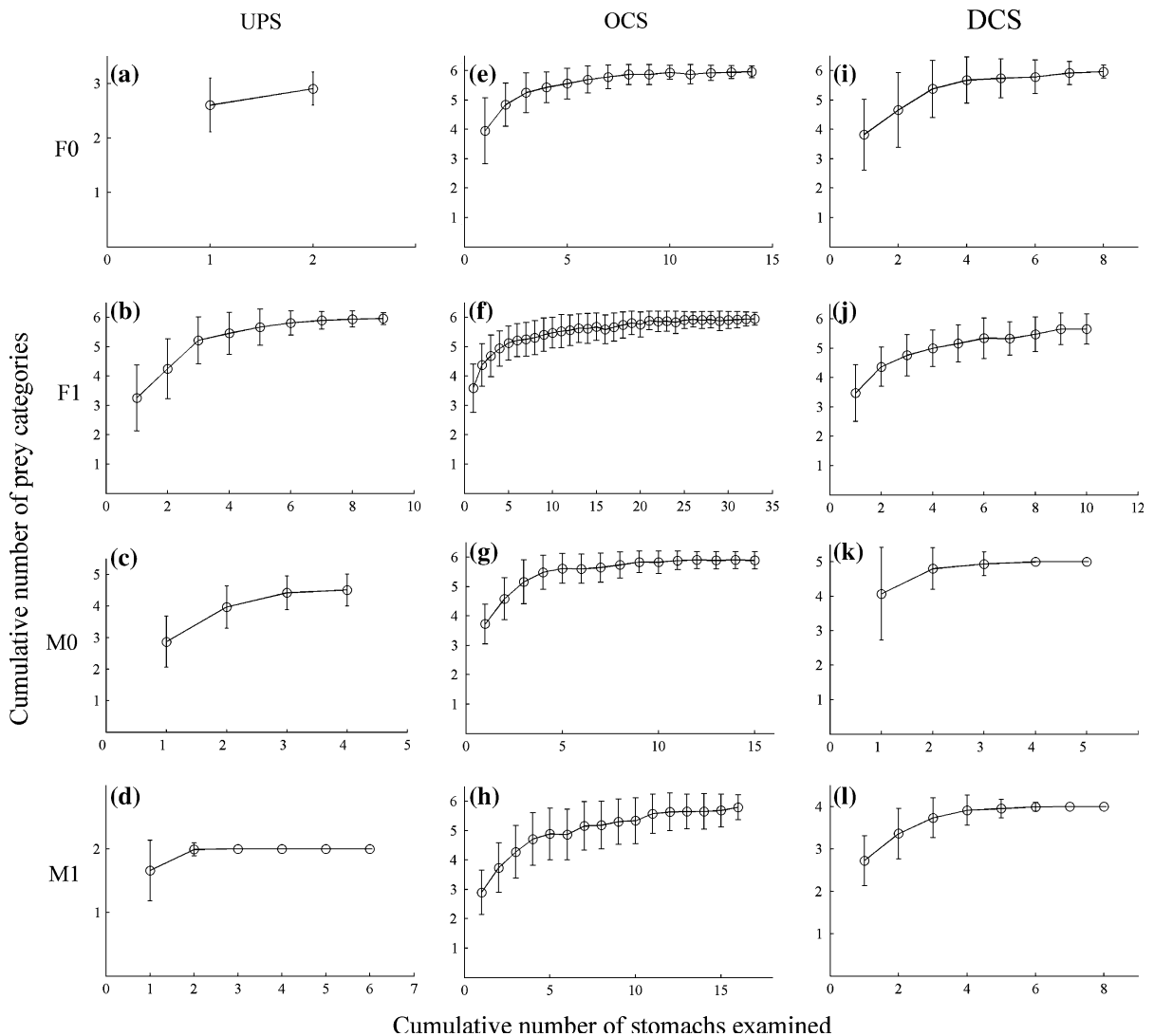
Fig. 4 Cumulative prey curves of the major prey categories for each combined factor grouping used in the analysis of the diet of *Bathyraja kincaidii*. Error bars represent the standard deviation of the plotted mean generated from 100 resamplings. For the following sex–maturity–season combinations, F = female, M = male, 0 = immature, 1 = mature, UPS = Upwelling season, OCS = Oceanic season, DCS = Davidson Current season

benthic crustaceans displayed a similar trend, but the maturity roles were reversed, immature skates having consumed more. Feeding on cephalopods by mature skates showed a marked increase from the OCS to DCS, though immature skates slightly decreased theirs.

In a qualitative examination of the numeric data, shrimp-like crustaceans were consumed in nearly equal proportion by skates during the UPS and the OCS; polychaetes and teleosts showed a similar pattern but the proportion ingested in the UPS was slightly less than the OCS but with a greater variance. The consumption of shrimp-like crustaceans in each of these two seasons was greater than the DCS, whereas predation on polychaetes and teleosts was less than during the DCS. Crab consumption during the UPS was similar to the other two seasons. The proportion of cephalopod prey taken by *B. kincaidii* was least in the UPS. There was a unique pattern in the proportion of small benthic crustacean prey, where consumption during the DCS was greater
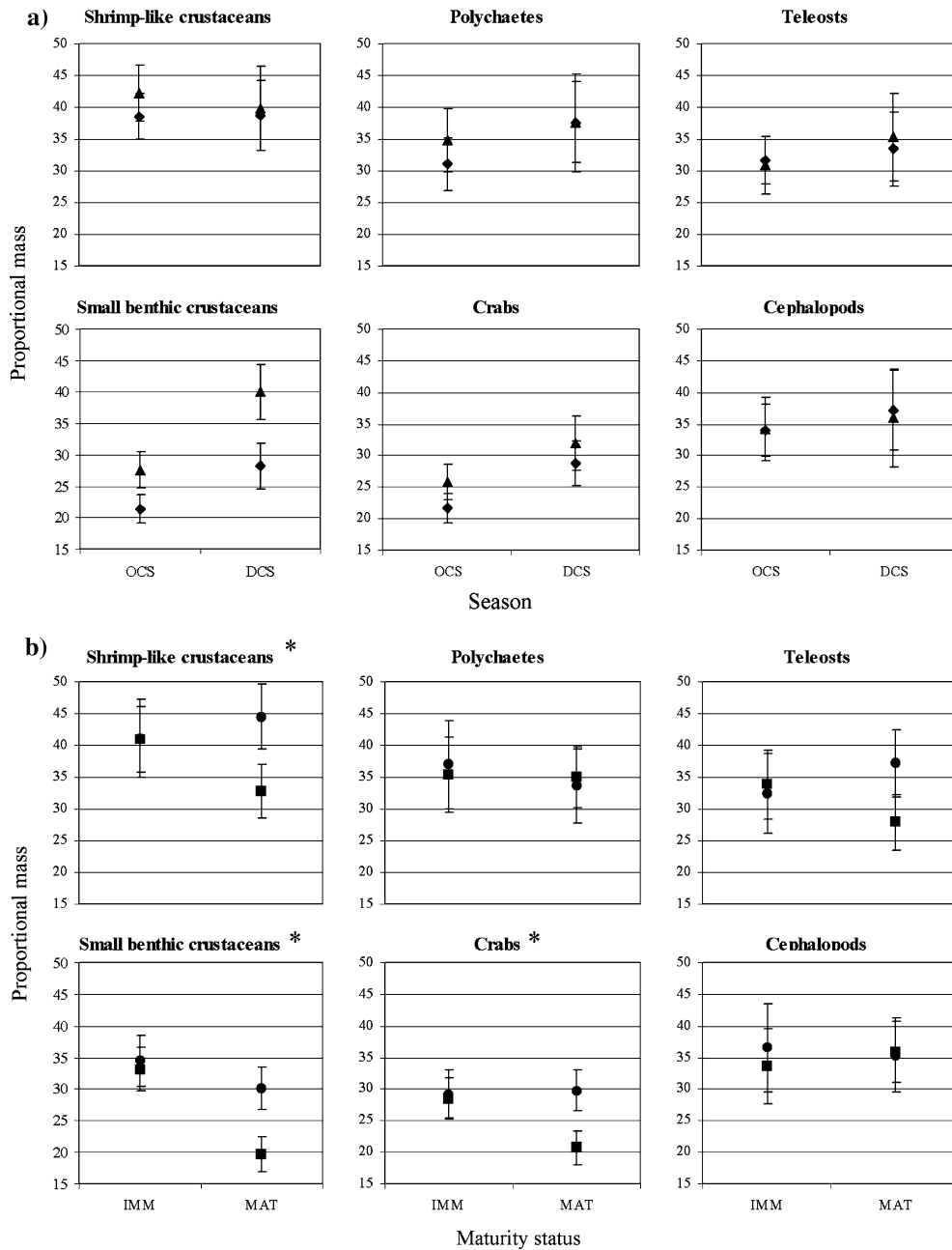
Fig. 5 Mean values and 95% confidence intervals of the gravimetric proportion of the six prey categories in the diet of *Bathyraja kincaidii*. (**a**) Maturity–season interaction, ▲ = immature skates, ◆ = mature skates. (**b**) Sex–matu-rity interaction, IMM = immature, MAT = mature, ■ = female skates, ● = male skates. *Significant ($p < 0.05$) for the interaction

than during the UPS which was in turn greater than the OCS.

Factor fit revealed that seasonal variation explained the most variance in both sets of *B. kincaidii* diet data (Table 2). By proportional number, season explained 17%, which was greater than the amount of variance explained by all variables in the mass model. Maturity stage was the second greatest factor by number and ranked third in importance by mass. This factor
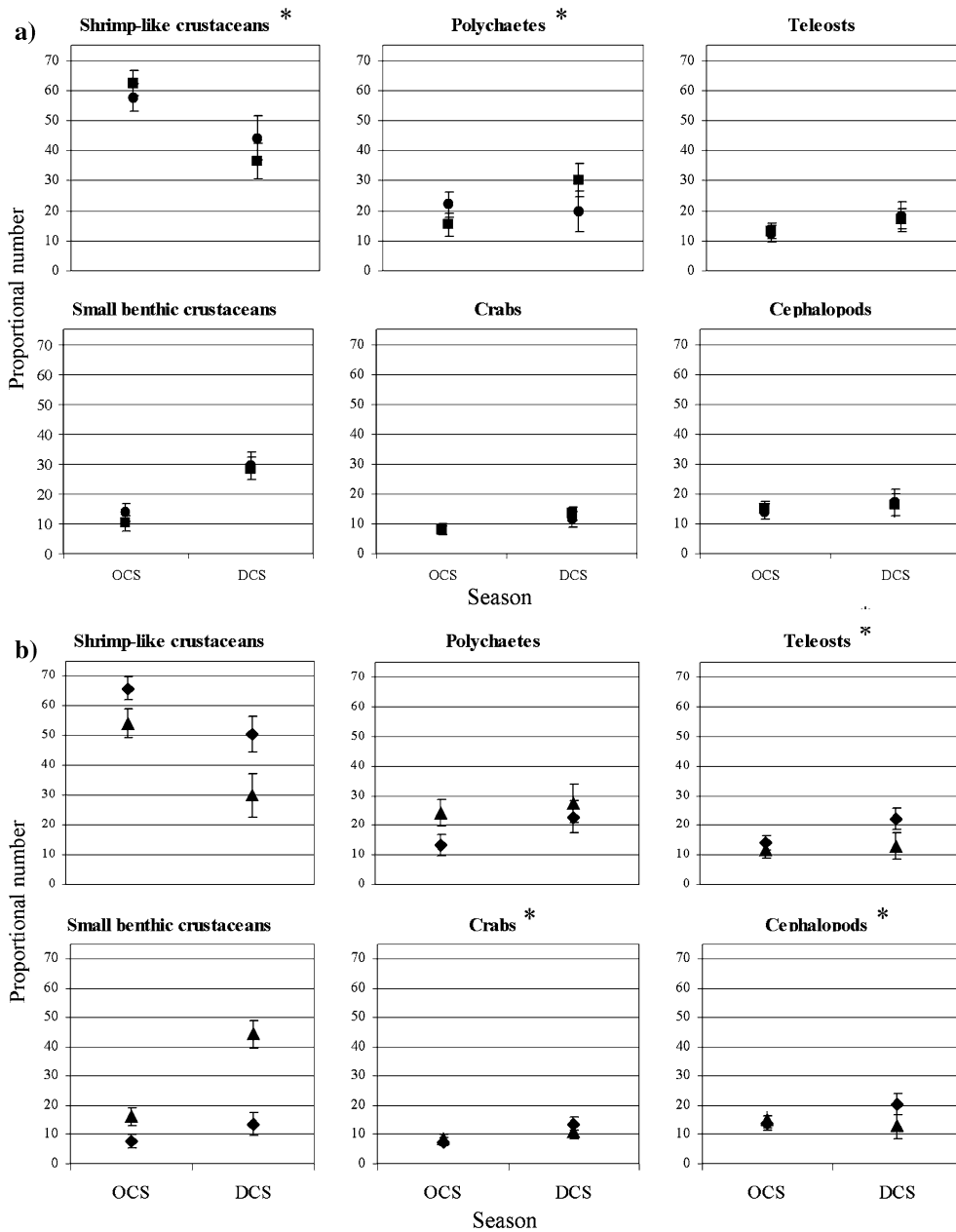
Fig. 6 Mean values and 95% confidence intervals of the numeric proportion of the six prey categories in the diet of *Bathyraja kincaidii*. (**a**) Sex–season interaction, ■ = female skates, ● = male skates. (**b**) Maturity–season, ▲ = immature skates, ◆ = mature skates. *Significant (p < 0.05) for the interaction

explained 14% of the variance by number, again more than the total explained in the mass model. Sex, which was a significant factor only for mass, explained the second most amount of variation in that model, but the second least amount numerically. Except for the maturity–season and sex–season interactions by number and the sex–maturity interaction by mass, the remaining interaction terms explained little of the variance in the diet.

Table 2 Factor fit (ω^2), Pillai's Trace p-value and the rank importance of both for the three main factors and their interactions resulting from the MANOVA performed on the gravimetric and numeric importance of the six main prey categories of *Bathyraja kincaidii*

Factor	ω^2	Rank	p-value	Rank
Gravimetric data				
Sex	2.05	2	0.03	4
Maturity	2.02	3	1.05×10^{-7}	1
Season	3.39	1	5.11×10^{-7}	2
Sex–maturity	1.85	4	0.13	5
Sex–season	0.21	5	0.23	6
Maturity–season	0.11	6	0.01	3
Sex–maturity–season	0.00	7	0.80	7
Error	90.37			
Numeric data				
Sex	0.04	6	0.53	6
Maturity	14.28	2	3.72×10^{-17}	1
Season	17.12	1	2.87×10^{-13}	2
Sex–maturity	0.01	7	0.86	7
Sex–season	2.31	4	0.04	4
Maturity–season	3.93	3	2.64×10^{-9}	3
Sex–maturity–season	0.61	5	0.29	5
Error	61.69			

Discussion

Crustaceans were by far the most important prey taxa to the overall diet of *B. kincaidii* from central California, comprising >72% of the prey by $\overline{\% N}$ and $\overline{\% IRI}$ and more than 47 $\overline{\% M}$. This is a trait shared with many other nearshore and offshore, small bodied (<700 mm TL) benthic skates (McEachran et al. 1976; Berestovskiy 1990; Ebert et al. 1991; Smale and Cowley 1992; Pedersen 1995; Ellis et al. 1996; Orlov 1998a; Muto et al. 2001; Braccini and Perez 2005; Dolgov 2005; Mabragaña et al. 2005). The most important lower taxon of this category was euphausiids, which are known to be an important, and often primary, prey for cetaceans, birds and fishes (Schoenherr 1991; Brodeur and Pearcy 1992; Ainley et al. 1996; Croll et al. 1998, 2005; Yamamura et al. 1998). Small benthic crustaceans, mostly gammarid amphipods, played only a minor role overall but were seasonally important, becoming the most important lower prey taxon by all three measures during the DCS. Crabs were not an important food for these skates.

Polychaetes (e.g. Onuphidae and Nephtyidae) were the second most important prey category overall and their importance in the diets of skates has been well documented (McEachran et al. 1976; Templeman 1982; Berestovskiy 1990; Ellis et al. 1996; Brickle et al. 2003; Dolgov 2005; Mabragaña et al. 2005). The taxa of polychaeta consumed appeared to be related to skate maturity, with small-bodied worms (e.g. Opheliidae) more important to immature skates and larger nephtyid worms nearly absent from immature skate stomachs but important to mature skates.

The two remaining prey categories, cephalopods and teleosts, played only minor roles in the diet of *B. kincaidii*. The reduced importance of cephalopods and teleosts in the diet of smaller batoids is well established (McEachran et al. 1976; Templeman 1982; Berestovskiy 1990; Ebert et al. 1991; Smale and Cowley 1992; Pedersen 1995; Ellis et al. 1996; Walmsley-Hart et al. 1999; Muto et al. 2001; Dolgov 2005), and has been observed in other *Bathyraja* species (Orlov 1998a; Brickle et al. 2003). Both of these categories were dominated by unidentifiable prey.

Some items found in the stomachs of *B. kincaidii* during this study were considered incidentally ingested rather than prey. The gastropods *Amphissa bicolor* and *Astyris gausapata* along with a piece of an unidentifiable bivalve shell comprised the molluscs. Echinoderms, the other category, were represented by a single piece of *Strongylocentrotus* sp. Out of the 7 occurrences of these items, 6 were from stomachs that had benthic prey items in them, such as crabs, polychaetes and crangonid shrimp, suggesting that these items could have been ingested while feeding upon other prey.

The dietary importance of benthopelagic, vertically migrating prey such as euphausiids, myctophid fishes and the shrimp *Sergestes similis* raised the question of where these skates could be feeding. Though it is possible they could migrate into the water column to feed, a more likely explanation is the interaction of shoreward currents and the migration of their prey. It has been suggested that when these migrators are at their shallower nighttime depths, currents may advect them over shallower shelf waters, so that when they descend in the daytime they are near or in contact with the benthos (Isaacs and Schwartzlose 1965; Pereyra et al. 1969; Croll et al. 1998;

Ressler et al. 2005). Within Monterey Bay, it has also been suggested that the canyon walls can further serve to concentrate the prey (Croll et al. 2005); the area map (Fig. 1) indicates that many skates used in this study came from trawls near canyon edges. This interaction of currents, a nearshore shelf and steep canyon walls could allow *B. kincaidii* to feed on concentrations of these prey the skate otherwise might not encounter in its benthic habitat.

While sorting stomachs, it became apparent that certain prey items were biased in how they were considered important to the diet because of their differential digestion and degradation. Often with cephalopod and teleost prey there was little or no flesh remaining in the stomach, leaving only beaks and otoliths or other bones to be used, which underestimated the importance by mass of those prey. Similarly, polychaetes were often partially digested and at times counted by jaw parts rather than whole animals (except for opheliids which were almost exclusively whole). Even though these categories comprised the second, third and fourth greatest portions of the diet by mass, those values are considered to underestimate their importance to a certain degree. Because of this, the numeric abundance of these prey categories may more accurately estimate their importance to the diet. Significant differences for these numerically biased prey were only found when testing the numeric data. Shrimp-like and small benthic crustaceans showed the opposite relationship. These items, though not always whole, were rarely in an advanced state of digestion. However, their eyes, the characters used to enumerate them, were often degraded, somewhat underestimating their numeric importance. Similar to the other biased group above, these categories composed the first and third greatest percentages by number in the diet despite their bias. Despite this possible bias, these prey did indicate differences by number, but not always for the same factors or interactions as the mass data. It is possible that differences in the findings between the numeric and gravimetric data may have been influenced more by the digestion rates of certain prey rather than their importance in the diet. Analyses of both mass and number would be beneficial in such cases. A

second possible source of bias could be from a low sample size (ten stomachs or less) in each sex–maturity grouping from the DCS. Though cumulative prey curves indicated those samples were enough to describe the richness of the diet, it could be argued they were inadequate for use in the statistical tests.

It is interesting that the data revealed differences in the diet between the sexes, though only by mass. Although not always analyzed, male and female diets frequently do not differ in elasmobranchs (Abdel-Aziz et al. 1993; Cortés et al. 1996; Alonso et al. 2001; Braccini and Perez 2005; Braccini et al. 2005), though sexual differences in diets have been observed in some species (King and Clark 1984; Gray et al. 1997; Orlov 1998b). In this study, consumption of the three major crustacean categories differed by sex. As previously stated, there were significant sex–maturity interactions which could explain these differences. Ingestion of these prey categories was not found to differ by sex when skates were immature but mature males consumed significantly more of each than mature females, which led to the result that males consumed more crustaceans than females.

Though the frequent significant interactions precluded the conclusion that differences in the diet could be due solely to main factors, fit revealed that season explained the most variance in the diet. Previous studies have also noted intra- and inter-annual changes in the diets of elasmobranchs (McEachran et al. 1976; Pedersen 1995; Cortés et al. 1996; Muto et al. 2001; Braccini and Perez 2005; Braccini et al. 2005). These results, coupled with previous studies on prey abundances, suggest that seasonal changes in the diet of *B. kincaidii* may be related to seasonal variation in the abundance of euphausiids, their most important prey. However, the majority of the variance remained unexplained in the gravimetric data, indicating additional factors are responsible for much of the variation in the diet by mass.

Euphausiid abundances have been found to vary intra-annually due to localized oceanographic changes, particularly upwelling, and inter-annually due to large scale El Niño/La Niña events (Brinton 1976; Ainley et al. 1996; Tanasichuk 1998a, b; Yamamura et al. 1998; Marinovic et al. 2002; Brinton and Townsend

2003). Though the timing can vary, when cool, nutrient rich water is upwelled, a predictable chain of events ensues (see Cushing 1971 for review) where phytoplankton increase in abundance followed by an increase in zooplankton, such as euphausiids. Because of variability and a lag between spawning and adulthood, peaks in euphausiid abundance can occur months after phytoplankton abundances begin to increase (Croll et al. 2005).

In the Monterey Bay area, upwelling most often occurs from late March/early April until late October/early November, peaking in June (Marinovic et al. 2002; Croll et al. 2005; Pacific Fisheries Environmental Laboratory 2006). This period encompasses the UPS and OCS used in this study, during which time euphausiids were most important to the diet of *B. kincaidii*. This is also the time of greatest euphausiid abundance in the study area (Marinovic et al. 2002; Croll et al. 2005). Upwelling decreases sharply starting in late July, and taking into account the 3- to 4-month time lag suggested by Croll et al. (2005), a decrease in the abundance of juvenile and adult euphausiids should first be seen in November, which corresponds to the start of the DCS. This decrease in abundance has been previously noted for euphausiids in Monterey Bay (Marinovic et al. 2002; Croll et al. 2005), *Euphausia pacifica* off southern California (Cailliet and Ebeling 1990) and for both *E. pacifica* and *Thysanoessa spinifera* off Vancouver Island (Brinton 1976; Tanasichuk 1998a, b).

The remaining shrimp-like crustaceans important in the diet of *B. kincaidii* included various shrimps and mysids, mostly unidentifiable. One of the more important identified shrimp species was *Sergestes similis*. In Monterey Bay, Barham (1957) found this species had a nearly constant abundance throughout the year due to two populations with a 6-month reproductive lag. There is no information currently available on the abundances of deep-water mysids in Monterey Bay, but Mauchline (1980) suggests that abundances of most species fluctuate seasonally with reproduction.

Myctophids were the most important identifiable teleosts in the diet of *B. kincaidii*. *Stenobrachius leucopsarus* abundance varies seasonally, peaking in winter and lowest from March to June (Neighbors and Wilson 2006). Barham (1957) noted that in Monterey Bay, *S. leucopsarus* was captured throughout the year, but was most abundant during the months of the DCS by a recalculated average. *Diaphus theta*, another myctophid consumed, was absent in all but one of the samples taken during the UPS, but like *S. leucopsarus* it was present in much greater numbers during the DCS (Barham 1957). These data suggest that myctophids are more abundant in the DCS than either of the other two seasons.

Little information is available on the seasonal abundance of *Loligo opalescens*, the most important identifiable squid species in the diet, aside from fishery dependant data. This is because of the difficulty in sampling this species with conventional gear such as trawls, which adults can easily evade or escape (Cailliet and Vaughan 1983). The fishery lands maximum catches from May to July (McInnis and Broenkow 1978; Hardwick and Spratt 1979; Cailliet and Vaughan 1983; Yaremko 2001). Assuming that catch was directly related to abundance (ignoring problems with fishing effort), October to March is the period of lowest *Loligo* abundance in Monterey Bay, suggesting that these squid were more abundant during the UPS and early OCS than in the DCS.

Data on the seasonality of deep-water small benthic crustaceans and polychaetes in the area is currently lacking. Slattery (1980) claimed that shallower amphipod species showed peaks in recruitment during spring and summer (UPS and early OCS), but in deeper water there was a reduced seasonality. Because there is no clear evidence, discussion of possible reasons for the fluctuation in importance of these prey in the diet is not discussed.

Synthesizing the abundances of the various prey from other studies, an explanation for the patterns observed in the diet of *B. kincaidii* is possible. Beginning in the UPS, euphausiids were likely highly abundant and remained so until approximately November. During this time they were the dominant prey of both males and females, but were more important to mature skates than immature skates. Also during this season, polychaetes were important prey to *B. kincaidii*, but were more important to

immature skates. Squids and crabs were consumed but were not important to the diet. Though they did not contribute much to the diet, *Sergestes similis* was likely fairly abundant.

During the OCS euphausiids likely remained highly abundant and were the most important prey of *B. kincaidii*. However, there was a dramatic increase in the importance of myctophids and squid such as *Loligo opalescens*, which could be explained by an increased abundance in the area. These prey were exploited by both sexes, but were more important to mature than immature skates. Polychaetes remained secondarily important but the importance of gammarid amphipods declined.

Decreases in phytoplankton, likely associated with the DCS, led to decreased numbers of euphausiids. Presumably since their primary prey was no longer available in the same abundance, *B. kincaidii* began to prey more upon shrimps such as *S. similis*, which remained at roughly the same abundance all year. Mysids were also of greater importance to the diet in this season, more so than euphausiids. The importance of euphausiids in the diet decreased from an average of 47 $\overline{\% \text{ N}}$, 21 $\overline{\% \text{ M}}$ and 55 $\overline{\% \text{ IRI}}$ in the UPS/OCS to 11, 6 and 6%, respectively, during the DCS. Though the overall importance of shrimp-like crustaceans declined somewhat during the same time period from an average of 77 $\overline{\% \text{ N}}$, 45 $\overline{\% \text{ M}}$ and 75 $\overline{\% \text{ IRI}}$ to 43, 34 and 54%, respectively, it remained the most important prey category because of the increased importance of shrimps and mysids which masked the decline of euphausiids. *Bathyraja kincaidii* continued to prey on myctophids, which likely peaked in abundance during this season; they remained more important to mature skates than immature ones. Gammarid amphipods significantly increased in the diet and were much more important to immature skates, replacing teleosts and cephalopods that the mature skates fed upon. Polychaetes also increased in the diet, again more in immature skates. Squids remained important items in the diet, but not as much as during the OCS. This may reflect, but cannot be fully explained by, their likely minimal abundance during this season. Further sampling of the shelf-slope benthos should lead to a more complete understanding of any seasonal trends in abundance and to further discussion of the causes behind the observed seasonal dietary fluctuations of *B. kincaidii*.

Conclusion

Bathyraja kincaidii is a major predator of benthic and benthopelagic crustaceans. By mean number, mass and IRI the dominant prey were shrimp-like crustaceans, which were comprised primarily of euphausiids, but also contained shrimps and mysids. Although differences in the diet by season, maturity status and sex could not be ascribed solely to those factors because of frequent significant interactions, factor fit indicated that these main factors better explained the observed variance in the data than the interactions. The difference in findings between the numeric and gravimetric data may be related more to differences in digestion of certain prey categories than their importance by these measures. The seasonal variation in the diet is most likely attributable to the availability of euphausiids, the skate's primary prey. In the DCS when euphausiids are less abundant, *B. kincaidii* relies on secondary prey such as gammarid amphipods, shrimps, mysids, polychaetes and myctophids. Further research is needed to accurately assess the seasonal abundances of these prey. This is to determine whether the cause for their increased importance is related to a relative increase in their abundance compared to the lower euphausiid biomass or if they display comparatively similar or lower absolute abundances during this period and *B. kincaidii* actively chooses them.

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