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Diet and ecomorphology of the sandpiper skate, Bathyraja kincaidii (Garman, 1908) from the eastern North Pacific

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DIET AND ECOMORPHOLOGY OF THE SANDPAPER SKATE, *BATHYRAJA KINCAIDII* (GARMAN,1908) FROM THE EASTERN NORTH PACIFIC

A thesis submitted to the faculty of
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Master of Science
in
Marine Science

by
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ABSTRACT

DIET AND ECOMORPHOLOGY OF THE SANDPAPER SKATE, *BATHYRAJA KINCAIDII* (GARMAN,1908) FROM THE EASTERN NORTH PACIFIC

by Christopher Scott Rinewalt

To determine diet, the stomach contents of sandpaper skates, *Bathyraja kincaidii* (Garman, 1908), were examined from a limited depth and geographic area off central California and from a wider depth and area range along the eastern North Pacific (ENP). The overall diet was dominated by euphausiids and shrimps, but polychaetes, squids, and gammarid amphipods were important secondary prey. Shrimp-like crustaceans, polychaetes, and teleosts were of similar importance in both data sources, but small benthic crustaceans and crabs were comparatively more important in the diet of skates from the ENP whereas cephalopods were more important in central Californian samples. A three-factor MANOVA demonstrated significant differences in the importance of major prey categories by sex, maturity status, and oceanographic season in the central California data. 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 environmental abundance changes in the most important prey, euphausiids, were coupled with changes in the importance of other prey. Differences in the diet by sex, maturity status, and geographic zone of capture occurred in the ENP. Geographic zone explained the most variance in the diet, though much less than that explained by the central California data. Information on prey availability for these samples was limited, but it

appears that latitudinal variation in euphausiids, again the most important prey, may be correlated with changes in the importance of other prey categories.

An ecomorphological study of the oral and dental morphology of *B. kincaidii* was conducted to determine if the intra-specific differences in diet could be linked with associated differences in morphology. Many of the structures associated with feeding grew allometrically, both positively and negatively, and the growth relationships were often different between the sexes. The results of a three-factor MANCOVA revealed that there were frequent significant differences by all of the factors (sex, maturity status, and geographic zone) and their interactions among all of the measured variables. However, variation between the sexes explained approximately one third of all the variance in the measurements in both data sets. The sex*maturity interaction explained the second most amount of variance, indicating that relational differences in the morphology of male and female skates further changed as they matured. The differences among the factor levels in oral and dental morphology were compared with the differences among the same levels determined from the diet study and it was concluded that intra-specific variation in morphology did not correlate well with intra-specific differences in diet. Based on the lack of a relationship, I suggest that intra-specific differences in the morphology of skates, as with other batoids, are related more to mating. The increased mouth width, amount of palatoquadrate protrusion, shorter pre-oral length, and teeth with higher and longer cusps of mature males allows them to better capture and hold females during courtship but such differences do not satisfactorily account for differential exploitation of any prey category.

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CHAPTER 1. DIET ANALYSIS

INTRODUCTION

The trophic ecology of a species, determined through diet analysis, gives insight to the place of both predator and prey in the food web. Diet studies can provide information on habitat use of predator and prey as foraging habitat may be different than where an animal has previously been observed. This kind of study also can 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 are the most speciose elasmobranch order, occurring in nearshore temperate environments and deep-water tropical and boreal regions (Compagno 1990). Skates are frequently taken as bycatch around the world in important fisheries that target hake (*Merluccius* spp.), whiting (*Micromesistius australis australis*), cod (*Salilota australis*), monkfish (*Lophius gastrophysus*) and shrimp (*Pleoticus muelleri*), and 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 also may compete with commercial species by sharing the same food resources (Berestovskiy 1990, Pedersen 1995, Orlov 1998a, Dolgov 2005). As with other elasmobranchs, these fishes are usually upper trophic level predators (Berestovskiy 1990, Orlov 1998a, Alonso et al. 2001, 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 indicate that thorough dietary studies are needed to determine their place in the ecosystem (Stevens et al. 2000).

Elasmobranchs, including skates, are relatively long lived and late to reproduce relative to teleosts (Compagno 1990, Camhi et al. 1998, Frisk et al. 2001, Zorzi et al. 2001). Because of these life history attributes, they face problems related to overfishing, such as the reduction of breeding biomass and slow recovery to pre-fishing levels when overfished. These biological attributes, 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 1981-1994, and were often greater than the combined landings of all other elasmobranch species (PacFin Database 2006). Additionally, landings have fluctuated greatly, increasing from 199 metric tons (mt) in 1995 to 1372 mt in 1997 then falling to 141 mt in 2003. Though not as strong, fluctuations were also indicated from landings within the Monterey Bay National Marine Sanctuary (Starr et al. 2002). Landings peaked in 1983 with 91 mt, followed by twelve years of relatively stable landings below 48 mt, to an increase of 110 mt in 1997, decreasing to 46 mt landed in 2000. In Oregon, commercial skate landings have displayed the same trend in both increase and fluctuation over the same time period, with a high of 938 mt in 2003 (Camhi, 1999; PacFin Database 2006). The total landings of skates in Oregon from 1995-2003, undifferentiated by species, was greater than thirteen times the combined total commercial landings of all other elasmobranchs. In Washington, the skate landings have remained comparatively low, ranging from < 100 mt to just over 300 mt over the same two decades. This catch never surpassed the remaining elasmobranch catch, which was predominantly spiny dogfish*, Squalus acanthias* (PacFin Database 2006). However, the skate catch has shown a fluctuating trend, most notable since 1997. It should be noted that no effort data were available for these landings. Prior to the current landings increase, skates were frequently discarded and it is unknown whether these increased landings are the result of increased catch retention or if fishermen are collecting a greater number of skates than before (Camhi 1999; Zorzi et al., 2001). In either case, 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 and 1372 m (most commonly between 200 to 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). Currently there is some question as to the validity of the species (Ebert 2003). Ishihara and Ishiyama (1985) synonymized *B. kincaidii* with *Bathyraja interrupta* based on morphometrics and meristics, claiming that geographic variation may account for the differences between them. However, the authors did note that there were differences in the size of egg cases between the two species, something they noted may not be due solely to geographic variation. Craig (1993), in a later examination of the *Bathyraja* genus, concluded that there were sufficient meristic and qualitative differences between the two species to separate them. Few studies have been conducted on its life history, yet it is frequently caught in trawls in the ENP. 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*, the teleost *Citharichthys sordidus*, a pinnotherid crab and the mysid, *Acanthomysis nephrophthalma*. Ebert (2003) reported anecdotal information on the diet, 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, maturity stages, and among oceanographic seasons for skates from the Monterey Bay area and between sexes, maturity stages, and among geographic zones from the slope waters of northern Washington to southern California.

MATERIALS AND METHODS

Sample sources, general sorting and measurements

Sandpaper skates, *Bathyraja kincaidii*, were collected during approximately monthly trawl surveys along the central California coast from March 2002 to February 2005 by the National Marine Fisheries Service (NMFS) Santa Cruz Lab (SCL) (Figure 1) and from the NMFS Northwest Fisheries Science Center West Coast Groundfish Survey (WCGS) trawls from June to October 2003 (Figure 2). Specimens from SCL surveys 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). Specimens from the WCGS trawls were collected during 118 hauls of varying depth.

Skates from both sources were frozen on board the vessel and later processed at which time the stomachs were removed and frozen for later sorting. Stomach contents were sorted without sieving at 6.3 to 16x magnification using a dissecting microscope. Prey items were identified, counted, and weighed wet to the nearest 0.001 g. Any prey item < 0.001 g was given a mass of 0.0005 g for use in calculations. Any material that was not identifiable to any taxonomic level was excluded from enumeration and weighing. An “unidentified digested material” category was not included in this analysis because it does not enhance the understanding of an animal’s diet, but only gives evidence to the rate of digestion and gastric evacuation, which was not examined in this study. The importance of non-biological categories, such as gravel, was not recorded. Prey taxa were grouped into nine taxonomic categories: polychaetes, cephalopods, small benthic crustaceans, shrimp-like crustaceans, crabs, unidentifiable crustaceans, teleosts, molluscs and echinoderms.

Diet description

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), $\overline{\%M}$ is the mean percentage mass of a given prey category, and %FO is the percentage frequency of occurrence of a given prey category from all stomachs. To estimate precision for %N and %M of the prey, mean importance and standard error were calculated based on importance values from each stomach examined (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 (Pinkas et al. 1971, Hyslop 1980). This index was chosen because it easily conveys all the important aspects of a prey category into a single metric (Cortés 1997, Cortés 1998). Also, the IRI is the most widely used feeding index (Hahn and Delariva 2003), allowing for comparisons with other studies of diet, provided care is taken when assigning prey categories for comparison. This index was modified to incorporate percentage mass instead of percentage volume:

$$\overline{IRI}_j = (\overline{\%N}_j + \overline{\%M}_j) * \%FO_j$$

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

$$\overline{\%IRI}_j = (\overline{IRI}_j / \Sigma\, \overline{IRI})*100$$

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. A curve employing the number of prey taxa was used as it appears to be more conservative than a curve based upon diversity values (Robinson 2006).

Diet analysis

The monthly SCL samples were divided among 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 to July) is characterized by the upwelling of cold, nutrient-rich water that can move far offshore due to strong southbound winds. This is followed by the Oceanic Season (OCS) (August to 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 to 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.

Similarly, the WCGS samples were divided among four geographic zones. Rather than divide the sampled area via political boundaries, previously described faunal breaks were used. The northernmost zone extends from the Canadian border to Cape Blanco (approximately 42.8° N- zone 4). Oceanic copepods and intertidal mussels and barnacles have significantly different assemblages and recruitment rates, respectively, north and south of the Cape (Connolly et al. 2001, Peterson and Keister 2002). Additionally, Cape Blanco is the northernmost boundary of the California Current; north of the Cape, cold, nutrient rich upwelled waters remain nearshore while south of the Cape these upwelled waters can be transported far offshore, over the deep shelf/ slope region (Barth et al. 2000). The third zone consists of the waters south of Cape Blanco to the northern edge of Monterey Bay (approximately 37.0° N) whereas the second zone extends from 37.0° N to Point Conception (approximately 34.4° N). Previous researchers have found that this division of the California Current is supported by faunal range cluster analyses of various crab, ascidian, mollusc, and fish taxa (Valentine 1966, Hayden and Dolan 1976, Horn and Allen 1978). Zone 1 consists of the area south of Point Conception to the Mexican border.

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/ four geographic zones for each data set (Somerton 1991, Paukert and Wittig 2002). Compound indices should not be used because they can conceal the information of individual measurements, so number and mass of the major prey categories were used separately in the analysis (Tirasin and Jørgensen 1999). The proportion of each category 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). A sequential Bonferroni comparison test was used to determine which geographic zones were responsible for the detected differences in diet categories (Rice 1989). This test was chosen as it has more power than the standard Bonferroni test, but is more conservative than the Least Significant Difference test. Except for these multiple comparisons, all other statistical tests were conducted with SPSS 11.0.1 for Windows. The two data sources, WCGS and SCL, were considered different populations a priori as there was no spatio-temporal overlap, and therefore were analyzed separately.

The diet data were tested based upon the major prey categories previously described. Without grouping prey, there will almost certainly be significant differences in food items simply because of the variation among individual predators and/or an excessive amount of variables (food taxa). Six of the taxonomic categories (polychaetes, shrimp-like crustaceans, small benthic crustaceans, crabs, cephalopods and teleosts), accounting for the twelve variables (number and mass), were used in the statistical tests. Unidentifiable crustaceans (pieces of crustaceans that could not be placed into any of the other crustacean categories), molluscs and echinoderms were excluded as they contributed little to the diet (Olson 1974). Additional randomized cumulative prey curves were created for each level of the three factors (e.g. immature females in the OCS, etc.) using these taxonomic categories. Because only major prey categories were statistically tested, a further qualitative examination of the importance of prey at lower taxonomic levels was included for each of the three main factors. Taxa were considered to be important if they comprised > 5% of $\overline{\%N}$, $\overline{\%M}$ or $\overline{\%IRI}$. These percentages should not be confused with the transformed proportions used in the statistical tests.

A multivariate factor fit model using the three fixed factors (sex, maturity status, and oceanographic season/ geographic zone) 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

Sample sources

In total, 140 *B. kincaidii* stomachs were collected from the SCL trawls, of which 8 (5.7%) were empty. Additionally, 2 (1.4%) specimens had incomplete haul tag information, which precluded their use in certain statistical analyses. The number of skates collected per haul ranged from 1 to 26 individuals (mean 5.4 ± 1.3 SE) and they ranged in size from 327 to 585 mm TL (mean 482 ± 4.6 SE mm TL, Figure 3). Examined by season, 21 skates with stomach contents were collected during the UPS, 78 from the OCS and 31 in the DCS. The majority of samples, however, were collected in January (22%), October (17%), and November (41%). The depth distribution of the specimens also was 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 (Figure 4).

In total, 368 specimens were examined from the WCGS trawls, 6 (1.6 %) with empty stomachs. There were 2 (0.5 %) stomachs from the WCGS that contained only unidentifiable crustacean prey or items considered incidentally ingested and another 7 (1.9 %) that had incomplete haul tag information, which precluded their use in any analysis other than general diet description. Between 1 and 14 skates were collected per haul (mean 3.1 ± 0.2 SE). Fourteen skates were collected in zone 1, 44 from zone 2, 136 from zone 3, and 159 from zone 4. Skates from the WCGS trawls had a greater TL range than those from SCL trawls, 195 to 660 mm TL (mean 479 ± 4.2 SE mm TL, Figure 5).

Skates were collected as shallow as 70.6 m to as deep as 1162.2 m (mean 347.2 m ± 17.7 SE m). There was a leveling in the randomized cumulative prey curve, requiring approximately 310 samples to describe prey richness (Figure 6).

Diet description

Bathyraja kincaidii consumed a wide variety of invertebrates and teleosts (Table 1). Taxonomically, with 67 of 94 lowest identifiable taxa (LIT), the majority of the prey items were crustaceans, most of which were amphipods (23) and shrimp or shrimp-like crustaceans (27). Amphipods from 12 families were ingested whereas the shrimp-like crustaceans were taxonomically dominated by hippolytid shrimps of the *Eualus* and *Spirontocaris* genera. To a lesser extent, crangonid shrimps and the euphausiid *Thysanoessa* spp. were consumed. Crabs also were well represented, with 13 LIT, the majority of which were *Pagurus* spp. Teleosts were the second most taxonomically diverse group with 12 LIT, which were composed mostly of the myctophids *Diaphus theta*, *Tarletonbeania crenularis*, and *Stenobrachius leucopsarus*. Various groundfish such as *Sebastes* spp., *Citharichthys* sp., and *Eopsetta exilis* comprised the remaining identified teleosts. Polychaetes ranked third with 9 LIT. Within this group only one family, Onuphidae, had more than one identifiable species present. Cephalopods were the least abundant group taxonomically, with 4 LIT. They were composed primarily of three identifiable squid, *Abraliopsis felis*, *Gonatus* sp., and *Loligo opalescens*, with a single identifiable octopod, *Octopus rubescens*. However, the low taxonomic diversity of this group could be attributed to the digestion of cephalopod beaks, which allowed the prey to be identified to this taxonomic level, but not any further.

The mean number (62.7 %), mass (46.2 %) and IRI (69.1 %) indicated the overall diet of *Bathyraja kincaidii* was dominated by shrimp-like crustaceans (euphausiids, mysids and shrimps), which were found in > 96 % of the stomachs examined (Figure 7, Table 2). Polychaetes were the second most important prey and were slightly more important by mass (20.1 %) than number (14.9 %) and IRI (16.6 %), and displayed a large frequency of occurrence (72 %). Cephalopods (4.4 $\overline{\%N}$, 9.2 $\overline{\%M}$, 39 %FO and 3.5 $\overline{\%IRI}$) and teleosts (5.3 $\overline{\%N}$, 10.1 $\overline{\%M}$, 46 %FO and 4.7 $\overline{\%IRI}$) also were more important by mass, but were consumed by much less of the sampled population. Small benthic crustaceans were of nearly equal importance by number and mass (8.9 $\overline{\%N}$, 6.8 $\overline{\%M}$, 43.8 %FO and 4.5 $\overline{\%IRI}$). Based on $\overline{\%IRI}$, the remaining four prey categories, crabs (1.6 %), unidentifiable crustaceans (0.05 %), molluscs (0.01 %), and echinoderms (< 0.01 %) comprised a minimal portion of the diet.

Examination of the minor groups in the overall diet indicated what lower taxa were most important to *Bathyraja kincaidii*. The inseparable conglomerates of euphausiids, shrimps, and mysids collectively dominated the shrimp-like crustacean group, of which the euphausiid/ shrimp mix was the most important. Following these mixes were shrimps, of which unidentifiable shrimps made up the greatest portion. Onuphidae was the most important polychaete family and were found in 32.5 % of the stomachs examined. There were no lower taxa of teleosts that were considered important in the diet, but were primarily unidentifiable remains followed by the family Myctophidae. Gammarid amphipods comprised the majority of small benthic crustaceans, with only trace amounts of the remaining taxa. Cephalopods mainly consisted of squid, most of which were unidentifiable. The remaining prey categories, like teleosts, had no important lower taxa. The majority of the crab category, however, was unidentifiable remains along with pagurids and axiids, the molluscs were mostly gastropods and the echinoderms were predominantly the urchin *Strongylocentrotus* sp.

When the sample sources were examined separately a similar pattern emerged. The majority of the diet of both sources, by mean number, mass and IRI, was comprised of shrimp-like crustaceans and a large portion of the diet, again by all three measures, was composed of polychaetes (Tables 3 and 4). The importance of cephalopods by mass was much greater in the SCL samples as was the frequency of occurrence, which led to their increased overall importance in those samples. The importance of teleosts in the diet of WCGS samples was slightly less by mass and frequency of occurrence, indicating a lower overall importance compared with the SCL data. Small benthic crustaceans and crabs were more important to skates from the WCGS based on all measures of importance (Figures 8 and 9).

Differences were found in the importance of minor prey groups between the two sources. In the stomachs from the WCGS samples, the euphausiid, shrimp, and mysid mixes dominated the diet. However, the diet of SCL skates was dominated by euphausiids rather than the mixes and were composed mainly of unidentifiable remains with *Thysanoessa spinifera* the most important identifiable species; unidentifiable shrimp were of secondary importance. Onuphid polychaetes were the most important family for both data sources. Nephtyids were, however, the second most important family to SCL samples, because of their comparatively greater mean mass and frequency of occurrence, whereas unidentifiable polychaetes ranked second in the WCGS samples because of their comparatively greater mean mass and high frequency of occurrence. The importance of myctophid fishes was somewhat greater in the SCL samples by all measures, but this category was only important by mass. The sources differed markedly in their importance of lower cephalopod taxa. Squids were more important to the diet of SCL samples, but a large percentage of skates from both sources consumed them. Though not important, octopods were consumed more by skates from SCL trawls by all measures. Gammarid amphipods were consumed similarly by skates from both sources, but were more frequently consumed by WCGS skates. No lower taxa of crab prey were considered important to the diet from either source, but each were more important to WCGS samples. These samples also displayed a greater taxonomic diversity than those collected in the SCL, of which axiid crabs were the most important.

Diet analysis

The additional randomized cumulative species curves for each level of the three factors examined in the SCL data indicated two groups for which there were not enough stomachs collected. There were only two stomachs from immature females during the UPS, which was not enough to test statistically (Figure 10a). Additionally, the curve for immature males in the UPS was inconclusive (Figure 10c). Removing only those samples would have made the design non-orthogonal, so all stomachs from the UPS were removed from the quantitative analysis. The diets of these stomachs were qualitatively compared with the diets of skates from the other two seasons. The remaining randomized curves indicated enough stomachs were collected to describe the richness of the diet for the remaining combination of factors (Figure 10).

There were groups from WCGS trawls for which there were not enough stomachs collected. There was only a single mature female and immature male stomach each from zone 1 (no curve generated). By the same reasoning as above, all stomachs from this zone were removed and qualitatively examined in relation to the other zones. The randomized curves generated for the remaining combinations revealed an adequate amount of samples were collected to describe their prey richness (Figure 11).

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The assumptions for parametric tests were violated in the SCL data set. Levene's test on the prey groups was significant only for polychaetes ($p= 0.004$) and Box's M also was significant ($p< 0.01$) for 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 ($p< 0.01$) indicating that overall the data set did not have equality of variances or covariances. 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 ($p=0.028$, df= 6, 96), maturity status ($p<0.01$, df= 6, 96) and oceanographic season ($p<0.01$, df= 6, 96) with a significant interaction of maturity-season ($p= 0.014$, df =6, 96). Pairwise comparisons revealed that male *B. kincaidii* ingested a significantly greater proportion of shrimp-like crustaceans, small benthic crustaceans, and crabs than females. Immature skates consumed more small benthic crustaceans and crabs than mature individuals. Greater proportions of small benthic crustaceans and crabs were ingested during the DCS than in the OCS.

Although there was a significant maturity*season interaction, no prey category had significant interactions when examined by univariate tests (Figure 12a). Most likely this was the combination of all prey categories that caused the interaction, but two prey groups stood out. The consumption of shrimp-like crustaceans by mature skates did not change from the OCS to the DCS, but there was a sharp decrease in their consumption by immature skates. The proportion of small benthic crustaceans consumed by both maturity stages increased from the OCS to the DCS, but immature skates had a greater increase than mature skates.

Aside from the significant interaction of maturity*season, there were significant sex*maturity interactions for three prey groups, though overall that interaction was not significant ($p=0.13$, df= 6, 96, Figure 12b). All three crustacean prey categories were significant for this interaction ($p<0.03$ for each). In all cases (and for teleost prey, $p=0.051$ for this interaction), immature males and females consumed nearly equal proportions of each of the respective categories but mature males consumed significantly more of each than mature females.

The proportional mass of prey consumed by *B. kincaidii* during the UPS was qualitatively similar to the diets of the other two seasons. Predation on polychaetes, teleosts and cephalopods was nearly equal among all three oceanographic seasons, though for the latter two categories the mean proportion consumed during the UPS was least but with a greater standard error. Shrimp-like crustaceans, however, were consumed in a greater proportion during the UPS than the other two seasons, which were similar to each other. Consumption of small benthic crustaceans and crabs during the UPS was greater than that during the OCS; for the former prey category this was less than the proportion ingested during the DCS, whereas for the latter the UPS and DCS were similar. The sex*season interaction revealed that males and females consumed small benthic crustaceans in equal proportions during the UPS, whereas in the other 2 seasons males had a greater proportion of this prey in their diet than females. Male and female skates ingested an equal proportion of teleosts in the UPS and DCS, but during the OCS, males ingested a significantly greater proportion than females. For the remaining prey groups, the diets of male and female skates were either the same among all three oceanographic seasons, or if different, they had the same trend among the three seasons. There did not appear to be a maturity*season interaction in the UPS. When the UPS data were included in the analysis there was not much difference in the consumption of shrimp-like crustaceans between the maturity levels. The consumption of small benthic crustaceans and crabs by skates differed between maturity stages each season. Immature skates ingested more of these prey than mature skates, and both prey categories were consumed in nearly equal proportions during the UPS and DCS, which were greater than the proportion consumed during the OCS.

Testing the numeric data revealed significant differences in the diet by maturity status ($p<0.01$, df= 6,96) and oceanographic 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 the shrimp-like crustacean and polychaete prey categories (Figure 13a). Both sexes decreased their consumption of shrimp-like crustaceans from the OCS to DCS, but females decreased more, having the greater consumption of the two sexes in OCS, but the lesser of the two during the DCS. Female skates greatly increased consumption of polychaetes from OCS to DCS, whereas males decreased slightly.

The significant maturity*season interaction was caused by teleost, small benthic crustacean, and cephalopod prey (Figure 13b). Mature skates greatly increased their consumption of teleosts from the OCS to the DCS, whereas that of immature skates increased only slightly. Predation on small benthic crustaceans by immature skates increased from the OCS to DCS, however, the consumption of these prey by mature skates displayed a much greater increase between the seasons. Mature skates ate more cephalopods in the OCS than the DCS, though immature skates consumed slightly less.

In a qualitative examination of the numeric data, shrimp-like crustaceans were consumed in nearly equal proportion by *B. kincaidii* during the UPS and the OCS; polychaetes and teleosts had 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 during the DCS, whereas predation on polychaetes and teleosts was less than during the DCS. Crab consumption during the UPS was in between and qualitatively similar to the other two seasons. The proportion of cephalopod prey taken 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 than during the UPS which was in turn greater than during the OCS. The maturity*season interaction revealed that small benthic crustaceans were consumed in greater proportion by immature skates in all seasons, but in the DCS the difference was much greater. Cephalopods were ingested in the same proportions by mature and immature skates during the UPS and the OCS, but in the DCS mature skates consumed a significantly greater proportion than immature skates. Mature skates consumed a greater proportion of shrimp-like crustaceans than immature skates in the OCS and DCS, but during the UPS there was no difference between maturity stages. Polychaetes were ingested more by mature skates in the UPS (but with a greater standard error), which was the opposite pattern of the other two seasons. Qualitatively, there appeared to be a significant sex*season interaction due to shrimp-like crustacean, polychaete, and crab prey. Though the sexes fed equally on shrimp-like crustaceans during the UPS, females had a greater proportion in their diet during the OCS whereas males consumed more in the DCS. Polychaetes had the same interaction as in the quantitative analysis, as the proportion ingested during the UPS by males was nearly equal to that of females. Male skates consumed a greater proportion of crab prey during the UPS, but as before this proportion did not differ between the sexes in the other two seasons.

Factor fit revealed that seasonal variation explained the most variance by mass and number in the diet of *B. kincaidii* (Table 5). By proportional number, oceanographic season explained 17 % of the variance, which was greater than the total amount of variance explained by all variables in the mass model. Maturity status was the second greatest factor by number and ranked third in importance by mass. This factor 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. Though some factors differed by only 1 rank, the only agreement between factor fit and p-value for the mass data was for the sex*maturity*season interaction, which ranked last for both. By number, all factors but maturity status and oceanographic season, which were switched, agreed between p-value and fit.

The qualitative examination of lower taxa indicated some fine scale differences among the main factors. Nephtyids were the only polychaete prey important to the female skate diet, whereas only onuphids played an important role in the diet of males. Squids were the primary cephalopod prey for both sexes. Gammarid amphipods were the only important small benthic crustacean taxon for both female and male skates. Euphausiids were the most important lower taxon of the shrimp-like crustacean category for both sexes, followed by the unidentifiable shrimp-like mix, also for both sexes. Additionally, unidentifiable shrimp were important to both males and females.

Myctophid fishes were important in the female diet and unidentifiable teleosts in the male's. There were no important lower crab taxa consumed.

When examined by maturity status, additional patterns were revealed. Immature skates preyed mostly on onuphid and opheliid polychaetes, whereas mature individuals primarily consumed nephtyid and onuphid polychaetes. Squids remained the single most important cephalopod prey, and of nearly equal importance to both maturity stages. Gammarid amphipods were again the only important small benthic crustaceans, but only to the diets of immature skates. Euphausiids dominated the diet of mature skates, with the unidentifiable mix and unidentifiable shrimp secondarily important. The unidentifiable shrimp-like mix, however, was the most important group to immature skates, followed by euphausiids. Myctophids were the single important teleost group and only to mature skates. Again, there were no important crab taxa.

Qualitatively, the diet of *B. kincaidii* displayed some of the greatest qualitative differences by oceanographic season. There were two important polychaete taxa among the 3 seasons surveyed, onuphids in the UPS and DCS and nephtyids during the OCS and DCS. Cephalopod taxa also were mixed among seasons, with squid being the only taxon ingested in the UPS, and also important in the other two seasons. Octopods, however, were important during the OCS, whereas unidentifiable cephalopods were important in the DCS. Gammarid amphipods were nearly absent from the diet of *B. kincaidii* during the OCS, but were important during the UPS and the DCS. During the DCS they were the most important lower prey taxon in the diet. Euphausiids were the most important prey taxon overall during the UPS and OCS, followed by the unidentifiable mix. In the

UPS, hippolytid shrimp and unidentifiable shrimp were also important. During the DCS, unidentifiable shrimp were the most important shrimp-like crustaceans, but were far less important than the euphausiids from the other two seasons. Unique to the DCS was the increased importance of mysids compared to the OCS. Euphausiids were also important during the DCS, but again much less so than the other two seasons. Myctophids were the sole important teleost taxon and only during the OCS and DCS.

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As with the SCL samples, the WCGS data set did not meet the assumptions of parametric tests. Tests revealed that neither data series was homoscedastic. Levene's Test determined significantly different ($p<0.05$) variances among the factor groupings for shrimp-like crustaceans, teleosts, crabs and cephalopods for the mass data; Box's M also was significant ($p<0.01$) in the multivariate examination of variance. Using the numeric data, Levene's Test indicated significant differences ($p<0.05$) by groups for teleosts, small benthic crustaceans and crabs; Box's M again was significant ($p<0.01$). Examination of the residuals indicated that both data series had a normal distribution.

Testing of the mass data revealed significant differences in the diet by sex ($p<0.01$, df = 6, 323), maturity status ($p=0.025$, df = 6, 323) and geographic zone ($p<0.01$, df = 12, 648), but there also were significant maturity*zone ($p=0.001$, df = 12, 648) and sex*maturity ($p=0.019$, df = 6, 323) interactions. Male skates consumed a significantly greater ($p< 0.05$) proportion of shrimp-like crustaceans and polychaetes than females as determined by post-hoc pairwise comparisons. Immature skates ingested a greater proportion of polychaetes and small benthic crustaceans than mature skates. By zone, the proportion of shrimp-like crustaceans in the diet of skates from zones 3 and 4 were similar for each prey and both were significantly greater than in the diets from zone 2. The proportion of polychaetes consumed in zone 3 was also greater than that of zone 2. Conversely, the proportion of crabs in the diet of skates from zone 2 was significantly greater than those of zones 3 and 4.

The maturity*zone results indicated that only polychaete and crab prey did not display an interaction. Analysis of the means for each level did not indicate any clear overall trend among the remaining prey categories (Figure 14a). One evident trend was the clinal decrease in the proportion of cephalopods and teleosts consumed by mature skates from south to north. The consumption of teleosts by immature skates was greatest in zone 3 whereas that of cephalopods was lowest in that zone. Mature skates displayed a general increase in their consumption of shrimp-like crustaceans from south to north, whereas the proportion ingested by immature skates remained fairly consistent across zones, though skates from the northernmost zone did consume the greatest proportion. The ingestion of small benthic crustaceans displayed opposing trends by maturity status. Though they ingested equal proportions in zone 3, immature skates consumed their least proportion, and mature skates their greatest, in that zone.

The sex*maturity interaction was driven by teleosts and cephalopods (Figure 14b). The proportions of these prey categories consumed by female skates decreased when they matured, whereas the amount ingested by males increased slightly. Though it was not significant ($p > 0.05$), male skates slightly decreased their consumption of shrimp-like prey as they matured, whereas female skates increased theirs.

The proportional mass data from the fourteen excluded *B. kincaidii* stomachs from zone 1 qualitatively indicated that the consumption of most of the prey categories was similar to the other zones. There was a greater standard error due to a smaller samples size, but the ingestion of teleosts, small benthic crustaceans, and cephalopods in zone 1 was similar to that of the other three geographic zones. The consumption of crab prey in zone 1 was nearly equal to that of zones 3 and 4, all of which were less than the proportion taken by skates from zone 2. Polychaete prey consumption in zone 1 was much greater than that of the other three zones, whereas the ingestion of shrimp-like crustaceans in zone 1 was in between that of zone 2 and zones 3/ 4. Examining the maturity*zone interaction revealed that immature skates in zone 1 consumed more shrimp-like crustaceans than mature skates, which was similar to the pattern from zone 2; mature skates in zone 3 had a greater proportion of these prey in their diet whereas the proportions were equal between the maturities in zone 4. Polychaetes were found in a greater proportion of mature skate stomachs from zone 1, which was opposite the trend found in the other three zones. The sex*zone interaction indicated that teleosts, small benthic crustaceans, crabs and cephalopods were all consumed in nearly equal proportion by both sexes among each zone. Males ingested a greater proportion of shrimp-like crustaceans in zone 1, similar to zone 2, whereas the consumption in zones 3/ 4 was nearly equal between the sexes. Polychaetes were consumed in a much greater proportion by females in zone 1, whereas the ingestion of this category by females was equal to or slightly less than that of males in each of the other three zones.

Examining the proportional number data, there were significant differences in the diet by sex, ($p=0.048$, df = 6, 323), maturity status ($p<0.01$, df = 6, 323) and geographic zone ($p<0.01$, df = 12, 648), with significant interactions of maturity*zone ($p= 0.007$, df = 12, 648) and sex*maturity ($p= 0.010$, df = 6, 323). Results of post-hoc comparisons indicated that female skates consumed significantly more small benthic crustaceans than males. Mature skates ingested a greater proportion of teleosts and cephalopods than immature skates, whereas the opposite was the case for small benthic crustaceans. Among zones, all prey groups except polychaetes displayed differences in the proportion ingested. Shrimp-like crustaceans were consumed significantly more in zones 3 and 4 (which were not significantly different than each other) than zone 2. The opposite was true for teleosts, crabs and cephalopods, where skates consumed a greater proportion of these prey in zone 2 than zones 3 and 4 (again not significantly different). The consumption of small benthic crustaceans deviated from this pattern, with skates from zones 2 and 4 (not significantly different from each other) consuming a greater proportion than those in zone 3.

Cephalopod prey were responsible for the maturity*zone interaction. Mature skates displayed a significant decline in the proportion of cephalopods consumed from zone 2 to zones 3/ 4 (Figure 15a). The proportion ingested by immature skates remained relatively stable across all zones.

The sex*maturity interaction was caused by teleosts, crabs, and cephalopods. Female skates did not increase their consumption of teleost prey as they matured, but males did (Figure 15b). The patterns of crab and cephalopod ingestion were similar in that female skates slightly decreased their ingestion on these groups as they matured, whereas males increased theirs.

Qualitative examination of the numeric proportion of zone 1 prey of *B. kincaidii* yielded similar results compared to the mass data. Shrimp-like crustaceans were consumed in a slightly lower proportion by skates in zone 1 than zone 2, both of which were much lower compared with zones 3 and 4. Polychaetes composed a much greater proportion of the skate diet in zone 1 than in all other zones. Teleost and crab prey proportions were similar for skates in zones 1, 3 and 4, all of which were lower than that of zone 2. Cephalopods were taken nearly equally in zones 1 and 2, which was marginally greater than the proportions taken from zones 3 and 4. Lastly, small benthic crustaceans were preyed on nearly equally in all zones, though least in zone 3. Shrimp-like crustacean and polychaete prey differed between maturity levels in zone 1 skate diets, as revealed by the maturity*zone interaction. Immature skates consumed a greater proportion of shrimp-like crustaceans than mature ones, whereas the opposite was true for polychaetes. There did not appear to be any overall pattern in the consumption of prey categories among the four zones. There was a distinct clinal zigzag pattern of consumption of crabs and small benthic crustaceans by immature skates; predation on these groups was greater in zones 2 and 4 than in zones 1 and 3. Examining the sex*zone interaction, consumption of shrimp-like crustaceans and polychaetes again differed in skates from zone 1. Male *B. kincaidii* consumed a greater proportion of shrimp and vice versa for polychaetes. Additionally, male skates ingested more cephalopods than females within zone 1.

Although the amount of variance in the diet explained by the model was low for both the proportional mass and number of prey, geographic zone, maturity status, and the interaction of these two factors accounted for the greatest explained dietary variance (Table 6). The sex*maturity interaction was next by numeric data, followed by the sex*maturity*zone interaction (which was non-significant). Sex, although significant in the model, explained the second least amount of variance in the diet by number, followed by the sex*zone interaction. Sex explained slightly more variation in the mass model and ranked 4th in factor fit. The remaining interactions in the mass model comprised the least important factors in explaining dietary variance. When the ranks of the factors were compared between significance of fit and p-value by mass, zone, sex*zone and sex*mat*zone agreed (Table 6). The remaining factors differed by a ranking of one except for maturity status, which explained the second most amount of variance in the model but was ranked fifth by p-value. All of the factors except maturity status and geographic zone, which were switched in rank between fit and p-value, agreed in the numeric model.

Additionally, lower taxa of the six prey categories were examined qualitatively for each of the main effects. Only unidentifiable polychaetes were important in the diet of female sandpaper skates. Onuphids were the most important polychaetes for male skates, followed by unidentifiable polychaetes. There were no cephalopods that were considered important in the diet of either sex, but squids were the dominant taxon. Small benthic crustaceans were predominately gammarid amphipods in the diet of both sexes, but were more important to females. The unidentifiable mix of shrimps, euphausiids and mysids was the most important group of shrimp-like crustaceans, followed by euphausiids, for both sexes. Additionally, crangonid shrimps and unidentifiable shrimps were important to female *B. kincaidii* whereas unidentifiable shrimps were important to males. There were no lower taxa of crabs or teleosts considered important to either sex.

By maturity status, onuphids were important in the diets of immature skates, but not to mature skates, whereas unidentifiable polychaetes were important for both maturity stages. Squids were the only important cephalopod component of the diet, and only for mature skates, whereas gammarid amphipods were the only important small benthic crustaceans and only to immature skates. The unidentifiable mix was the most important taxon of shrimp-like crustaceans for both maturity stages, though more to mature skates. Euphausiids and unidentifiable shrimps were also important to the diet of immature skates. Unidentifiable shrimps were the next most important taxon to mature skates, followed by crangonid shrimps and identifiable euphausiids.

The two most important shrimp-like crustacean taxa to skates from zone 1 were unidentifiable and crangonid shrimps. These were followed by euphausiids and the unidentifiable mix. In zone 2, euphausiids and the unidentifiable mix were most important taxa, followed by unidentifiable shrimps. The unidentifiable mix was the most important taxon to the diet of skates in zones 3 and 4. In zone 3, the remaining important group were euphausiids, whereas in zone 4 unidentifiable shrimps were second, followed by crangonid shrimps.

Among the four zones, unidentifiable polychaetes were frequently important contributors to the diet. In zone 1, this group, followed closely by opheliids and nephtyids were important. In zone 2, however, only opheliids were important. Onuphids were the most important lower taxon in the diet of skates from zone 3 along with unidentifiable polychaetes. In the northernmost zone, 4, unidentifiable polychaetes and the unidentified polychaete A were the important taxa.

The importance of lower taxa from the remaining prey categories varied geographically, but was often greatest in the two southernmost zones. Squids were the single important cephalopod, and only to skates in zones 1 and 2. Two lower taxa of crabs were important to the diet of *B. kincaidii* but in only two of the zones; unidentifiable crabs in zone 1 and axiid crabs in zone 2. Similarly, two teleost taxa were important contributors to the diet. Myctophids were considered important to the diet of skates from zones 1 and 2; unidentifiable teleosts were also consumed in zone 2. Unlike the other secondary taxa, gammarid amphipods were important prey in all zones.

DISCUSSION

Crustaceans were the most important prey taxa to the overall diet of *Bathyraja kincaidii*, composing > 75% of the prey by $\overline{\%N}$ and $\overline{\%IRI}$ and more than 60 $\overline{\%M}$. 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, Platell et al. 1998, Muto et al. 2001, Braccini and Perez 2005, Dolgov 2005, Mabragaña et al. 2005), rays (Abdel-Aziz, 1994, Valadez-Gonzalez et al. 2001, Ismen 2003), sharks (Ellis et al. 1996, Braccini et al. 2005) and teleosts (Wakefield 1984, Garrison and Link 2000, Platell and Potter 2001). Additionally, smaller individuals of larger (> 700 mm TL) species in these habitats also prey significantly on crustaceans (McEachran et al. 1976, Ajayi 1982, King and Clark 1984, Smale and Cowley 1992, Abdel-Aziz et al. 1993, Ellis et al. 1996, Smale and Compagno 1997, Orr and Bowering 1997, Alonso et al. 2001, Hovde et al. 2002, Brickle et al. 2003, Ebert and Cowley 2003). Most crustaceans taken by *B. kincaidii* were shrimp and shrimp-like crustaceans (euphausiids and mysids), which were found in 96% of the stomachs that contained food. Euphausiids are important, and often primary, prey for cetaceans, birds, and fishes (Schoenherr 1991, Brodeur and Pearcy 1992, Ainley et al. 1996, Croll et al. 1998, Yamamura et al. 1998, Croll et al. 2005). Although they were taxonomically diverse, crabs and small benthic crustaceans (predominantly gammarid amphipods) played minor roles in the overall diet.

Polychaetes were the second most important category overall, and as with the crustaceans, their importance in the diets of skates and other elasmobranchs has been well documented (McEachran et al. 1976, Templeman 1982, Gordon and Duncan 1989, Berestovskiy 1990, Ellis et al. 1996, Platell et al. 1998, Brickle et al. 2003, Ebert and Cowley 2003, Dolgov 2005, Mabragaña et al. 2005). The most important members of this group were the Onuphidae and unidentifiable polychaete remains. In the SCL data, the taxa of polychaetes consumed appeared to be related to skate maturity status, 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 played only minor roles in the diet of *B. kincaidii*. Teleosts were fairly diverse, but the most important taxon was unidentifiable remains. Other researchers have noted a similar minor importance of teleosts in the diet of small batoids (McEachran et al. 1976, Templeman 1982, Ebert et al. 1991, Smale and Cowley 1992, Pedersen 1995, Muto et al. 2001, Platell and Potter 2001) and specifically *Bathyraja* spp. (Orlov 1998a, Brickle et al. 2003). Cephalopods ranked just behind teleosts in importance. The majority of this category were unidentifiable squids due to the partial digestion of beaks. However the majority of octopods were identified as *Octopus rubescens*. As with the other groups of prey items, the minor importance of cephalopods in the diet of small benthic fishes has been previously established (Templeman 1982, Berestovskiy 1990, Smale and Cowley 1992, Ellis et al. 1996, Orr and Bowering 1997, Orlov 1998a, Walmsley-hart et al. 1999, Garrison and Link 2000, Hovde et al. 2002, Brickle et al. 2003, Dolgov 2005).

Echinoderms, composed of an unidentifiable ophiuroid and *Strongylocentrotus* sp., and molluscs, represented by *Amphissa bicolor*, *Astyris gausapata*, *Rictaxis punctocaelatus* and an unidentifiable bivalve, were considered incidentally ingested rather than prey. In all four cases of the occurrence of echinoderms, only small pieces of spines, test and disc were recovered. Of the 14 occurrences of molluscs, 12 were from stomachs that contained benthic prey items such as crabs, polychaetes and Crangonid shrimp, indicating they could have been ingested while feeding on other items. The lone bivalve encountered in the examination comprised < 0.01% by mass of the items in that stomach. For the remaining 13 gastropods, only in two cases did they comprise more than 4% by mass of the stomach contents. Additionally, in only a single instance was there more than one of these items in a stomach; one mature female had a single *Astyris gausapata* and a single *Rictaxis punctocaelatus* that totaled < 2% by mass of the stomach contents. With a combined frequency of occurrence < 4%, it seems these items should have occurred in more stomachs if they were actively incorporated into the diet. This combination of factors led to these items being excluded from the prey analyses; the values for the remaining prey items in Tables 2, 3 and 4 were calculated without including these items, whereas the values for the molluscs and echinoderms were calculated with all stomach contents included.

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 based upon 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, shoreward currents may advect them over shallower shelf waters, so that when they descend in the daytime they are near or in contact with the seafloor (Isaacs and Schwartzlose 1965, Pereyra et al. 1969, Chess et al. 1988, Croll et al. 1998, Ressler et al. 2005). Within Monterey Bay, it has been suggested that the canyon walls can further serve to concentrate prey (Croll et al. 2005); the area map indicates that many skates used in this study came from trawls near canyon edges (Figure 1). This interaction of currents, a nearshore shelf and, in Monterey Bay, 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 three categories were only detected in tests of their numeric importance in the SCL data. Similarly, the importance of teleosts and cephalopods in the WCGS samples displayed differences in their numeric importance, yet polychaetes displayed differences only with the mass data.

Shrimp-like and small benthic crustacean prey displayed 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 frequently destroyed. These categories composed the first and third greatest percentages by number in the diet, but again, these estimates are believed to somewhat underestimate their importance. Thus, the mass data may have more accurately represented their importance. Despite this, differences in the importance of these categories were still detected by proportional number, but not always for the same factors or interactions as their mass data. It is possible that differences in the findings between 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.

Another possible source of bias could be from a low sample size (ten stomachs or less) in each sex-maturity grouping from the DCS in the SCL data. Though cumulative prey curves indicated those samples were enough to describe the richness of the diet, it could be argued they were too few and could have biased the importance of prey for that season. Though the use of cumulative prey curves is an accepted (and imperative) step in the description of diet, further discussion and examination into methods for determining the proper diet statistic (prey number, mass, IRI, richness or diversity) and sufficient sample size for use in statistical testing of diet data is needed.

An interesting result from these statistical tests was the significant difference in the diet between the sexes. Although not always analyzed, male and female diets frequently do not differ in elasmobranchs (Abdel-Aziz et al. 1993, Cortés et al. 1996, Platell et al. 1998, Alonso et al. 2001, Morato et al. 2003, 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). Significant differences were detected for all three crustacean categories and polychaetes across both sample sources. Yet, because of significant interactions, it was determined that only polychaete prey by mass and small benthic crustacean prey by number differed between the sexes in the WCGS samples. Though the significant interactions do not allow for the conclusion that the remaining differences were due to sex alone, they do indicate that sex had a significant effect on the diet, but this effect differed with maturity status and geographic zone.

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Though frequent significant interactions precluded the conclusion that differences in the diet of SCL samples could be due solely to the main factors, fit revealed that oceanographic season explained the most variance in the diet. Previous studies have also noted intra- and interannual changes in the diets of elasmobranchs (McEachran et al. 1976, Pedersen 1995, Cortés et al. 1996, Muto et al. 2001, Ismen 2003, Braccini and Perez 2005, Braccini et al. 2005). These results, coupled with previous studies on prey abundances from the area, indicate 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. Depth is one factor that may account for some dietary variance. Significant differences were detected in the diet of *Raja rhina* by depth, specimens that were collected in the same sampling regime as *B. kincaidii* (Robinson 2006). Another factor that may account for the unexplained variation is larger scale temporal variation. The SCL samples were collected from 2002-2005, so yearly fluctuations in prey species could possibly affect their importance in the diet.

Euphausiid abundances vary intra-annually due to localized oceanographic changes, particularly upwelling, and inter-annually due to large scale El Niño/ La Niña events (Brinton 1976, Brinton 1981, Brodeur and Pearcy 1992, Mackas et al 1997, Mackas 1992, Ainley et al. 1996, Lavaniegos et al. 1998, Tanasichuk 1998a, Tanasichuk 1998b, Yamamura et al. 1998, Tanasichuk 1999, Benson et al. 2002, Marinovic et al. 2002, Brinton and Townsend 2003, Croll et al. 2005). Though the timing can vary, when cool, nutrient rich water is upwelled, a predictable chain of events ensues (see Cushing 1971 for review). During this time, phytoplankton increase in biomass 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) (Figure 16). This period encompasses the UPS and OCS used in the present 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 three to four 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, Tanasichuk 1998b).

The remaining shrimp-like crustaceans important in the diet of *B. kincaidii* included various shrimps and mysids, mostly unidentifiable. If it can be assumed that the identifiable species also comprise the unidentifiable group and represent the same proportion in the diet, then the most important 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 six month reproductive lag. There is no information currently available on the abundances of deep-water mysids in Monterey Bay, but Mauchline (1980) suggested that abundances of most species fluctuate seasonally with reproduction.

Myctophids were the most important identifiable teleosts in the diet of *B. kincaidii*. *Stenobrachius leucopsaurus* abundance varies seasonally, with estimates from Monterey Bay peaking in winter and lowest from March-June (Neighbors and Wilson, Jr.

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 indicate 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-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-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 had 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 items 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* were 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* to the diet, 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 of greater importance to the diet in this season, more so than euphausiids. Although the overall importance of shrimp-like crustaceans declined somewhat during the same time period, it remained the most important prey category because of this increased importance of shrimps and mysids which masked the dramatic decline of euphausiids from the UPS/

OCS to DCS. *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 prey abundance and to further discussion of the causes behind the observed seasonal dietary fluctuations of *B. kincaidii*.

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Similar to the SCL samples, a dimensional factor, geographic zone, explained more variance in the diet than sex, maturity status or their interactions. The amount of explained dietary variance among all factors, however, was much less than that of the SCL samples. Depth may again be a source of this unexplained variation, given that the depth range of WCGS samples was greater than SCL samples. Additionally, there is the possibility that these were merely weak statistical effects detected by a large sample size and differences in diet based on these factors are not necessarily biologically significant (Graham and Edwards 2001). Unlike the SCL data, scant information is available on latitudinal variation in the abundances of the prey of *B. kincaidii*. There are general descriptions of the distribution of euphausiids which report that *Euphausia pacifica* and *Thysanoessa spinifera*, the two most important euphausiids in the diet, are transitional zone species and are present throughout the study area (Ponomareva 1966, Mauchline and Fisher 1969).   Additionally, published information on historical data from 1949 to 1958 indicated some degree of latitudinal variation in the abundances of these two species (Brinton 1962). The information available on decapod prey abundance is primarily limited to landing data for the most commercially important species (Wicksten 1984, Wicksten 1989, see also Otto and Jamieson 2003), of which only *Pandalus jordani* was consumed. This species has been found to display marked horizontal differences in abundance. A similar lack of information on non-commercial species abundance exists for teleost prey with *Sebastes* spp the most important commercially collected prey. As the data indicate, however, *P. jordani* and *Sebastes* spp. composed little of the overall diet from these samples, so discussions of their latitudinal differences in the diet of *B. kincaidii* would not be that informative. Some information is available for polychaete distributions from the study area, but lacks information on abundance (see Appendix I listing of polychaete identification guides). Taking into account these limitations, what evidence there is for prey abundance and distribution is presented.

In the southernmost zone, 1, the increased importance of shrimps and polychaetes in the diet, and the lower overall importance of shrimp-like crustaceans compared to the other zones, may be because of the overall lower abundance of euphausiids in the area. Historical evidence indicates that euphausiid abundance could be comparatively lesser within zone 1. During the period from 1955-1959, krill were less abundant in the area of zone 1 compared with the area from just south of Monterey Bay to just north of San Francisco Bay (spanning the northern area of zone 2 and the southern area of zone 3)

(Mullin and Conversi 1989). However, from 1960-1969, no significant difference in the abundance of euphausiids could be detected for the same regions, lending evidence to the highly variable spatio-temporal nature of this group. Similarly, Brinton (1962), using combined data from 1949-1958, found that except for an inshore area of southern California and two areas further north (discussed later), there was a relatively homogenous abundance of 500-4999 *Euphausia pacifica* / 1000 m^3 (see Figure 28, ibid) whereas *Thysanoessa spinifera* was found in abundances of 50-499 individuals/ 1000 m^3 in the area of zone 1 (see Figure 53, ibid). This indicates that euphausiids could also, at times, be fairly abundant within this area. It is unclear whether the diet from this zone reflected a period of low krill abundance and skates fed on the relatively more abundant shrimps or whether the skates preyed more upon shrimps regardless of euphausiid abundance. There is no available abundance data on the remaining prey categories in this zone.

The diet of skates from zone 2 was again dominated by shrimp-like crustaceans, and the importance of this category closely matched their overall importance in the WCGS samples. The dominance of euphausiids and the shrimp-like crustacean mix could possibly be explained by the historical findings, as before. Brinton (1962) noted that the greatest abundance of *Euphausia pacifica* was slightly offshore within this zone, from the area of Point Conception to San Francisco Bay (southern portion of study zone 3), reaching densities of > 5000 individuals/ 1000 m^3. *Thysanoessa spinifera* also displayed greater abundances (50-499 individuals/ 1000 m^3) in the southern half of zone 2, yet historically it was conspicuously absent from the Monterey Bay area (recall that this species was the most important identifiable euphausiid from the SCL stomachs). Perhaps because of this increased euphausiid abundance, *B. kincaidii* decreased consumption of polychaetes. The increase in euphausiids, however, does not easily explain the increased importance of crab prey in the diet, of which the Axiidae (*Calocarides* spp.) comprised over 20% of the diet by mass, the greatest mass for all prey taxa from that zone. Although it is unclear why because of a lack of prey abundance information, within this zone, *B. kincaidii* replaced polychaetes in its diet with cephalopods, teleosts and most importantly, axiid crabs. It is possible that axiid crabs were more abundant in this area and the skates consumed them in proportion to their abundance.

Within zone 3, shrimp-like crustaceans remained the major component of the diet and were predominantly the shrimp-like mix. As from above, *Euphausia pacifica* displayed their greatest abundance in the southern portion of this zone. However, in the mid-offshore area in southern Oregon/ northern California, densities were slightly decreased to 50-499 individuals/ 1000 m^3. *Thysanoessa spinifera* displayed a similar trend; this species had its greatest density (> 500 individuals/ 1000 m^3) outside of San Francisco Bay, and steadily decreased until < 50 individuals/ 1000 m^3 were collected in southern Oregon. Despite this general decrease in the northern limits of zone 3, euphausiids remained important prey for skates in this area. Although there was no abundance information, small benthic crustaceans, crabs, cephalopods, and teleosts displayed a general decrease in their importance compared to the other three zones. *Octopus rubescens* first appeared in the diet within this zone, which was interesting given this species importance in the diet of *B. kincaidii* from the SCL samples, yet none were found in the diet of skates from zone 2. Pagurid and galatheid crabs, along with crab larvae, were first encountered in the diet within this zone. Additionally, *B. kincaidii* consumed *Sternaspis* cf. *fossor* and two unidentified polychaetes (albeit infrequently and comprising a low importance) which were not ingested in other zones.

Skates from the northernmost zone, 4, again preyed predominantly on shrimp-like crustaceans. The importance of lower taxa, however, changed considerably. Euphausiids comprised < 1 $\overline{\%\mathrm{IRI}}$ of the diet, whereas the unidentified shrimp-like mix made up 43 $\overline{\%\mathrm{IRI}}$, which could be related to availability based on the historical data. *Euphausia pacifica* displayed its lowest abundance in this area and *T. spinifera* was absent from all plankton samples except those from northernmost area of Washington outside of Puget Sound. Within this zone, skates began to prey upon the shrimp *Pandalus jordani*. This may be because the greatest abundance of this species occurs off central Oregon and Washington (Dahlstrom 1970), specifically in the Columbia region between 43º00’ N and 47º30’ N (PacFin 2006b). However, this species is also considered abundant off northern California/ southern Oregon, so its absence in the diet of skates from zone 3 cannot be explained by abundance alone. *Bathyraja kincaidii* also increased consumption of gammarid amphipods, possibly as a result of decreased euphausiid abundances.

CONCLUSION

Bathyraja kincaidii is a major predator of benthic and benthopelagic crustaceans. By mass and number, the dominant prey were shrimp-like crustaceans, composed primarily of euphausiids, but also included shrimps and mysids. Although there were differences in the diet by geographic zone, oceanographic season, maturity status and sex, some differences could not be ascribed solely to those factors because of significant interactions. Factor fit indicated that these main factors explained more of the observed variance in the diet data than the interactions, and the temporal (oceanographic season) and spatial (geographic zone) factors explained the most overall. The difference in the importance of prey between the numeric and gravimetric data may be related to differences in digestion of certain prey groups and may not represent actual differences in their importance by these measures. The seasonal variation in the diet of SCL samples was likely attributable to the availability of euphausiids, the skate's primary prey. In the DCS, when euphausiids are less abundant, *B. kincaidii* relied more 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. Due to a general lack of information on latitudinal variation in the abundance of most prey items, the causes for differences in the diets of WCGS samples by geographic zone remain unknown. However, for euphausiid prey, geographic variation may play a key role in determining their importance in the diet.

CHAPTER 2. MORPHOLOGICAL EXAMINATION

INTRODUCTION

In conjunction with a diet study, it can be beneficial to examine a species' ecomorphology, the role an organism's form plays in how the organism interacts with its environment and other organisms (Norton et al. 1995). Previous researchers have qualitatively examined and generally described the gross morphology of fishes and their place in the ecosystem (e.g. Compagno 1990), but not until recently have these data been used quantitatively with diet descriptions. Ecomorphological studies have incorporated gut length, mouth placement, mouth size, and jaw protrusibility to associate fishes with their diet (Labropoulou and Eleftheriou 1997, Castillo-Rivera et al. 2000, Platell and Potter 2001, Xie et al. 2001, Schafer et al. 2002). The feeding morphology of a species can give insight into particular inter- and intra-specific differences (or similarities) detected in the diet. Sex and maturity status (or size classes) are two of the most common factors related to differences in diet, and it is possible that changes in morphology related to these factors may play a role in these dietary differences.

Sexual dimorphism in elasmobranchs is fairly widespread, and is particularly common in the batoids. These differences are manifested as variation in body size, sexually dimorphic teeth and as the alar and malar thorns unique to adult male skates (Hubbs and Ishiyama 1968, McEachran et al. 1976, McCourt and Kerstitch 1980, Nordell 1994, Braccini and Chiaramonte 2002a, Ebert 2005). Thorns are believed to assist in maintaining the males' attachment to females during mating (Price 1967, Luer and Gilbert 1985). The importance of variation in the tooth morphology of skates, however, has been a contested matter. Feduccia and Slaughter (1974) suggested that differences in dentition were utilized to alleviate niche overlap between the sexes, but a reply by McEachran (1977) indicated that a diet study of more than 1600 skates from four species with sexually dimorphic teeth did not display any differences in diet between the sexes. Herman et al. (1995, 1996) noted that sexual and ontogenetic variation is common among the extant skate genera, but there was no discussion of how this variation related to diet. Conversely, the dentition of adult male and female *Bathyraja griseocauda* collected off Chile were not significantly different from one another (Sáez and Lamilla 2004). A dietary study of this species, from the Falkland Islands, found an ontogenetic shift in the diet, but did not examine possible gender differences (Brickle et al. 2003). Given the widespread nature of dental dimorphism in batoids, an examination of feeding morphology in concert with diet data could provide insight into the way in which morphology may influence diet.

There is a general lack of quantitative data concerning the relationship of feeding morphology and diet in skates, particularly on an intra-specific basis. Certain factors that may be important were suggested by Ellis et al. (1996): predator size, mouth structure, dentition and species distribution. Though these were used in an inter-specific comparative context, the first three factors also could be important in describing diet within a species relative to this variation. To date, studies by Braccini and Chiaramonte (2002b) and Braccini and Perez (2005) provide the most insight into these relationships for skates. These authors detected a mix of ontogenetic and sexual differences in morphology, and a distinct ontogenetic shift in diet, but no difference in diet was found between males and females. From these results, they suggested that such sexual dimorphisms probably did not play a role in determining diet, but that ontogenetic changes in diet could be related to a release from certain morphological constraints and/or better ability to find prey.

This study further tested if differences in the morphology of skates were correlated with diet. The oral and dental morphology of *Bathyraja kincaidii* was examined for intra-specific differences related to sex, maturity status and geographic zone of capture. These findings were then examined in conjunction with the results from the diet study to determine what role, if any, morphology has in determining intra-specific differences in diet.

MATERIALS AND METHODS

Sandpaper skates, *Bathyraja kincaidii*, were collected from June through October 2004 by the NMFS Northwest Fisheries Science Center West Coast Groundfish Survey. These specimens were collected from 49 hauls of varying depths, frozen onboard, and later thawed for processing and examination.

To examine the role morphology may play in explaining diet, the following were measured to the nearest 0.01 mm using dial calipers (Figure 17):

Mouth width (MW) - the distance between the labial flaps at either end of the mouth. The actual jaw is wider than this measurement, but the flaps constrain the mouth width to this distance.

Pre-oral length (POL) - in a relaxed state, the distance from the tip of the snout to the edge of the portion of the upper jaw just before it bears teeth.

Palatoquadrate protrusion (PROT) - the maximum distance the upper jaw can extend away from the ventrum, measured as the distance from the furthest point on the upper jaw, at full extension, to the labial skin flap where the palatoquadrate rests when retracted. Though this may not be a true measure of the actual amount of protrusion the skate uses, it is the maximum amount of which it is capable.

Additionally, teeth were examined to assess their possible role in dietary variation. The second tooth row to the left of the median row on the lower jaw of the skate was removed. Each tooth in the row was photographed digitally in both a lateral and dorsal aspect with the SPOT Advanced program v. 4.0.9 for Windows using a SPOT RT Slider 2.3.1 camera attached to a Leica MZ125 dissecting microscope. The photographs were analyzed with

Image-Pro Plus v. 4.1.1.2 calibrated to the appropriate zoom settings employed by the microscope. The following were measured to the nearest 0.1 nm (Figure 18):

Crown width (CW) - the distance between the lateral portions of the crown.

Crown length (CL) - the distance between the anterior and posterior portions of the crown.

Cusp height (CuH) - the perpendicular height of the cusp measured from the base of the crown to the tip of the cusp.

Cusp length (CuL) - the straight line distance from the anterior portion of the crown where the cusp erupts to the tip of the cusp.

Only those teeth which appeared to be complete and unworn were measured. If one aspect of a tooth was usable (e.g. base width) but another was broken or worn (e.g. cusp height), the valid measurement was determined and used and the broken or worn one was discarded. The measurements for each tooth in a row were used to calculate a mean value for each skate which was then used in the analysis. Preliminary analyses were conducted by creating log-log plots of disc width against the above seven measurements, as suggested by Alexander (1971), to discern how these features changed with the growth of the skate. The slope of the regression from each measurement was then compared with a slope of 1 (indicating isometric growth) using a t-test to determine statistical significance (Zar 1996). Similar to the diet data, a three factor multivariate analysis of covariance (MANCOVA) was used on the data to test the null hypotheses that there were no differences in either mouth or tooth morphology for the same sex, maturity status, and geographic zones described in the dietary analysis. Pillai’s Trace was again used as the reported test statistic owing to its robustness to the violations of parametric assumptions (Olson 1974). Evidence exists that the use of proportions in statistical testing of morphological measurements, especially in instances where the growth of structures is allometric, can lead to inaccurate results (Packard and Boardman 1987). Thus, the decision was made to use a MANCOVA with disc width (DW, the straight line measurement from the lateral tip of the left pectoral fin to the lateral tip of right pectoral fin) as the covariate to account for the variability in oral and dental measurements with the size of the skate. The use of total length (TL) as an estimator of body has size has been suggested to be superior to DW as it displays the least amount of measurement error compared with other body measurements (Francis 2006). However, preliminary log-log plots in which the morphometric measurements were regressed against DW and TL had similar slopes and r^2 values for both body size estimators (nearly all the regressions using DW had slightly greater r^2 values). Arcsine transformed proportions were not used because unlike the diet data, these measurements did not have any '0' data points. Tooth and mouth data were tested separately to examine any possible contrasts in how they varied. A sequential Bonferroni test was used to determine which geographic zones were different from one another when a morphological difference was found for that factor (Rice 1989). Aside from the multiple comparisons, all other statistical tests were conducted with SPSS 11.0.1 for Windows. The magnitude of effects (ω^2) for each factor was calculated for sex, maturity status, and geographic zone of capture (Graham and Edwards 2001).

RESULTS

Sample information

A total of 179 specimens was examined (80 females, 99 males), with a range of 1 to 12 skates collected per haul (mean 3.6 ± 0.4 SE); 20 skates were collected in zone 1, 36 from zone 2, 51 from zone 3 and 72 from zone 4 (Figure 19). Skates ranged in size from 236 to 628 mm TL (mean 487 ± 6.3 SE mm TL) (Figure 20). Skates were collected from 54.6 m to 589.2 m depth (mean 268.5 ± 20.5 SE m). The number of teeth examined in each tooth row ranged from 3 to 11 (mean 5.9 ± 0.1 SE). There were three skates for which tooth crown widths and lengths were not collected because all teeth in the row were damaged, however the cusps were intact and those measurements were used. Additionally, there was one skate for which no mouth measurements were taken.

Oral morphology

The preliminary log-log plots indicated that each of the three oral measurements varied with size in a different manner between the sexes (Figure 21). Mouth width displayed isometric growth (a constant rate of growth in relation to change in disc width) for females whereas this measurement was slightly positively allometric (the slope of the regression line >1) in males, meaning that mouth width increased proportionately as they grew (Table 7). There was an isometric relationship in the pre-oral length of females, but a negatively allometric (slope of regression line <1) one for males. This indicated that the pre-oral lengths of males became proportionately smaller as they grew. The protrusion distance of females displayed negative allometry, whereas males displayed a significantly positive allometric relationship. Also evident from the plots was that mouth width and pre-oral length growth had relatively low variances at any size, whereas protrusion distance had greater variation, especially for the large immature and mature skates of both sexes. These results indicate that as they grow, the amount of protrusion of which females are capable and the pre-oral length of males decreases proportionately, whereas both the protrusion distance and mouth width of males increase proportionately.

The assumptions for parametric tests were violated in this data set. Levene's test indicated that separately, pre-oral length ($p=0.081$) had equal variances among the groups, but mouth width ($p=0.017$) and protrusion distance ($p<0.001$) did not. Box's M test also indicated significant ($p<0.001$) differences in variance for all measurements together. An examination of the residuals indicated that the data for these measurements were distributed normally, though mature males had much greater protrusion distances than all other groups (Figure 22). The specific assumption of homogeneity of the regression coefficients was not violated ($p>0.33$ for each interaction).

There were significant differences in the oral measurements by sex, maturity status ($p<0.01$, df= 3, 159 for both factors), and geographic zone ($p<0.01$, df= 9, 483) with significant sex*maturity ($p<0.01$, df= 3, 159), sex*zone ($p=0.044$, df= 9, 483), maturity*zone ($p<0.01$, df= 9, 483), and sex*maturity*zone ($p=0.048$, df= 9, 483) interactions. Pairwise comparisons determined that male *B. kincaidii* had significantly greater mouth widths and protrusion distances, whereas females displayed greater pre-oral lengths. Mature skates had a greater amount of protrusion. Skates examined from zones 2 and 3 displayed similar size mouth widths, which were both greater than that of skates from zone 4. Skates from zone 2 had smaller pre-oral lengths than skates from zone 4. Finally, skates from the two southern-most zones, 1 and 2, displayed more upper jaw protrusion than those from zone 3, which in turn had greater distances than skates from zone 4.

The sex*maturity interaction was caused by pre-oral length and protrusion distance. As skates matured, the pre-oral length of females increased slightly whereas that of males decreased; the mean measurement of females was greater than that of males for both maturity states (Figure 23a). The protrusion distance of females decreased somewhat as they matured, but that of males increased significantly and remained greater than females.

The maturity*zone interaction was caused by both mouth width and protrusion distance. There was no change in the mouth width of immature skates throughout zones. Mature skates, however, displayed a significantly smaller mouth width in zone 4 (Figure 23b). The palatoquadrate protrusion measured in skates from zones 1 and 4 were not different between maturities, but in zones 2 and 3 mature skates displayed a much greater amount of protrusion. Immature skates showed a continual decrease in their protrusion distance with increasing latitude, whereas there was a slight increase in this measurement for mature skates from zone 1 to zone 2, which then decreased northward.

Though overall there was a significant sex*zone interaction, post-hoc tests indicated that no oral measurement was different between immature and mature skates ($p>0.24$ for all, Figure 23c). It may have been the multivariate combination of the three measurements that indicated a significant difference between the maturity states.

However, the mouth width of skates from zone 1 was similar between the sexes, but for the remaining three zones, males displayed greater mouth widths.

A post-hoc test indicated that only protrusion distance was responsible for the significant sex*maturity*zone interaction. The data indicated that in zones 1 and 3, immature males displayed greater amounts of protrusion than immature females, whereas in the other zones, immature skates of both sexes had nearly equal protrusion distances (Figure 24). The difference in the amount of protrusion between mature males and females in zone 2 also was greater than that of the other three zones. Additionally, the mean protrusion distance of females in zones 2 and 3 did not change as they matured, whereas that of females from zones 1 and 4 decreased sharply.

Factor fit indicated that sex explained the most amount of variance (32 %) in the mouth morphology data (Table 8). The sex*maturity interaction (ranked second) and geographic zone (ranked third) explained nearly equal amounts of morphological variance. The maturity*zone interaction ranked fourth in importance and together these four factors accounted for 52 % of the variation in oral morphology. The variance explained by the remaining three factors was < 2 %. There was nearly complete agreement between rank importance of factor fit and p-value, with the sex*maturity interaction and zone inverted as were the two factors explaining the least amount of variance, the sex*zone and sex*maturity*zone interactions.

Dental morphology

As with the oral measurements, log-log plots revealed that the growth of teeth varied between males and females (Figure 25). Tooth crown widths grew with negative allometry for both sexes, but the growth of male crown widths was less than females (Table 7). There was little difference in this measurement between large immature and mature males. The growth of crown lengths for both sexes was slightly negatively allometric. The growth of cusp height in females was isometric, but males had positive allometric growth of this feature. The cusp lengths of males and females grew with positive allometry, but the slope of the regression line for males was greater than that of females indicating the growth of this feature in males is proportionately greater than that of females. The values of all four of the measurements tended to continue to increase with size in mature females, but in mature males they leveled off; crown width and cusp height also displayed a large amount of variation with size. As the skates grew, the teeth of both sexes tended to get proportionately shorter and narrower. However the cusps of the teeth of both sexes grew proportionately longer, though more so in males; the cusps of males also become proportionately higher.

The assumptions of parametric tests also were violated in the tooth measurement data. Levene's test revealed that only cusp length data did not have equal variances among groups ($p<0.01$), but Box's M also was significant ($p<0.01$). The examination of the residuals indicated the data were normally distributed, though mature males had greater cusp heights and cusp lengths than all other sex-maturity groups (Figure 26). The regression coefficients were determined to be homogeneous for all treatments ($p>0.40$ for each interaction).

There were significant differences in dental morphology by sex, maturity status ($p<0.01$, df= 4, 156 for both), and geographic zone ($p<0.01$, df= 12, 474), along with a significant sex*maturity ($p<0.01$, df= 4, 156) interaction. Pairwise comparisons revealed that male *B. kincaidii* had greater cusp heights and cusp lengths, whereas females had greater crown widths. The crown widths of immature skates were greater than that of mature individuals but mature skates displayed greater cusp lengths. The cusp lengths of skates from zone 1 were greater than those of skates from zone 4.

Crown width, cusp height, and cusp length led to the significant sex*maturity interaction. Immature females displayed slightly greater crown widths than immature males, but the difference between the sexes increased significantly as they matured (Figure 27a). Immature males had slightly greater cusp heights and lengths than immature females, but similarly, the differences between the sexes were significantly greater for mature individuals. Of the mature skates, females displayed greater crown widths than males, whose mean measurement was less than that of immature skates, whereas mature males had greater cusp heights than those of mature females and immature skates. For both maturity stages, the cusp lengths of males were greater, but the difference between the sexes was much greater in mature skates.

Although there was not an overall significant maturity*zone interaction, a post-hoc test indicated that crown width differed significantly ($p=0.02$) among the zones. The crown width of skates from zones 1, 2, and 3 was slightly greater in immature skates (Figure 27b). However, the difference in this measurement between maturity states was much greater in zone 4. There appeared to be a trend of slightly increased crown widths from south (zone 1) to north (zone 3), but in zone 4 the crown width of mature skates decreased sharply.

There was also a significant interaction in cusp height (p=0.033) although the sex*maturity*zone interaction was not significant. In zones 2, 3, and 4, cusp heights of immature skates of both sexes were similar (Figure 28). As they matured, this measurement slightly decreased for females whereas that of males increased. Within zone 1, however, the cusp height of male teeth remained consistent as they matured but that of females increased, such that there was no difference between mature males and females.

Factor fit again revealed that sex explained the greatest amount of variance in the data (34 %) (Table 8). The sex*maturity interaction explained the second greatest amount of variation in dental morphology (12.6 %). Maturity status and geographic zone of capture together explained 4.3 % and were the final factors to explain > 1 % of the morphological variance in the data. In total, these four factors explained 51 % of the variance in tooth morphology whereas the remaining three factors accounted for 1.2 % of the explained variance. There was complete agreement between the rankings of factor fit and p-value.

DISCUSSION

There were clear, significant differences detected in the oral and dental morphology of *Bathyraja kincaidii* by all three of the main factors along with frequent interactions. However, of all the factors and interactions, sex accounted for >32 % of the variance in the examined morphology. This was manifested in differences for all examined variables except tooth crown length. Although there were distinct differences in morphology between the sexes, it is questionable whether differences detected in the diet were reflected by these differences in morphology. Recall that in the 2003 WCGS diet data, sex explained < 1 % of the variance, indicating the possibility that any differences detected in the diet were because of a large number of samples and may not be biologically relevant. The sex*maturity interaction explained the second most amount of variance in the morphology data, revealing that the link between these two factors played an important role in how morphology varied. Ontogenetic and sexually dimorphic differences in teeth are fairly widespread in elasmobranchs, with the teeth of mature males differing from that of immature males and females (Ebert et al. 1991, Herman et al. 1995, 1996, Motta and Wilga 2001). Yet again, this interaction explained < 1 % of the variance in the diet data.

Further evidence for the lack of a relationship between intra-specific variation in morphology and diet is evident from a comparison of the results of the tests on the morphological variables to those of the 2003 WCGS diet data. If the examined morphological variables had an effect on diet, differences among the factor levels of the former should correlate well with differences in the latter, either positively or negatively.

Male *B. kincaidii* had greater mouth widths, protrusion distances, and tooth cusp heights and lengths; males also ingested significantly more shrimp-like crustaceans and polychaetes. If there was a direct link between these significantly greater morphological measurements and a significant increase in these prey categories, it should be expected that for any other factor (maturity status, geographic zone and interactions), the relationship should remain (or display a significant decrease in a prey category in the case of a negative correlation). For example, protrusion distance and cusp length were greater in mature individuals, with both measurements displaying sex*maturity interactions whereby they increased significantly for males as they matured but decreased slightly for females. Yet, immature and mature skates did not differ in their consumption of shrimp-like crustaceans, nor was there a sex*maturity interaction for this prey. Furthermore, polychaetes were consumed more by immature skates, which is contrary to what would be predicted.

Likewise, there was no clear relationship between morphology and diet by geographic zone of capture. Mouth width, PROT, and CuL were greater in skates from the southern zones (1 and 2) than in the northern zones (3 and 4). Yet, shrimp-like crustaceans were more important to the diet of skates from the northern zones, and polychaetes only showed and increased importance in the diet of skates from zone 1. The only possible relationship supported by the data was that increased PROT and CuL may negatively affect the consumption of small benthic crustaceans, whereas an increase in CW would positively affect consumption. However, these relationships did not hold when accounting for variances in morphology by geographic zone. Intuitively, it is unlikely that these differences in morphology could be so strong as to lead to differences in diet for one factor (sex) but then not in another (maturity status, geographic zone) or their interactions. Unfortunately, the skates used in the diet and morphological tests were collected in different years. It could be possible, as discussed in the previous chapter, that temporal variation could allow for the diet of samples from 2004 to be different from those in 2003 (and thus have different relationships among the factors), but the degree to which this is the case is unknown.

Early in the examination of such relationships for skates, Feduccia and Slaughter (1974) suggested that differences in the dentition of skates were used to exploit different prey to reduce intra-specific competition, though no specific diet data was cited. McEachran (1977) issued a reply in which he refuted these claims. In his examination of more than 1600 specimens from four species with dimorphic teeth, none were found to display significant differences in the diet between the sexes for either maturity status.

This lack of a relationship between intra-specific differences in morphology and diet was noted in a study of the sandskate, *Psammobatis extenta* (Braccini and Chiaramonte 2002b). As males grew, POL was negatively allometric (based on total length, TL) whereas females displayed isometry for this measurement. The MW of males displayed positive allometry whereas females showed negative allometry and there were strong differences in dentition. Females retained a rounded cusp throughout their size range, whereas the teeth of males changed from a rounded to a pointed cusp, the change in tooth morphology with TL corresponding closely to the changes in maturity status with size (Braccini and Chiaramonte 2002a). Yet, given these differences in morphology between the sexes, there was no difference in the diets of males and females for this species, though an ontogenetic change was noted (Braccini and Perez 2005).

Additional, less exhaustive, studies on other batoids have led to similar conclusions. Smale and Cowley (1992) found that despite the morphological differences in the teeth of adult *Raja* cf. *clavata*, males and females consumed similar prey. A separate diet study of *R. clavata* from the Azores (Morato et al. 2003) further indicated similarity in the diet between the sexes, despite noted differences in their teeth. The teeth of mature male Patagonian skates, *Bathyraja macloviana*, display well developed cusps whereas the teeth of all females and immature males also have cusps, but are smaller and blunter than those of mature males (Scenna et al. 2006). There were no significant differences found in the proportions of the major prey categories between the sexes of mature individuals; Horn's Index was found to be 0.98 (a value of 1.00 indicates identical diets). A comparison of the diet of immature skates was not possible because of a lesser sample size. Teeth of the stingray *Dasyatis akajei* qualitatively differed between the sexes in mature individuals, whereas those of immature rays were similar (Taniuchi and Shimizu 1993). As they matured, males developed a long curved cusp whereas females had teeth of similar shape as the larger immature specimens, but with irregular pointed posterior edges. The stomach contents, based solely on frequency of occurrence, indicated some difference in the lower taxa consumed, but were similar in their major prey categories; changes in the diet with the onset of maturity were displayed. Based on the body of evidence from these previously published and the current results, it appears that variation in the feeding morphology of skates plays little, if any, role in any detectable intra-specific differences in their diet.

With the amount of evidence against the role of morphology accounting for intra-specific differences in diet of skates, it is likely these morphological differences serve another purpose, namely mating. Accounts of the courtship of skates and rays indicate that males bite and hold the pectoral fins of females before and during copulation (Price 1967, McCourt and Kerstitch 1980, Luer and Gilbert 1985). It is believed that the more cuspidate dentition of males allows them to better grip females to aid in reproduction. Round stingrays, *Urobatis halleri*, which have been documented engaging in such behavior, display sexually dimorphic teeth when mature (Nordell 1994). The teeth of adult males have a single, long cusp whereas females retain a molariform dentition similar to immature individuals. Adult females also have a relatively thicker disc than that of immature females, presumably to reduce damage that the sharper dentition of adult males may cause during copulatory biting; females with severely damaged discs were rarely seen.

Perhaps the most striking evidence for the primary role of sexual dental dimorphism in mating was found in the Atlantic stingray, *Dasyatis sabina* (Kajiura and Tricas 1996). Females displayed typical molariform batoid teeth with rounded crowns throughout the year. Males also had this tooth shape, but only for a few months during the year. From October to June, males developed strongly monocuspidate teeth which were significantly different from females. Like other batoids, even with such morphological differences, there was no difference in the diet between the sexes (Cook

1994 cited in Kajiura and Tricas 1996). The time at which these teeth began to emerge corresponded closely with the mating season. The authors determined that this change in dentition could benefit the male's gripping of the female's pectoral fin during mating, with a significant increase in force required to break a pectoral fin free from jaws bearing the cuspidate teeth compared with jaws bearing molariform teeth. Combined with this stronger grip, the greater mouth width of male *B. kincaidii* would allow for more surface area of a female's pectoral fin to be grasped by the jaws, further strengthening the hold and increasing the probability of successfully reproducing.

In addition to sex, geographic location was a source of morphological variation in *B. kincaidii*, more so for oral than dental measurements. Protrusion distance decreased with increasing latitude whereas mouth width generally increased with latitude, but it is unclear as to why only these measurements displayed a pattern. The pre-oral, pre-nasal, and pre-orbital lengths of *Raja miraletus* decreased clinally in samples from the Mediterranean Sea to South Africa (McEachran et al. 1989). It was suggested that varied hydrographic conditions served to isolate or reduce gene flow among the populations, giving rise to these morphological differences. Though the geographic area in the present study is smaller by comparison, perhaps the same conditions that led to the suggested geographical differences in abundance of their prey (see Chapter 1) could have also created semi-isolated populations of *B. kincaidii*, allowing these slight, but discernable, morphological differences to develop. A study of *Raja ocellata* in the northeast Atlantic revealed that specimens from an isolated allopatric population in the Gulf of St. Lawrence displayed some morphological characters that were dramatically different than specimens from a population sympatric with another skate, *Raja erinacea*, further south (McEachran and Martin 1977). The authors claimed this was evidence of character displacement to reduce competition in the sympatric population. In the present study, a similar possibility could exist given the geographically varied abundance of other skate species (such as other *Bathyraja* spp. and *Raja* spp.) along the eastern North Pacific (Pacific Shark Research Center 2007). This could further interact with geographically isolated populations (as postulated above), causing the varied morphological differences detected in this study.

This is the first study to consider cusp length in a quantitative analysis of tooth morphology in batoids. The cusp length measurement displayed the greatest difference among the factor levels and contributed the most amount of explained variance to the factor fit model. A quantitative examination of the teeth of the skate *Bathyraja griseocauda* revealed no significant differences in tooth width or height between mature males and females (Sáez and Lamilla 2004). Considering this, cusp length may be a more pertinent measurement to describe the important difference in tooth morphology between the sexes and as the skate matures. For species with recurved dentition similar to *B. kincaidii*, length, rather than height, better describes the size of the cusp relative to its purpose. An increase in length could increase the penetration depth of the tooth, which would allow for a better grip on the pectoral fin of the female. A firmer grasp would require an increase in the force necessary to break the two apart, as determined by Kajiura and Tricas (1996). By the same reasoning, greater cusp length also could increase the likelihood of capturing prey, at least those items that require capture or processing by the jaws as opposed to those that are engulfed and swallowed. If this benefit was employed by the skates, as indicated previously, not all groups with greater cusp lengths (males and mature skates) consistently fed more on any prey category.

This is also the first reported study to quantitatively examine palatoquadrate protrusion in skates within an ecological context. This measurement contributed either the most or the second most (behind pre-oral length) amount of variation explained by the factors. Protrusion is believed to play an important role in the feeding behavior of elasmobranchs (Motta and Wilga 2001). Batoids can display the greatest amount of protrusion of all elasmobranchs owing to their euhyostylic jaw suspension coupled with the lack of ligamentous connections to the cranium (Wilga et al. 2001, Wilga 2002). In this type, the jaws are suspended solely from an anteriorly directed hyomandibula; the jaws are free to move as far away from the head as is allowed by the skin that covers the labial portion of the palatoquadrate. Ecologically, the function of palatoquadrate protrusion in elasmobranchs is in need of further experimental study, but it appears the function can vary from taxa to taxa (see Motta and Wilga 2001 for summary). Early examination suggested that palatoquadrate protrusion served to facilitate the closing of jaws by decreasing the distance needed to be traveled by the Meckel's cartilage (lower jaw) and facilitated prey capture and processing (cutting or removing pieces of large prey) in certain species (Motta and Wilga 2001).

Information on the upper jaw protrusion in batoids has primarily come from functional analyses in three species. Whereas kinematic analyses were beyond the scope of this simple examination, such results give some insight to the findings of the present study. Each of the three taxa examined displayed distinct uses of palatoquadrate protrusion. The Atlantic guitarfish, *Rhinobatos lentiginosus,* used protrusion to capture food between its jaws by decreasing the amount of time for jaw closure and during processing manipulation (Wilga and Motta 1998). *Narcine brasiliensis*, the lesser electric ray, employed protrusion to quickly anterio-ventrally expand its jaws to decrease the distance to its food and during the winnowing process to aid in the removal of debris (Dean and Motta 2004). The exact use of protrusion during feeding by the cownose ray, *Rhinoptera bonasus,* is currently unclear, but it was suggested that ligamentous connections, used to strengthen the jaws for durophagy, may passively cause palatoquadrate protrusion with expansion of the lower jaw (Sasko et al. 2006).

Based on these results, increased protrusion distance can be added to the list of morphological features that benefit male skates in reproduction. It has been suggested that a wider mouth, shorter snout, more cuspidate teeth, and alar and malar spines work together to ensure a more successful mating attempt (Braccini and Chiaramonte 2002b). If used in a similar manner as *R. lentiginosus*, protrusion would increase the likelihood of capturing the female's pectoral fin by decreasing both the distance between individuals and the time it takes to close the jaw. As much as protrusion has been analyzed in a feeding context, studies are lacking in the reproductive aspect, which appears to be equally important in batoids. Though it would be quite difficult for *B. kincaidii*, given its habitat and available methods for live capture, a functional morphological study of batoids comparing the distance and timing of protrusion behavior in dietary and reproductive contexts would give important insight into any differences that exist between these two uses.

CONCLUSION

Among the three main factors, significant differences were found for a majority of the morphological measurements tested. Overall, the most common differences encountered were by sex (with differences in 6 of the 7 measurements), the sex*maturity interaction (5 measurements) and geographic zone of capture (4 measurements). These types of differences have frequently been reported in morphological studies on batoids. Of the geographical differences detected, only protrusion clearly indicated a latitudinal cline. The interaction of sex and maturity status provided an important basis for understanding morphological development in batoids. As males matured, there was a dramatic change in their morphology, with an increase in their mean mouth width, amount of upper jaw protrusion, tooth cusp height and length accompanied by a decrease in pre-oral length. Despite these differences in morphology between the sexes and maturity stages, they were not well correlated with changes in the diet for those factors. The data indicate that reproduction plays a greater role than diet in shaping intra-specific morphological variation. The extreme morphology of mature male skates allows them to better capture females and maintain the close contact needed for successful mating, without affecting their diet.

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Table 1. Taxonomic list of all items found in the stomachs of *Bathyraja kincaidii*.

- Annelida
  - Polychaeta
    - Aciculata
      - Onuphidae
        - *Mooreonuphis* sp.
        - *Onuphis* sp.
      - Lumbrineridae
        - *Lumbrineris* sp.
      - Nephtyidae
        - *Nephtys* sp.
    - Canalipalpata
      - Sternaspidae
        - *Sternaspis* cf. *fossor*
      - Terebellidae
    - Scolecida
      - Opheliidae
        - *Ophelina acuminata*
    - Unknown
      - Polychaete A
      - Polychaete E
- Echinodermata
  - Echinoidea
    - Strongylocentrotidae
      - *Strongylocentrotus* sp.
  - Ophiuroidea (unid)
- Mollusca
  - Bivalvia (unid)
  - Gastropoda
    - Cerithiidae
      - *Bittium* sp.
    - Columbellidae
      - *Amphissa bicolor*
      - *Astyris gausapata*
    - Acteonidae
      - *Rictaxis punctocaelatus*
  - Cephalopoda
    - Octopoda
      - Octopodidae
        - *Octopus rubescens*
    - Teuthida
      - Enoploteuthidae
        - *Abraliopsis felis*
      - Gonatidae
        - *Gonatus* sp.
      - Loliginidae
        - *Loligo opalescens*
- Crustacea
  - Eumalacostraca
    - Pericarida
      - Amphipoda
        - Gammaridea
          - Ampeliscidae
            - *Ampelisca unsocalae*
            - *Byblis bathyalis*
            - *Byblis* sp.
          - Eusiridae
            - *Rhachotropis clemens*
            - *Rhachotropis oculata*
          - Gammaridae
            - *Maera danae*
          - Isaeidae
            - *Photis lacia*
            - *Photomedeia prudens*
          - Liljeborgiidae
            - *Liljeborgia cota*
          - Lysianassidae
            - *Hippomedon columbianus*
            - *Lepidepecreum serraculum*
            - *Wecomedon wecomus*
          - Oedicerotidae
            - *Bathymedon* sp.
            - *Monoculodes glyconica*
          - Pardalascidae
            - *Nicippe tumida*
          - Phoxocephalidae
            - *Foxiphalus cognatus*

Table 1. continued

        - *Heterophoxus oculatus*
        - *Rhepoxynius* sp.
        - Synopiidae
        - *Syrrhoe longifrons*
        - *Syrrhoe* sp.
- Hyperiidea
    - Paraphronimidae
        - *Paraphronima crassipes*
        - *Paraphronima* sp.
- Caprellidea
    - Protellidae
        - *Mayerella banksia*
- Isopoda
    - Aegidae
        - *Rocinela angustata*
    - Idoteidae
        - *Synidotea angulata*
- Cumacea
    - Diastylidae
        - *Diastylis* sp.
    - Nannastacidae
        - *Campylaspis* sp.
- Mysida
    - Mysidae
        - *Boreomysis californica*
        - *Holmsiella anomala*
        - *Inusitatomysis insolita*
        - *Meterythrops robusta*
        - *Pseudomma* cf. *truncatum*
- Eucarida
- Euphasiacea
    - Euphausiidae
        - *Euphausia pacifica*
        - *Nematoscelis difficilis*
        - *Thysanoessa inermis*
        - *Thysanoessa raschi*
        - *Thysanoessa spinifera*
- Decapoda
- Dendrobranchiata
    - Sergestidae
        - *Sergestes similis*
- Caridea
    - Hippolytidae
        - *Eualus avinus*
        - *Eualus berkelyorum*
        - *Eualus macropthalmus*
        - *Eualus* sp.
        - *Heptacarpus* sp.
        - *Spirontocaris holmesi*
        - *Spirontocaris lamellicornis*
        - *Spirontocaris ochotensis*
        - *Spirontocaris sica*
        - *Spirontocaris* sp.
    - Pandalidae
        - *Pandalus jordani*
        - *Pandalus* sp.
    - Pasiphaeidae
        - *Pasiphaea pacifica*
    - Crangonidae
        - Crangon alaskensis
        - *Metacrangon spinosissima*
        - *Neocrangon communis*
        - *Neocrangon resima*
- Thalassinidea
    - Axiidae
        - *Calocarides quinqueseriatus*
        - *Calocarides spinulicauda*
        - *Calocarides* sp.
- Brachyura
    - Majoidea
    - Pisidae
        - *Chorilia longipes*
        - *Scyra acutifrons*
    - Pinnotheridae
        - *Pinnixa occidentalis*
        - *Pinnixa* sp.

Table 1. continued

- Anomura
  - Paguridae
    - *Pagurus granosimanus*
    - *Pagurus ochotensis*
    - *Pagurus tanneri*
    - *Pagurus* sp.
  - Galatheidae
    - *Munida quadrispina*
    - *Munida* sp.
- Chordata
  - Vertebrata
    - Teleostei
      - Bothidae
        - *Citharichthys* sp.
      - Clupeidae
        - *Clupea pallasi*
      - Merlucciidae
        - *Merluccius productus*
      - Myctophidae
        - *Diaphus theta*
        - *Stenobrachius leucopsarus*
        - *Tarletonbeania crenularis*
      - Pleuronectidae
        - *Eopsetta exilis*
      - Scorpaenidae
        - *Sebastes* sp.
      - Zoarcidae
        - *Lycodapis mandibularis*

Table 2. The importance and standard error (SE) of prey items consumed by *Bathyraja kincaidii* based on mean percentage number (%N), mean percentage mass (%M), frequency of occurrence (%FO), mean Index of Relative Importance (IRI), and mean percentage Index of Relative Importance (%IRI) from the combined Santa Cruz Lab and West Coast Groundfish Survey samples sources at four taxonomic scales.

	$\overline{\%N}$	SE	$\overline{\%M}$	SE	%FO	$\overline{IRI}$	$\overline{\%IRI}$
Polychaetes	**14.85**	**0.91**	**20.08**	**1.27**	**72.01**	**2515.10**	**16.57**
Polychaetes	**14.85**	**0.91**	**20.08**	**1.27**	**72.01**	**2515.10**	**25.16**
Onuphidae	4.70	0.49	6.77	0.73	32.45	372.33	6.42
Onuphidae	4.70	0.49	6.77	0.73	32.45	372.33	9.61
Lumbrinereidae	0.30	0.10	0.39	0.19	3.85	2.68	0.05
Lumbrinereidae	0.30	0.10	0.39	0.19	3.85	2.68	0.07
Nephtyidae	1.30	0.29	4.10	0.71	11.76	63.56	1.10
Nephtys sp.	1.30	0.29	4.10	0.71	11.76	63.56	1.64
Polychaete A	2.74	0.36	1.02	0.24	22.52	84.65	1.46
Polychaete A	2.74	0.36	1.02	0.24	22.52	84.65	2.19
Polychaete E	0.43	0.17	0.50	0.24	2.84	2.66	0.05
Polychaete E	0.43	0.17	0.50	0.24	2.84	2.66	0.07
Other polychaetes	0.04	0.03	0.07	0.06	0.61	0.07	0.00
Sternaspis cf. *fossor*	0.02	0.01	0.01	0.01	0.41	0.01	0.00
Terebellidae	0.03	0.03	0.06	0.06	0.20	0.02	0.00
Opheliidae	2.92	0.48	2.73	0.49	15.21	85.97	1.48
Opheliidae	2.92	0.48	2.73	0.49	15.21	85.97	2.22
Polychaetes (unid)	2.40	0.37	4.48	0.61	38.54	264.96	4.57
Polychaetes (unid)	2.40	0.37	4.48	0.61	38.54	264.96	6.84
Cephalopods	**4.40**	**0.41**	**9.16**	**0.98**	**38.95**	**527.85**	**3.48**
Cephalopods	**4.40**	**0.41**	**9.16**	**0.98**	**38.95**	**527.85**	**5.28**
Octopoda	0.46	0.09	1.39	0.31	7.71	14.28	0.25
Octopus rubescens	0.44	0.08	1.37	0.31	7.30	13.27	0.34
Octopoda (unid)	0.01	0.01	0.02	0.01	0.41	0.01	0.00
Teuthida	3.19	0.36	7.25	0.91	30.22	315.43	5.44
Abraliopsis felis	0.16	0.08	0.35	0.24	1.42	0.71	0.02
Gonatus sp.	0.52	0.15	0.66	0.28	3.65	4.32	0.11
Loligo opalescens	0.18	0.07	1.56	0.50	2.23	3.89	0.10
Teuthida (unid)	2.36	0.33	4.68	0.70	23.12	162.64	4.20
Cephalopods (unid)	0.75	0.19	0.52	0.24	6.49	8.21	0.14
Cephalopods (unid)	0.75	0.19	0.52	0.24	6.49	8.21	0.21
Small benthic crustaceans	**8.92**	**0.75**	**6.75**	**0.78**	**43.81**	**686.58**	**4.52**

Table 2. continued

	$\overline{\%N}$	SE	$\overline{\%M}$	SE	%FO	$\overline{\text{IRI}}$	$\overline{\%\text{IRI}}$
Amphipods	**7.91**	**0.70**	**4.95**	**0.67**	**39.96**	**514.21**	**5.14**
Gammarid amphipods	7.83	0.70	4.94	0.67	39.55	504.94	13.03
Other Amphipods	0.10	0.06	0.02	0.02	1.01	0.12	0.00
Paraphronima crassipes	0.01	0.01	0.00	0.00	0.20	0.00	0.00
Paraphronima sp.	0.05	0.05	0.02	0.02	0.20	0.01	0.00
Caprellid amphipods	0.04	0.02	0.00	0.00	0.61	0.02	0.00
Isopods	**0.92**	**0.18**	**1.76**	**0.41**	**9.53**	**25.57**	**0.26**
Isopods	0.92	0.18	1.76	0.41	9.53	25.57	0.44
Rocinela angustata	0.52	0.15	1.17	0.34	3.85	6.53	0.17
Synidotea angulata	0.03	0.02	0.01	0.00	0.41	0.01	0.00
Isopods (unid)	0.37	0.09	0.58	0.23	5.27	5.04	0.13
Cumaceans	**0.09**	**0.07**	**0.03**	**0.02**	**0.81**	**0.10**	**0.00**
Cumaceans	0.09	0.07	0.03	0.02	0.81	0.10	0.00
Campylaspis sp.	0.02	0.01	0.01	0.01	0.41	0.01	0.00
Diastylis sp.	0.07	0.07	0.02	0.02	0.20	0.02	0.00
Cumaceans (unid)	0.01	0.01	0.00	0.00	0.20	0.00	0.00
Shrimp-like crustaceans	**62.66**	**1.30**	**46.17**	**1.55**	**96.35**	**10485.96**	**69.08**
Euphausiids/ mysids	**21.28**	**1.47**	**11.02**	**1.03**	**47.87**	**1546.05**	**15.46**
Euphausiidae	18.78	1.47	9.77	1.00	36.51	1042.39	17.97
Euphausia pacifica	1.15	0.27	1.05	0.24	10.55	23.16	0.60
Nematoscelis difficilis	0.07	0.07	0.19	0.19	0.20	0.05	0.00
Thysanoessa inermis	0.03	0.03	0.01	0.01	0.20	0.01	0.00
Thysanoessa raschi	0.01	0.01	0.00	0.00	0.20	0.00	0.00
Thysanoessa spinifera	1.75	0.35	1.44	0.30	12.37	39.42	1.02
Euphausiidae (unid)	15.75	1.32	7.08	0.84	27.99	639.12	16.50
Mysidae	2.50	0.40	1.25	0.31	17.85	66.88	1.15
Boreomysis californica	0.07	0.07	0.05	0.05	0.41	0.05	0.00
Holmsiella anomala	0.42	0.15	0.20	0.08	2.64	1.64	0.04
Inusitatomysis insolita	0.07	0.06	0.02	0.01	0.61	0.06	0.00
Meterythrops robusta	0.01	0.01	0.00	0.00	0.61	0.01	0.00
Pseudomma cf. *truncatum*	1.03	0.28	0.30	0.13	6.90	9.22	0.24
Mysidae (unid)	0.89	0.22	0.67	0.26	7.71	12.01	0.31
Shrimp-like decapods (unid)	**25.65**	**1.41**	**16.00**	**1.12**	**49.09**	**2044.43**	**20.45**
Shrimp-like decapods (unid)	25.65	1.41	16.00	1.12	49.09	2044.43	35.25
Euphausiid/ mysid mix	2.58	0.61	1.50	0.42	4.06	16.55	0.43

Table 2. continued

	$\overline{\%N}$	**SE**	**$\overline{\%M}$**	**SE**	**%FO**	**$\overline{IRI}$**	**$\overline{\%IRI}$**
Euphausiid/ mysid/ shrimp mix	5.16	0.74	3.62	0.60	10.95	96.15	2.48
Euphausiid/ shrimp mix	15.87	1.27	9.33	0.93	29.41	741.15	19.13
Shrimp/ mysid mix	2.03	0.47	1.56	0.39	4.67	16.75	0.43
Shrimps	**15.74**	**1.15**	**19.15**	**1.33**	**53.35**	**1861.14**	**18.62**
Crangonidae	2.45	0.43	4.49	0.68	15.01	104.14	1.80
Crangon alaskensis	0.35	0.20	0.47	0.25	1.01	0.83	0.02
Metacrangon spinosissima	0.12	0.06	0.31	0.17	1.01	0.44	0.01
Neocrangon communis	0.69	0.14	1.64	0.33	6.90	16.10	0.42
Neocrangon resima	0.02	0.01	0.15	0.10	0.61	0.10	0.00
Crangonidae (unid)	1.27	0.28	1.91	0.44	8.72	27.81	0.72
Hippolytidae	2.94	0.42	3.05	0.46	17.85	106.84	1.84
Eualus avinus	0.11	0.07	0.05	0.04	1.01	0.16	0.00
Eualus berkelyorum	0.00	0.00	0.01	0.01	0.20	0.00	0.00
Eualus macropthalmus	0.23	0.10	0.65	0.25	1.62	1.43	0.04
Eualus sp.	0.25	0.07	0.10	0.05	4.06	1.43	0.04
Heptacarpus sp.	0.10	0.10	0.11	0.11	0.20	0.04	0.00
Spirontocaris holmesi	0.51	0.16	0.53	0.17	3.45	3.59	0.09
Spirontocaris lamellicornis	0.00	0.00	0.00	0.00	0.20	0.00	0.00
Spirontocaris ochotensis	0.00	0.00	0.00	0.00	0.20	0.00	0.00
Spirontocaris sica	0.64	0.25	0.74	0.27	2.03	2.80	0.07
Spirontocaris sp.	0.97	0.22	0.83	0.19	7.51	13.49	0.35
Hippolytidae (unid)	0.12	0.08	0.02	0.02	0.61	0.08	0.00
Pandalidae	0.55	0.14	1.62	0.40	5.88	12.73	0.22
Pandalus jordani	0.23	0.11	0.90	0.35	1.83	2.06	0.05
Pandalus sp.	0.32	0.08	0.71	0.21	4.26	4.41	0.11
Pasiphaea pacifica	0.62	0.15	1.42	0.38	6.09	12.44	0.21
Pasiphaea pacifica	0.62	0.15	1.42	0.38	6.09	12.44	0.32
Sergestes similis	1.68	0.27	3.12	0.49	14.60	70.06	1.21
Sergestes similis	1.68	0.27	3.12	0.49	14.60	70.06	1.81
Shrimps (unid)	7.50	0.83	5.46	0.73	21.50	278.65	4.80
Shrimps (unid)	7.50	0.83	5.46	0.73	21.50	278.65	7.19
Crabs	**2.95**	**0.45**	**6.86**	**0.87**	**24.95**	**244.90**	**1.61**
Crabs	**2.95**	**0.45**	**6.86**	**0.87**	**24.95**	**244.90**	**2.45**
Axiidae	0.94	0.38	2.04	0.58	2.84	8.47	0.15
Calocarides quinqueseriatus	0.44	0.24	1.06	0.42	1.62	2.44	0.06

Table 2. continued

	$\overline{\%N}$	SE	$\overline{\%M}$	SE	%FO	$\overline{IRI}$	$\overline{\%IRI}$
Calocarides spinulicauda	0.01	0.01	0.15	0.15	0.20	0.03	0.00
Calocarides sp.	0.49	0.29	0.83	0.38	1.01	1.34	0.03
Brachyura	0.19	0.08	0.36	0.15	2.64	1.46	0.03
Chorilia longipes	0.01	0.01	0.08	0.08	0.20	0.02	0.00
Scyra acutifrons	0.01	0.01	0.02	0.02	0.20	0.01	0.00
Majoidea (unid)	0.12	0.07	0.20	0.11	1.01	0.32	0.01
Pinnixa occidentalis	0.01	0.01	0.01	0.01	0.41	0.01	0.00
Pinnixa sp.	0.01	0.01	0.01	0.01	0.20	0.00	0.00
Brachyura (unid)	0.03	0.01	0.05	0.03	0.81	0.06	0.00
Paguridae	0.34	0.10	1.78	0.45	4.87	10.34	0.18
Pagurus granosimanus	0.03	0.02	0.24	0.15	0.61	0.16	0.00
Pagurus ochotensis	0.01	0.01	0.08	0.08	0.20	0.02	0.00
Pagurus tanneri	0.11	0.07	0.63	0.26	1.42	1.05	0.03
Pagurus sp.	0.12	0.06	0.58	0.28	1.42	0.99	0.03
Paguridae (unid)	0.08	0.03	0.26	0.17	1.22	0.41	0.01
Galatheidae	0.38	0.12	0.51	0.21	3.25	2.90	0.05
Munida quadrispina	0.33	0.12	0.46	0.20	2.43	1.94	0.05
Munida sp.	0.02	0.02	0.05	0.05	0.41	0.03	0.00
Galatheidae (unid)	0.02	0.02	0.00	0.00	0.41	0.01	0.00
Crab larvae	0.28	0.14	0.11	0.05	2.84	1.09	0.02
Crab larvae	0.28	0.14	0.11	0.05	2.84	1.09	0.03
Crabs (unid)	0.82	0.15	2.06	0.44	11.76	33.88	0.58
Crabs (unid)	0.82	0.15	2.06	0.44	11.76	33.88	0.87
Unidentifiable crustaceans	**0.88**	**0.32**	**0.88**	**0.37**	**4.46**	**7.87**	**0.05**
Unidentifiable crustaceans	**0.88**	**0.32**	**0.88**	**0.37**	**4.46**	**7.87**	**0.08**
Unidentifiable crustaceans	0.88	0.32	0.88	0.37	4.46	7.87	0.14
Unidentifiable crustaceans	0.88	0.32	0.88	0.37	4.46	7.87	0.20
Teleosts	**5.33**	**0.52**	**10.10**	**1.03**	**46.04**	**710.51**	**4.68**
Teleosts	**5.33**	**0.52**	**10.10**	**1.03**	**46.04**	**710.51**	**7.11**
Myctophidae	1.49	0.33	4.22	0.75	10.34	59.00	1.02
Diaphus theta	0.30	0.10	1.01	0.36	2.84	3.73	0.05
Stenobrachius leucopsarus	0.66	0.21	2.20	0.56	4.46	12.76	0.33
Tarletonbeania crenularis	0.31	0.21	0.74	0.35	1.01	1.06	0.01
Myctophidae (unid)	0.22	0.08	0.27	0.10	2.84	1.37	0.04
Pleuronectidae	0.18	0.06	0.41	0.17	3.25	1.92	0.03

Table 2. continued

	$\overline{\%N}$	**SE**	$\overline{\%M}$	**SE**	**%FO**	$\overline{IRI}$	$\overline{\%IRI}$
Eopsetta exilis	0.10	0.05	0.18	0.10	1.42	0.39	0.01
Pleuronectidae (unid)	0.08	0.03	0.23	0.13	2.03	0.64	0.02
Sebastes sp.	0.59	0.13	1.13	0.28	7.71	13.23	0.23
Sebastes sp.	0.59	0.13	1.13	0.28	7.71	13.23	0.34
Other Teleosts	0.39	0.18	0.84	0.38	1.83	2.26	0.04
Citharichthys sp.	0.00	0.00	0.00	0.00	0.20	0.00	0.00
Clupea pallasi	0.13	0.08	0.25	0.20	0.61	0.23	0.01
Lycodapis mandibularis	0.07	0.07	0.18	0.18	0.20	0.05	0.00
Merluccius productus	0.18	0.14	0.38	0.27	0.41	0.23	0.01
Gadidae	0.02	0.01	0.03	0.02	0.41	0.02	0.00
Teleosts (unid)	2.68	0.35	3.50	0.58	27.99	173.05	2.98
Teleosts (unid)	2.68	0.35	3.50	0.58	27.99	173.05	4.47
Echinoderms	**0.29**	**0.21**	**0.24**	**0.20**	**0.81**	**0.43**	**0.00**
Echinoderms	**0.29**	**0.21**	**0.24**	**0.20**	**0.81**	**0.43**	**0.00**
Echinoidea	0.28	0.21	0.23	0.20	0.61	0.31	0.01
Strongylocentrotus sp.	0.28	0.21	0.23	0.20	0.61	0.31	0.01
Ophiuroidea	0.01	0.01	0.01	0.01	0.20	0.00	0.00
Ophiuroidea (unid)	0.01	0.01	0.01	0.01	0.20	0.00	0.00
Molluscs	**0.16**	**0.06**	**0.24**	**0.13**	**2.83**	**1.12**	**0.01**
Molluscs	**0.16**	**0.06**	**0.24**	**0.13**	**2.83**	**1.12**	**0.01**
Bivalvia	0.00	0.00	0.00	0.00	0.20	0.00	0.00
Bivalve (unid)	0.00	0.00	0.00	0.00	0.20	0.00	0.00
Gastropoda	0.16	0.06	0.24	0.13	2.63	1.03	0.02
Amphissa bicolor	0.03	0.02	0.05	0.05	0.61	0.05	0.00
Astyris gausapata	0.07	0.05	0.07	0.06	1.01	0.15	0.00
Rictaxis punctocaelatus	0.01	0.01	0.00	0.00	0.20	0.00	0.00
Gastropoda (unid)	0.05	0.03	0.11	0.10	1.01	0.16	0.00

Table 3. The importance and standard error (SE) of prey items consumed by *Bathyraja kincaidii* based on mean percentage number (%N), mean percentage mass (%M), frequency of occurrence (%FO), mean Index of Relative Importance (IRI), and mean percentage Index of Relative Importance (%IRI) from Santa Cruz Lab samples at four taxonomic scales.

	$\overline{\%N}$	SE	$\overline{\%M}$	SE	%FO	$\overline{IRI}$	$\overline{\%IRI}$
Polychaetes	**11.50**	**1.62**	**20.69**	**2.54**	**65.91**	**2121.84**	**13.78**
Polychaetes	**11.50**	**1.62**	**20.69**	**2.54**	**65.91**	**2121.84**	**20.67**
Onuphidae	4.65	1.10	5.98	1.49	26.52	281.94	4.43
Onuphidae	4.65	1.10	5.98	1.49	26.52	281.94	5.78
Nephtyidae	1.16	0.40	8.35	1.88	16.67	158.52	2.49
Nephtys sp.	1.16	0.40	8.35	1.88	16.67	158.52	3.25
Polychaete A	1.22	0.43	0.86	0.60	10.61	22.14	0.35
Polychaete A	1.22	0.43	0.86	0.60	10.61	22.14	0.45
Opheliidae	3.57	1.14	3.36	1.19	12.12	84.04	1.32
Opheliidae	3.57	1.14	3.36	1.19	12.12	84.04	1.72
Polychaetes (unid)	0.89	0.23	2.14	0.73	21.21	64.24	1.01
Polychaetes (unid)	0.89	0.23	2.14	0.73	21.21	64.24	1.32
Cephalopods	**5.30**	**0.73**	**19.43**	**2.57**	**53.03**	**1311.37**	**8.52**
Cephalopods	**5.30**	**0.73**	**19.43**	**2.57**	**53.03**	**1311.37**	**12.77**
Octopoda	1.00	0.24	3.98	1.02	16.67	83.04	1.30
Octopus rubescens	0.98	0.24	3.94	1.02	15.91	78.27	1.60
Octopoda (unid)	0.02	0.02	0.04	0.04	0.76	0.05	0.00
Teuthida	3.10	0.51	13.99	2.40	39.39	673.57	10.58
Abraliopsis felis	0.42	0.27	0.77	0.73	3.79	4.51	0.09
Gonatus sp.	0.15	0.13	0.61	0.61	1.52	1.14	0.02
Loligo opalescens	0.65	0.27	4.66	1.65	6.82	36.15	0.74
Teuthida (unid)	1.89	0.37	7.96	1.72	27.27	268.70	5.51
Cephalopods (unid)	1.19	0.57	1.46	0.85	5.30	14.04	0.22
Cephalopods (unid)	1.19	0.57	1.46	0.85	5.30	14.04	0.29
Small benthic crustaceans	**8.27**	**1.62**	**5.79**	**1.53**	**28.79**	**404.85**	**2.63**
Amphipods	**7.58**	**1.53**	**4.27**	**1.27**	**28.03**	**332.01**	**3.23**
Gammarid amphipods	7.39	1.52	4.20	1.27	27.27	316.13	4.96
Gammarid amphipods	7.39	1.52	4.20	1.27	27.27	316.13	6.48
Other Amphipods	0.19	0.19	0.06	0.06	0.76	0.19	0.00
Paraphronima sp.	0.19	0.19	0.06	0.06	0.76	0.19	0.00
Isopods	**0.69**	**0.31**	**1.53**	**0.77**	**5.30**	**11.77**	**0.11**
Isopods	0.69	0.31	1.53	0.77	5.30	11.77	0.18
Rocinela angustata	0.34	0.19	0.73	0.43	3.79	4.07	0.08

Table 3. continued

	%$\overline{N}$	SE	%$\overline{M}$	SE	%FO	$\overline{IRI}$	%$\overline{IRI}$
Isopods (unid)	0.35	0.25	0.80	0.65	1.52	1.73	0.04
Shrimp-like crustaceans	**68.74**	**2.45**	**39.83**	**2.98**	**98.48**	**10693.08**	**69.46**
Euphausiids/ mysids	**42.97**	**3.49**	**19.91**	**2.48**	**64.39**	**4048.96**	**39.44**
Euphausiidae	40.79	3.58	17.94	2.43	56.82	3336.70	52.40
Euphausia pacifica	0.86	0.45	0.65	0.49	6.82	10.28	0.21
Thysanoessa raschi	0.04	0.04	0.01	0.01	0.76	0.04	0.00
Thysanoessa spinifera	5.49	1.22	4.02	0.99	28.79	273.93	5.61
Euphausiidae (unid)	34.39	3.22	13.25	2.03	50.76	2418.29	49.56
Mysidae	2.18	0.82	1.97	0.86	9.85	40.89	0.64
Boreomysis californica	0.25	0.25	0.18	0.18	0.76	0.33	0.01
Holmsiella anomala	0.56	0.32	0.29	0.19	3.79	3.23	0.07
Mysidae (unid)	1.37	0.63	1.50	0.78	6.06	17.37	0.36
Shrimp-like decapods (unid)	**14.15**	**2.33**	**8.64**	**1.81**	**28.03**	**638.68**	**6.22**
Shrimp-like decapods (unid)	14.15	2.33	8.64	1.81	28.03	638.68	10.03
Euphausiid/ mysid mix	2.22	1.06	1.40	0.92	4.55	16.45	0.34
Euphausiid/ mysid/ shrimp mix	1.17	0.69	0.84	0.49	2.27	4.57	0.09
Euphausiid/ shrimp mix	10.11	2.09	5.32	1.45	18.18	280.50	5.75
Shrimp/ mysid mix	0.65	0.39	1.07	0.64	3.03	5.24	0.11
Shrimps	**11.62**	**2.01**	**11.29**	**2.05**	**40.91**	**937.34**	**9.13**
Crangonidae	1.11	0.34	1.50	0.68	9.85	25.69	0.40
Neocrangon communis	0.39	0.19	0.90	0.59	3.79	4.88	0.10
Crangonidae (unid)	0.72	0.29	0.60	0.34	6.06	8.00	0.16
Hippolytidae	2.64	0.93	2.91	0.97	9.85	54.60	0.86
Heptacarpus sp.	0.38	0.38	0.40	0.40	0.76	0.59	0.01
Spirontocaris holmesi	0.21	0.15	0.33	0.18	3.03	1.62	0.03
Spirontocaris sica	1.18	0.65	1.42	0.76	3.79	9.83	0.20
Spirontocaris sp.	0.75	0.53	0.70	0.40	2.27	3.30	0.07
Hippolytidae (unid)	0.12	0.12	0.06	0.06	0.76	0.14	0.00
Pasiphaea pacifica	0.77	0.36	0.60	0.41	6.82	9.30	0.15
Pasiphaea pacifica	0.77	0.36	0.60	0.41	6.82	9.30	0.19
Sergestes similis	1.87	0.74	2.45	0.96	8.33	36.01	0.57
Sergestes similis	1.87	0.74	2.45	0.96	8.33	36.01	0.74
Shrimps (unid)	5.24	1.31	3.84	1.29	19.70	178.77	2.81
Shrimps (unid)	5.24	1.31	3.84	1.29	19.70	178.77	3.66
Crabs	**0.97**	**0.35**	**1.83**	**0.86**	**12.88**	**36.05**	**0.23**

Table 3. continued

	$\overline{\%N}$	SE	$\overline{\%M}$	SE	%FO	$\overline{IRI}$	$\overline{\%IRI}$
Crabs	**0.97**	**0.35**	**1.83**	**0.86**	**12.88**	**36.05**	**0.35**
Brachyura	0.21	0.16	0.29	0.24	2.27	1.14	0.02
Majoidea (unid)	0.18	0.15	0.24	0.24	1.52	0.64	0.01
Brachyura (unid)	0.03	0.03	0.04	0.04	0.76	0.05	0.00
Paguridae	0.25	0.23	0.28	0.23	1.52	0.80	0.01
Pagurus tanneri	0.23	0.23	0.23	0.23	0.76	0.35	0.01
Paguridae (unid)	0.02	0.02	0.05	0.05	0.76	0.05	0.00
Crabs (unid)	0.52	0.22	1.26	0.75	9.85	17.48	0.27
Crabs (unid)	0.52	0.22	1.26	0.75	9.85	17.48	0.36
Unidentifiable crustaceans	**0.57**	**0.39**	**0.09**	**0.05**	**6.06**	**4.02**	**0.03**
Unidentifiable crustaceans	**0.57**	**0.39**	**0.09**	**0.05**	**6.06**	**4.02**	**0.04**
Unidentifiable crustaceans	0.57	0.39	0.09	0.05	6.06	4.02	0.06
Unidentifiable crustaceans	0.57	0.39	0.09	0.05	6.06	4.02	0.08
Teleosts	**4.64**	**0.75**	**12.34**	**2.09**	**48.48**	**823.10**	**5.35**
Teleosts	**4.64**	**0.75**	**12.34**	**2.09**	**48.48**	**823.10**	**8.02**
Myctophidae	2.10	0.66	6.43	1.79	15.91	135.77	2.13
Diaphus theta	0.58	0.31	1.56	0.90	4.55	9.73	0.20
Stenobrachius leucopsarus	1.33	0.59	4.34	1.57	8.33	47.23	0.97
Myctophidae (unid)	0.19	0.08	0.54	0.28	4.55	3.31	0.07
Pleuronectidae	0.05	0.04	0.30	0.29	1.52	0.53	0.01
Pleuronectidae (unid)	0.05	0.04	0.30	0.29	1.52	0.53	0.01
Sebastes sp.	0.50	0.21	1.55	0.61	8.33	17.07	0.27
Sebastes sp.	0.50	0.21	1.55	0.61	8.33	17.07	0.35
Teleosts (unid)	1.99	0.40	4.05	1.17	26.52	160.21	2.52
Teleosts (unid)	1.99	0.40	4.05	1.17	26.52	160.21	3.28
Echinoderms	**0.03**	**0.03**	**0.01**	**0.01**	**0.75**	**0.03**	**0.00**
Echinoderms	**0.03**	**0.03**	**0.01**	**0.01**	**0.75**	**0.03**	**0.00**
Echinoidea	0.03	0.03	0.01	0.01	0.75	0.03	0.00
Strongylocentrotus sp.	0.03	0.03	0.01	0.01	0.75	0.03	0.00
Molluscs	**0.19**	**0.09**	**0.21**	**0.19**	**4.51**	**1.80**	**0.01**
Molluscs	**0.19**	**0.09**	**0.21**	**0.19**	**4.51**	**1.80**	**0.02**
Bivalvia	0.01	0.01	0.00	0.00	0.75	0.01	0.00
Bivalve (unid)	0.01	0.01	0.00	0.00	0.75	0.01	0.00

Table 3. continued

	$\overline{\%N}$	**SE**	**$\overline{\%M}$**	**SE**	**%FO**	**$\overline{IRI}$**	**$\overline{\%IRI}$**
Gastropoda	0.17	0.09	0.21	0.19	3.76	1.45	0.02
Amphissa bicolor	0.07	0.06	0.20	0.19	1.50	0.40	0.01
Astyris gausapata	0.04	0.04	0.00	0.00	0.75	0.03	0.00
Gastropoda (unid)	0.07	0.06	0.01	0.01	1.50	0.13	0.00

Table 4. The importance and standard error (SE) of prey items consumed by *Bathyraja kincaidii* based on mean percentage number (%N), mean percentage mass (%M), frequency of occurrence (%FO), mean Index of Relative Importance (IRI), and mean percentage Index of Relative Importance (%IRI) from West Coast Groundfish Survey samples at four taxonomic scales.

	$\overline{\%N}$	SE	$\overline{\%M}$	SE	%FO	$\overline{IRI}$	$\overline{\%IRI}$
Polychaetes	**16.08**	**1.09**	**19.85**	**1.47**	**74.24**	**2667.22**	**17.53**
Polychaetes	**16.08**	**1.09**	**19.85**	**1.47**	**74.24**	**2667.22**	**25.25**
Onuphidae	4.72	0.53	7.06	0.83	34.63	407.87	6.53
Onuphidae	4.72	0.53	7.06	0.83	34.63	407.87	10.06
Lumbrinereidae	0.41	0.13	0.54	0.25	5.26	5.00	0.08
Lumbrinereidae	0.41	0.13	0.54	0.25	5.26	5.00	0.12
Nephtyidae	1.35	0.37	2.55	0.66	9.97	38.89	0.62
Nephtys sp.	1.35	0.37	2.55	0.66	9.97	38.89	0.96
Polychaete A	3.29	0.46	1.08	0.25	26.87	117.46	1.88
Polychaete A	3.29	0.46	1.08	0.25	26.87	117.46	2.90
Polychaete E	0.59	0.23	0.69	0.32	3.88	4.96	0.08
Polychaete E	0.59	0.23	0.69	0.32	3.88	4.96	0.12
Other polychaetes	0.06	0.04	0.10	0.09	0.83	0.13	0.00
Sternaspis cf. *fossor*	0.02	0.02	0.01	0.01	0.55	0.02	0.00
Terebellidae	0.03	0.03	0.09	0.09	0.28	0.03	0.00
Opheliidae	2.69	0.51	2.50	0.51	16.34	84.70	1.36
Opheliidae	2.69	0.51	2.50	0.51	16.34	84.70	2.09
Polychaetes (unid)	2.95	0.50	5.34	0.79	44.88	371.63	5.95
Polychaetes (unid)	2.95	0.50	5.34	0.79	44.88	371.63	9.17
Cephalopods	**4.07**	**0.50**	**5.40**	**0.87**	**33.80**	**319.96**	**2.10**
Cephalopods	**4.07**	**0.50**	**5.40**	**0.87**	**33.80**	**319.96**	**3.03**
Octopoda	0.26	0.08	0.45	0.17	4.43	3.14	0.05
Octopus rubescens	0.25	0.08	0.44	0.17	4.16	2.84	0.07
Octopoda (unid)	0.01	0.01	0.01	0.01	0.28	0.01	0.00
Teuthida	3.22	0.46	4.78	0.86	26.87	214.99	3.44
Abraliopsis felis	0.06	0.06	0.19	0.19	0.55	0.14	0.00
Gonatus sp.	0.65	0.19	0.68	0.31	4.43	5.93	0.15
Loligo opalescens	0.01	0.01	0.43	0.31	0.55	0.25	0.01
Teuthida (unid)	2.54	0.42	3.48	0.72	21.61	129.92	3.20
Cephalopods (unid)	0.59	0.16	0.17	0.08	6.93	5.26	0.08
Cephalopods (unid)	0.59	0.16	0.17	0.08	6.93	5.26	0.13
Small Benthic Crustaceans	**9.16**	**0.83**	**7.10**	**0.90**	**49.31**	**801.65**	**5.27**

Table 4. continued

	$\overline{\%N}$	SE	$\overline{\%M}$	SE	%FO	$\overline{IRI}$	$\overline{\%IRI}$
Amphipods	**8.04**	**0.78**	**5.20**	**0.78**	**44.32**	**586.93**	**5.56**
Gammarid amphipods	7.98	0.78	5.20	0.78	44.04	580.52	9.29
Gammarid amphipods	7.98	0.78	5.20	0.78	44.04	580.52	14.32
Other Amphipods	0.06	0.03	0.00	0.00	1.11	0.07	0.00
Paraphronima crassipes	0.01	0.01	0.00	0.00	0.28	0.00	0.00
Caprellid amphipods	0.05	0.03	0.00	0.00	0.83	0.04	0.00
Isopods	**1.00**	**0.22**	**1.85**	**0.48**	**11.08**	**31.59**	**0.30**
Isopods	1.00	0.22	1.85	0.48	11.08	31.59	0.51
Rocinela angustata	0.58	0.20	1.33	0.44	3.88	7.44	0.18
Synidotea angulata	0.04	0.03	0.01	0.01	0.55	0.02	0.00
Isopods (unid)	0.38	0.09	0.51	0.20	6.65	5.89	0.15
Cumaceans	**0.12**	**0.09**	**0.04**	**0.03**	**1.11**	**0.18**	**0.00**
Cumaceans	0.12	0.09	0.04	0.03	1.11	0.18	0.00
Campylaspis sp.	0.02	0.02	0.01	0.01	0.55	0.02	0.00
Diastylis sp.	0.09	0.09	0.02	0.02	0.28	0.03	0.00
Cumaceans (unid)	0.01	0.01	0.00	0.00	0.28	0.00	0.00
Shrimp-like crustaceans	**60.44**	**1.52**	**48.49**	**1.81**	**95.29**	**10379.76**	**68.23**
Euphausiids/ mysids	**13.35**	**1.32**	**7.77**	**1.03**	**41.83**	**883.19**	**8.36**
Euphausiidae	10.73	1.28	6.79	1.00	29.09	509.47	8.16
Euphausia pacifica	1.25	0.32	1.20	0.27	11.91	29.14	0.72
Nematoscelis difficilis	0.09	0.09	0.26	0.26	0.28	0.10	0.00
Thysanoessa inermis	0.05	0.05	0.01	0.01	0.28	0.02	0.00
Thysanoessa spinifera	0.38	0.10	0.49	0.17	6.37	5.55	0.14
Euphausiidae (unid)	8.94	1.18	4.82	0.84	19.67	270.63	6.68
Mysidae	2.62	0.45	0.98	0.29	20.78	74.76	1.20
Boreomysis californica	0.00	0.00	0.00	0.00	0.28	0.00	0.00
Holmsiella anomala	0.37	0.16	0.17	0.09	2.22	1.20	0.03
Inusitatomysis insolita	0.10	0.08	0.02	0.02	0.83	0.10	0.00
Meterythrops robusta	0.02	0.01	0.01	0.00	0.83	0.02	0.00
Pseudomma cf. *truncatum*	1.41	0.38	0.42	0.17	9.42	17.19	0.42
Mysidae (unid)	0.71	0.19	0.37	0.21	8.31	8.98	0.22
Shrimp-like decapods (unid)	**29.85**	**1.68**	**18.70**	**1.35**	**56.79**	**2756.79**	**26.10**
Shrimp-like decapods (unid)	29.85	1.68	18.70	1.35	56.79	2756.79	44.14
Euphausiid/ mysid mix	2.72	0.74	1.53	0.47	3.88	16.48	0.41
Euphausiid/ mysid/ shrimp mix	6.61	0.96	4.64	0.80	14.13	158.98	3.92

Table 4. continued

	$\overline{\%N}$	SE	$\overline{\%M}$	SE	%FO	$\overline{IRI}$	$\overline{\%IRI}$
Euphausiid/ shrimp mix	17.98	1.54	10.79	1.15	33.52	964.39	23.79
Shrimp/ mysid mix	2.54	0.63	1.74	0.47	5.26	22.49	0.55
Shrimps	**17.24**	**1.38**	**22.03**	**1.63**	**57.89**	**2273.29**	**21.52**
Crangonidae	2.94	0.57	5.58	0.89	16.90	143.99	2.31
Crangon alaskensis	0.47	0.28	0.64	0.35	1.39	1.55	0.04
Metacrangon spinosissima	0.17	0.09	0.42	0.24	1.39	0.81	0.02
Neocrangon communis	0.80	0.17	1.92	0.40	8.03	21.82	0.54
Neocrangon resima	0.02	0.01	0.21	0.13	0.83	0.19	0.00
Crangonidae (unid)	1.48	0.37	2.39	0.58	9.70	37.54	0.93
Hippolytidae	3.04	0.46	3.10	0.52	20.78	127.70	2.04
Eualus avinus	0.15	0.10	0.07	0.06	1.39	0.31	0.01
Eualus berkelyorum	0.00	0.00	0.01	0.01	0.28	0.00	0.00
Eualus macropthalmus	0.31	0.14	0.89	0.34	2.22	2.66	0.07
Eualus sp.	0.34	0.09	0.14	0.06	5.54	2.67	0.07
Spirontocaris holmesi	0.62	0.21	0.61	0.22	3.60	4.41	0.11
Spirontocaris lamellicornis	0.00	0.00	0.00	0.00	0.28	0.00	0.00
Spirontocaris ochotensis	0.00	0.00	0.01	0.01	0.28	0.00	0.00
Spirontocaris sica	0.45	0.23	0.49	0.24	1.39	1.30	0.03
Spirontocaris sp.	1.05	0.23	0.88	0.22	9.42	18.13	0.45
Hippolytidae (unid)	0.11	0.09	0.01	0.01	0.55	0.07	0.00
Pandalidae	0.75	0.19	2.21	0.55	8.03	23.74	0.38
Pandalus jordani	0.31	0.15	1.23	0.48	2.49	3.84	0.09
Pandalus sp.	0.44	0.11	0.97	0.28	5.82	8.22	0.20
Pasiphaea pacifica	0.57	0.15	1.73	0.50	5.82	13.34	0.21
Pasiphaea pacifica	0.57	0.15	1.73	0.50	5.82	13.34	0.33
Sergestes similis	1.61	0.25	3.37	0.58	16.90	83.99	1.34
Sergestes similis	1.61	0.25	3.37	0.58	16.90	83.99	2.07
Shrimps (unid)	8.33	1.03	6.05	0.88	22.16	318.66	5.10
Shrimps (unid)	8.33	1.03	6.05	0.88	22.16	318.66	7.86
Crabs	**3.67**	**0.60**	**8.71**	**1.13**	**29.36**	**363.55**	**2.39**
Crabs	**3.67**	**0.60**	**8.71**	**1.13**	**29.36**	**363.55**	**3.44**
Axiidae	1.29	0.51	2.78	0.79	3.88	15.79	0.25
Calocarides quinqueseriatus	0.60	0.33	1.45	0.57	2.22	4.55	0.11
Calocarides spinulicauda	0.01	0.01	0.20	0.20	0.28	0.06	0.00
Calocarides sp.	0.68	0.40	1.13	0.52	1.39	2.50	0.06

Table 4. continued

	$\overline{\%N}$	SE	$\overline{\%M}$	SE	%FO	$\overline{IRI}$	$\overline{\%IRI}$
Brachyura	0.18	0.09	0.39	0.19	2.77	1.60	0.03
Chorilia longipes	0.02	0.02	0.11	0.11	0.28	0.04	0.00
Scyra acutifrons	0.02	0.02	0.03	0.03	0.28	0.01	0.00
Majoidea (unid)	0.10	0.08	0.18	0.12	0.83	0.23	0.01
Pinnixa occidentalis	0.02	0.01	0.01	0.01	0.55	0.02	0.00
Pinnixa sp.	0.01	0.01	0.01	0.01	0.28	0.01	0.00
Brachyuran (unid)	0.03	0.02	0.05	0.03	0.83	0.07	0.00
Paguridae	0.37	0.11	2.33	0.60	6.09	16.49	0.26
Pagurus granosimanus	0.04	0.02	0.33	0.21	0.83	0.30	0.01
Pagurus ochotensis	0.01	0.01	0.11	0.11	0.28	0.03	0.00
Pagurus tanneri	0.07	0.03	0.77	0.34	1.66	1.40	0.03
Pagurus sp.	0.16	0.09	0.79	0.38	1.94	1.84	0.05
Paguridae (unid)	0.10	0.05	0.33	0.24	1.39	0.60	0.01
Galatheidae	0.52	0.16	0.70	0.28	4.43	5.41	0.09
Munida quadrispina	0.45	0.16	0.63	0.28	3.32	3.62	0.09
Munida sp.	0.03	0.02	0.06	0.06	0.55	0.05	0.00
Galatheidae (unid)	0.03	0.02	0.01	0.00	0.55	0.02	0.00
Crab larvae	0.38	0.19	0.15	0.07	3.88	2.03	0.03
Crab larvae	0.38	0.19	0.15	0.07	3.88	2.03	0.05
Crabs (unid)	0.93	0.19	2.35	0.53	12.47	40.93	0.66
Crabs (unid)	0.93	0.19	2.35	0.53	12.47	40.93	1.01
Unidentifiable crustaceans	**1.00**	**0.42**	**1.17**	**0.50**	**4.16**	**9.03**	**0.06**
Unidentifiable crustaceans	**1.00**	**0.42**	**1.17**	**0.50**	**4.16**	**9.03**	**0.09**
Unidentifiable crustaceans	1.00	0.42	1.17	0.50	4.16	9.03	0.14
Unidentifiable crustaceans	1.00	0.42	1.17	0.50	4.16	9.03	0.22
Teleosts	**5.58**	**0.65**	**9.28**	**1.18**	**45.15**	**671.23**	**4.41**
Teleosts	**5.58**	**0.65**	**9.28**	**1.18**	**45.15**	**671.23**	**6.35**
Myctophidae	1.26	0.37	3.40	0.79	8.31	38.80	0.62
Diaphus theta	0.20	0.08	0.81	0.36	2.22	2.24	0.06
Stenobrachius leucopsarus	0.42	0.19	1.41	0.50	3.05	5.59	0.14
Tarletonbeania crenularis	0.42	0.29	1.01	0.47	1.39	1.98	0.05
Myctophidae (unid)	0.23	0.11	0.17	0.08	2.22	0.87	0.02
Pleuronectidae	0.23	0.08	0.45	0.20	3.88	2.64	0.04
Eopsetta exilis	0.14	0.06	0.24	0.14	1.94	0.74	0.02
Pleuronectidae (unid)	0.09	0.04	0.21	0.15	2.22	0.67	0.02

Table 4. continued

	$\overline{\%N}$	SE	$\overline{\%M}$	SE	%FO	$\overline{IRI}$	$\overline{\%IRI}$
Sebastes sp.	0.62	0.16	0.98	0.31	7.48	11.93	0.19
Sebastes sp.	0.62	0.16	0.98	0.31	7.48	11.93	0.29
Other Teleosts	0.54	0.24	1.15	0.52	2.49	4.21	0.07
Citharichthys sp.	0.00	0.00	0.00	0.00	0.28	0.00	0.00
Clupea pallasi	0.17	0.12	0.34	0.28	0.83	0.43	0.01
Lycodapis mandibularis	0.09	0.09	0.25	0.25	0.28	0.09	0.00
Merluccius productus	0.24	0.19	0.52	0.37	0.55	0.42	0.01
Gadidae	0.02	0.02	0.04	0.03	0.55	0.03	0.00
Teleosts (unid)	2.93	0.45	3.30	0.67	28.53	177.85	2.85
Teleosts (unid)	2.93	0.45	3.30	0.67	28.53	177.85	4.39
Echinodermata	**0.38**	**0.29**	**0.33**	**0.28**	**0.55**	**0.39**	**0.00**
Echinodermata	**0.38**	**0.29**	**0.33**	**0.28**	**0.55**	**0.39**	**0.00**
Echinoidea	0.37	0.29	0.31	0.28	0.55	0.38	0.01
Strongylocentrotus sp.	0.37	0.29	0.31	0.28	0.55	0.38	0.01
Ophiuroidea	0.01	0.01	0.01	0.01	0.28	0.01	0.00
Ophiuroidea (unid)	0.01	0.01	0.01	0.01	0.28	0.01	0.00
Mollusca	**0.15**	**0.08**	**0.25**	**0.16**	**2.22**	**0.88**	**0.01**
Mollusca	**0.15**	**0.08**	**0.25**	**0.16**	**2.22**	**0.88**	**0.01**
Gastropoda	0.15	0.08	0.25	0.16	2.22	0.88	0.01
Amphissa bicolor	0.01	0.01	0.00	0.00	0.28	0.00	0.00
Astyris gausapata	0.09	0.07	0.10	0.08	1.11	0.21	0.01
Rictaxis punctocaelatus	0.01	0.01	0.00	0.00	0.28	0.00	0.00
Gastropoda (unid)	0.04	0.03	0.14	0.13	0.83	0.15	0.00

Table 5. 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* taken in SCL samples.

Gravimetric Data

Factor	ω^2	**rank**	**p-value**	**rank**
Sex	2.05	2	0.03	4
Maturity status	2.02	3	1.05×10^{-7}	1
Oceanographic 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

Factor	ω^2	**rank**	**p-value**	**rank**
Sex	0.04	6	0.53	6
Maturity status	14.28	2	3.72×10^{-17}	1
Oceanographic 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			

Table 6. 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* taken in WCGS samples.

Gravimetric Data

Factor	**ω^2**	**rank**	**p-value**	**rank**
Sex	0.62	4	1.93×10^{-4}	2
Maturity status	0.78	3	0.02	5
Geographic zone	2.00	1	4.74×10^{-6}	1
Sex*maturity	0.56	5	0.02	4
Sex*zone	0.50	6	0.38	6
Maturity*zone	1.63	2	7.9×10^{-4}	3
Sex*maturity*zone	0.21	7	0.53	7
Error	93.70			

Numeric Data

Factor	**ω^2**	**rank**	**p-value**	**rank**
Sex	0.35	6	0.05	5
Maturity status	1.14	3	3.38×10^{-5}	1
Geographic zone	4.94	1	1.41×10^{-4}	2
Sex*maturity	0.68	4	0.01	4
Sex*zone	0.01	7	0.97	7
Maturity*zone	2.18	2	6.51×10^{-3}	3
Sex*maturity*zone	0.59	5	0.71	6
Error	90.12			

Table 7. Linear regression slopes, resultant t-test and p-values and description of the proportional growth of the seven morphological measurements taken on *Bathyraja kincaidii*

	Female				**Male**			
Measurement	**Slope**	**t -value**	**p-value**	**Growth**	**Slope**	**t -value**	**p-value**	**Growth**
MW	1.01	0.89	>0.20	Isometry	1.08	2.72	<0.01	+ Allometry
POL	0.97	1.61	>0.10	Isometry	0.70	6.40	<0.01	- Allometry
PROT	0.82	4.15	<0.01	- Allometry	1.71	6.36	<0.01	+ Allometry
CW	0.74	5.24	<0.01	- Allometry	0.21	19.24	<0.01	- Allometry
CL	0.92	2.64	0.01	- Allometry	0.81	4.87	<0.01	- Allometry
CuH	0.98	1.16	>0.20	Isometry	1.30	4.73	<0.01	+ Allometry
CuL	1.42	4.83	<0.01	+ Allometry	2.41	7.58	<0.01	+ Allometry

Table 8. 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 MANCOVA performed on the three oral and four dental morphology measurements taken on *Bathyraja kincaidii*

Oral morphology

Factor	**ω^2**	**rank**	**p-value**	**rank**
Sex	32.01	1	8.11×10^{-30}	1
Maturity status	0.97	5	5.95×10^{-3}	5
Geographic zone	8.41	3	1.57×10^{-14}	2
Sex-maturity	8.93	2	5.24×10^{-13}	3
Sex-zone	0.15	7	0.04	6
Maturity-zone	3.01	4	9.78×10^{-7}	4
Sex-maturity-zone	0.61	6	0.048	7
Error	45.92			

Dental morphology

Factor	**ω^2**	**rank**	**p-value**	**rank**
Sex	34.05	1	7.39×10^{-40}	1
Maturity status	2.52	3	1.01×10^{-6}	3
Geographic zone	1.77	4	1.28×10^{-3}	4
Sex-maturity	12.58	2	3.15×10^{-22}	2
Sex-zone	0.01	7	0.77	7
Maturity-zone	0.73	5	0.07	5
Sex-maturity-zone	0.41	6	0.27	6
Error	47.93			

Figure 1. Area map of central California indicating locations and number of *Bathyraja kincaidii* captured in Santa Cruz Lab trawls whose stomachs were used in the diet analysis. Size of bar indicates length of trawl.

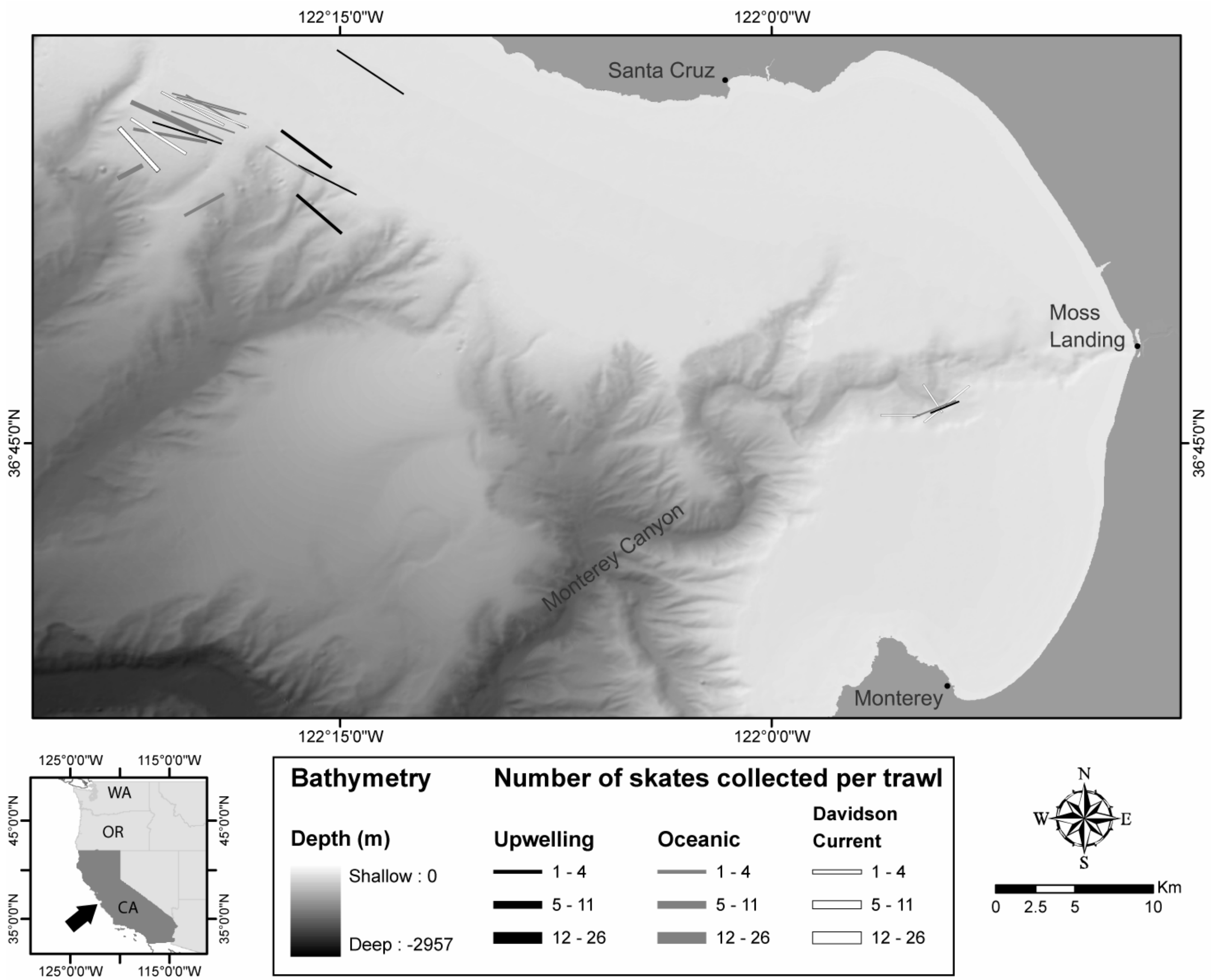
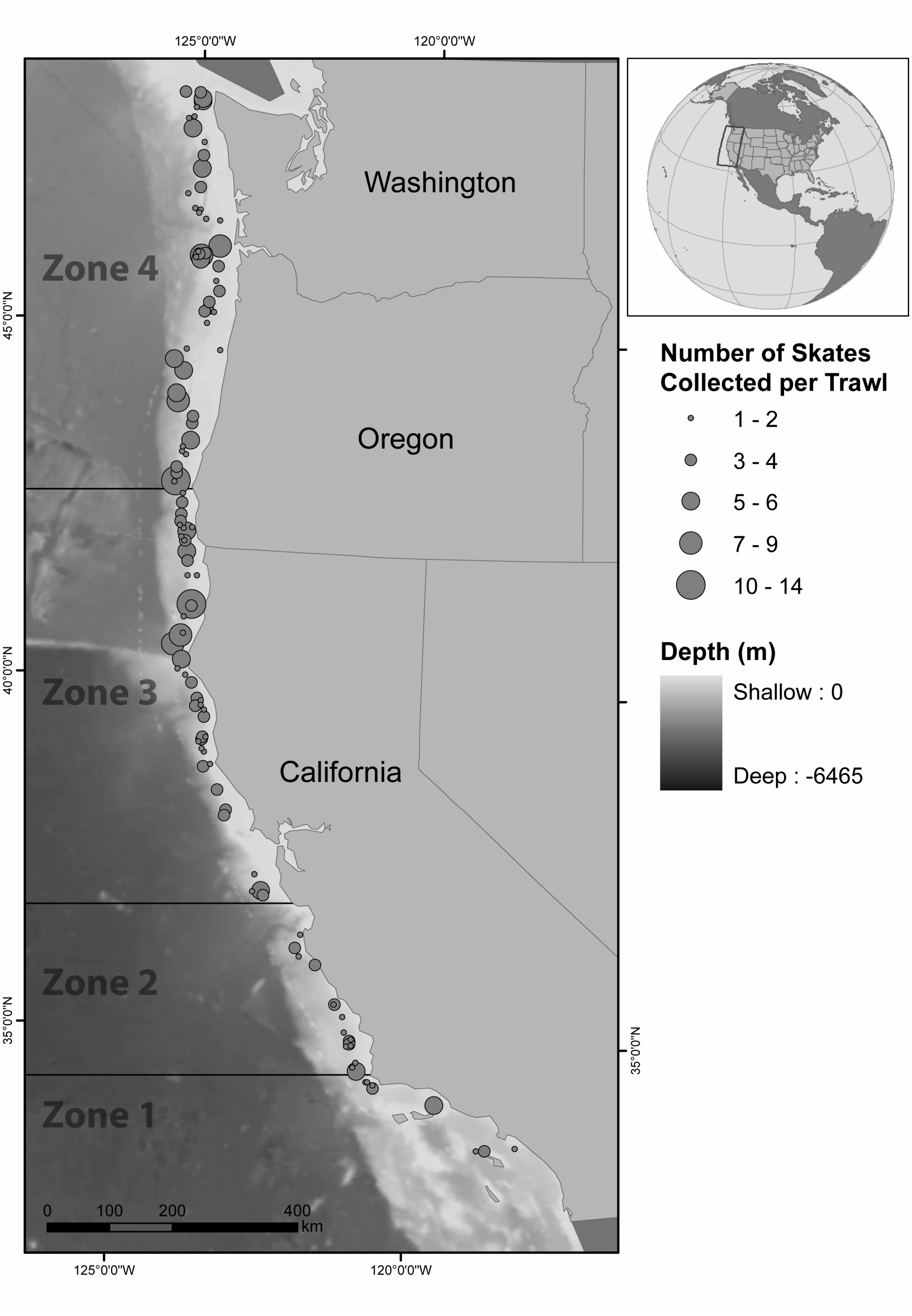

122°15'0"W
122°0'0"W
36°45'0"N
Santa Cruz
Moss Landing
Monterey Canyon
Monterey
125°0'0"W
115°0'0"W
45°0'0"N
35°0'0"N
WA
OR
CA
Bathymetry
Depth (m)
Shallow : 0
Deep : -2957
Number of skates collected per trawl
Upwelling
Oceanic
Davidson Current
1 - 4
5 - 11
12 - 26
N
E
S
W
0
2.5
5
10
Km

Figure 2. Area map of the eastern North Pacific indicating locations and number of *Bathyraja kincaidii* captured in West Coast Groundfish Survey trawls whose stomachs were used in the diet analysis.



125°0'0"W
120°0'0"W
45°0'0"N
40°0'0"N
35°0'0"N
Washington
Oregon
California
Zone 4
Zone 3
Zone 2
Zone 1
0
100
200
400
km
Number of Skates Collected per Trawl
1 - 2
3 - 4
5 - 6
7 - 9
10 - 14
Depth (m)
Shallow : 0
Deep : -6465

Figure 3. Histogram of the total lengths of male and female *Bathyraja kincaidii* collected in Santa Cruz Lab trawls.

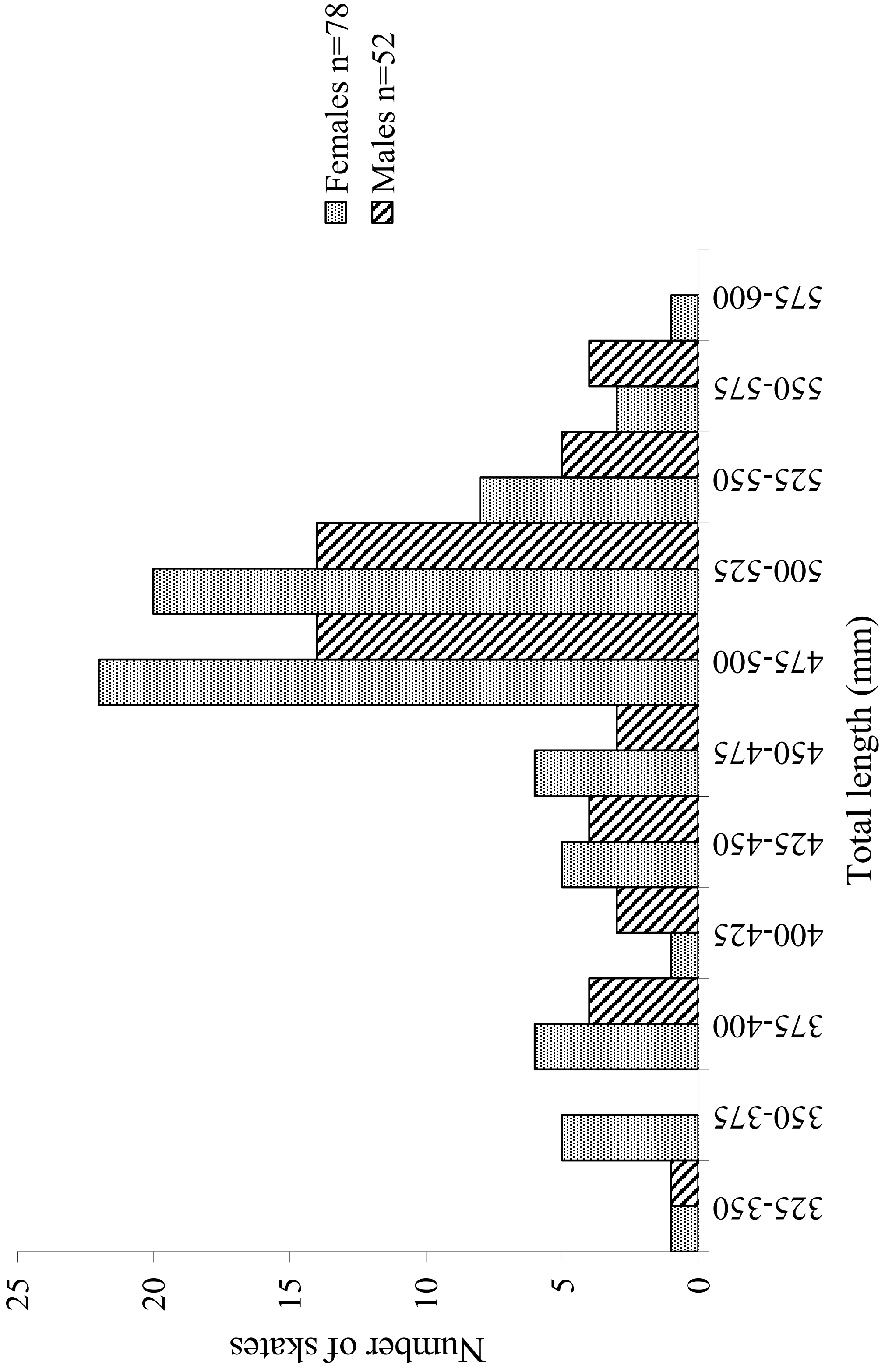

Females n=78
Males n=52
Number of skates
0
5
10
15
20
25
325-350
350-375
375-400
400-425
425-450
450-475
475-500
500-525
525-550
550-575
575-600
Total length (mm)

Figure 4. Cumulative prey curve for all prey items collected in *Bathyraja kincaidii* stomach samples from Santa Cruz Lab trawls. Error bars represent the standard deviation of the plotted mean generated from 100 resamplings.

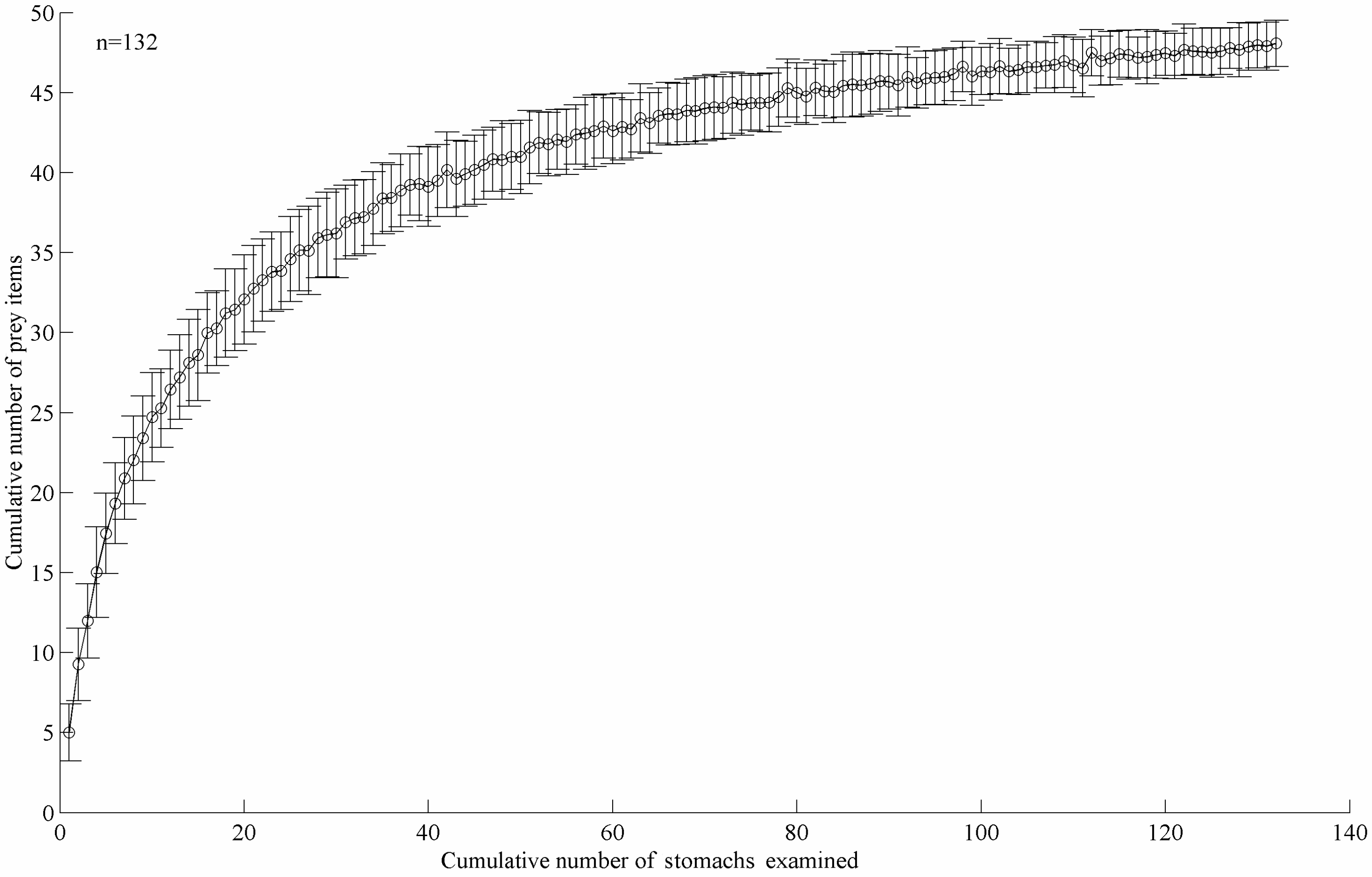

n=132
Cumulative number of prey items
0
5
10
15
20
25
30
35
40
45
50
Cumulative number of stomachs examined
0
20
40
60
80
100
120
140

Figure 5. Histogram of the total lengths of male and female *Bathyraja kincaidii* collected in West Coast Groundfish Survey trawls.

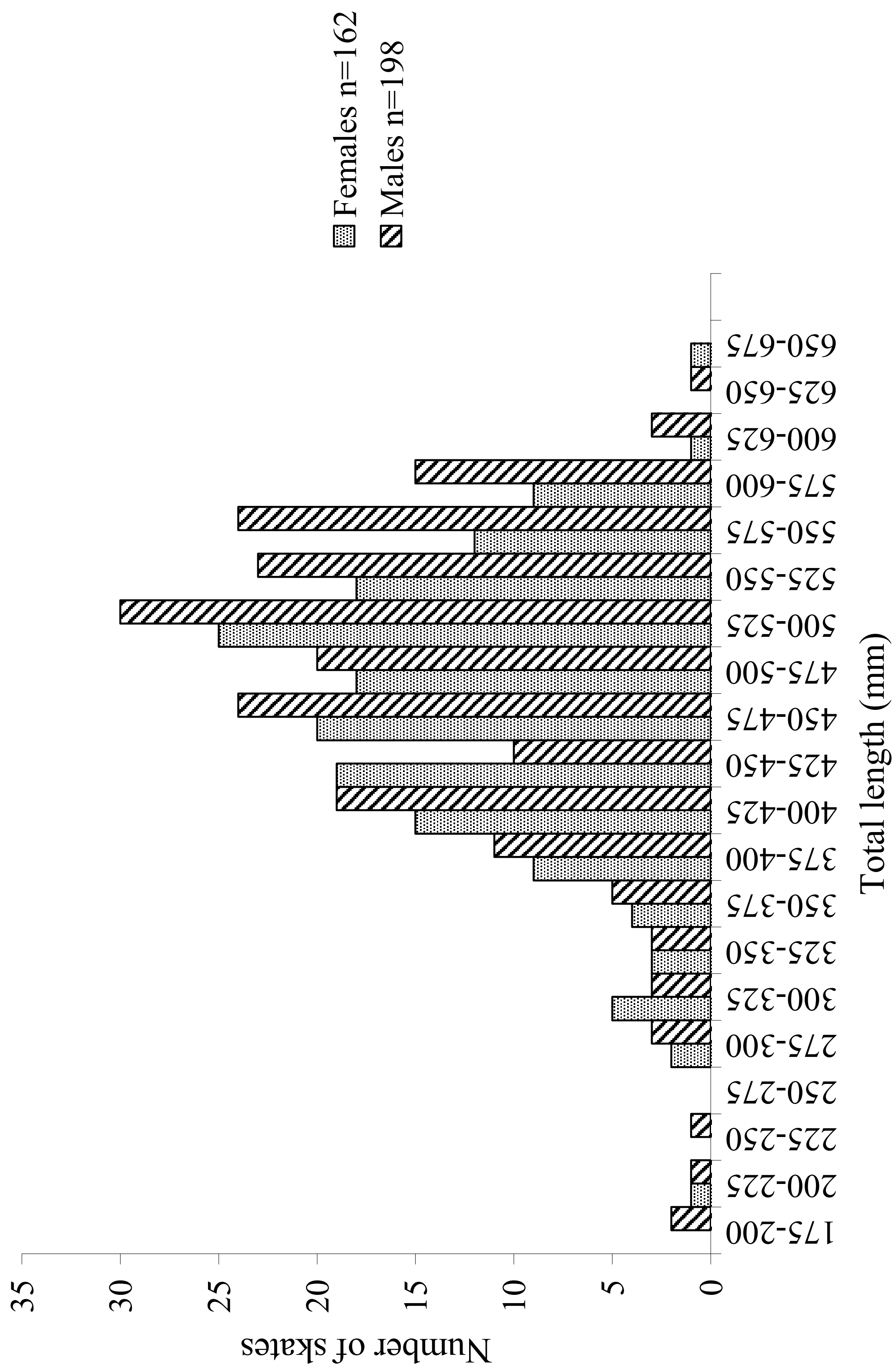

Females n=162
Males n=198
Number of skates
0
5
10
15
20
25
30
35
Total length (mm)
175-200
200-225
225-250
250-275
275-300
300-325
325-350
350-375
375-400
400-425
425-450
450-475
475-500
500-525
525-550
550-575
575-600
600-625
625-650
650-675

Figure 6. Cumulative prey curve for all prey items collected in *Bathyraja kincaidii* stomach samples from West Coast Groundfish Survey trawls. Error bars represent the standard deviation of the plotted mean generated from 100 resamplings.

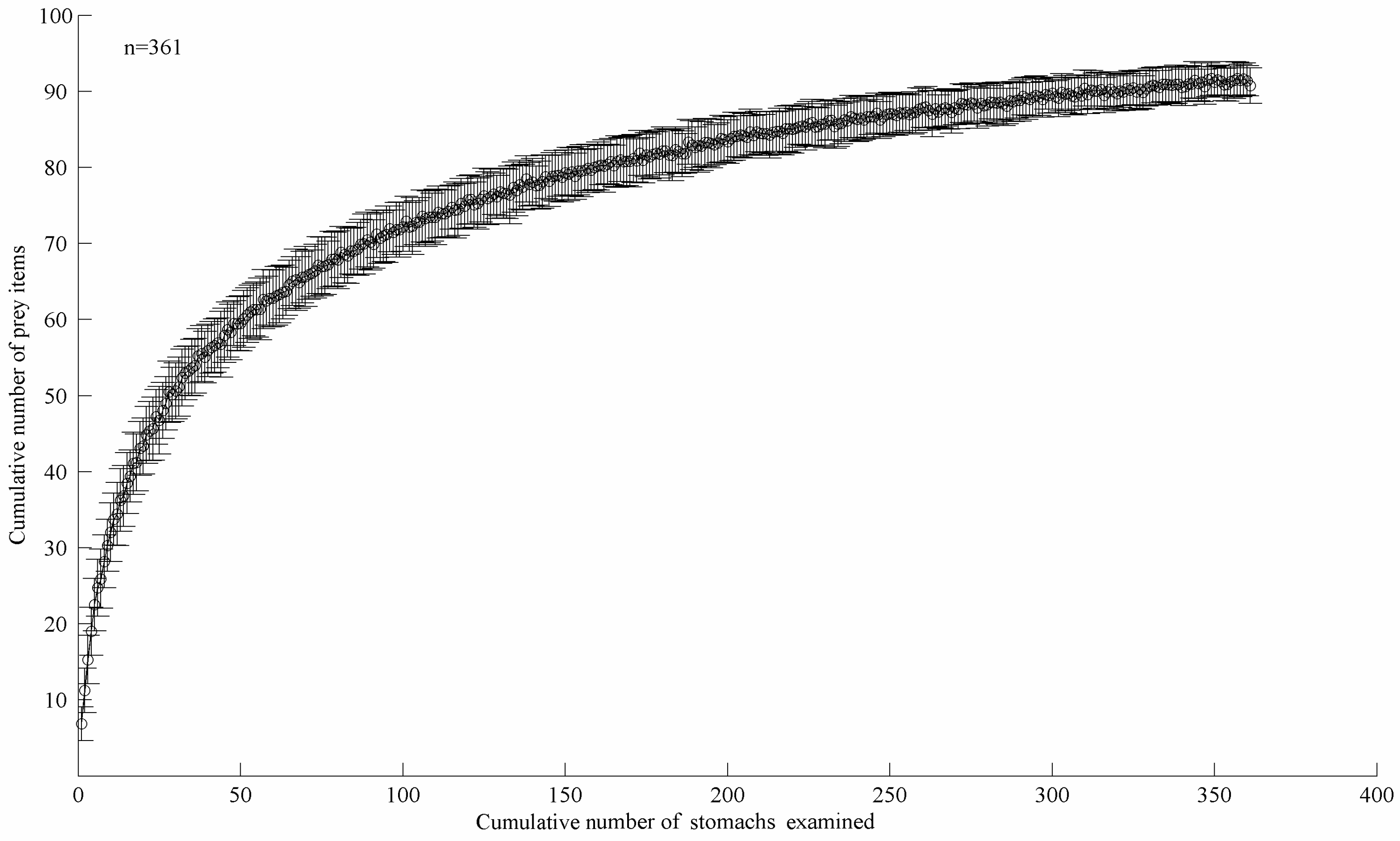

n=361
Cumulative number of prey items
100
90
80
70
60
50
40
30
20
10
0
50
100
150
200
250
300
350
400
Cumulative number of stomachs examined

Figure 7. Graphical representation of the component indices of importance for major prey categories in the diet of *Bathyraja kincaidii* from both sample sources. Numbers in parentheses indicate %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.

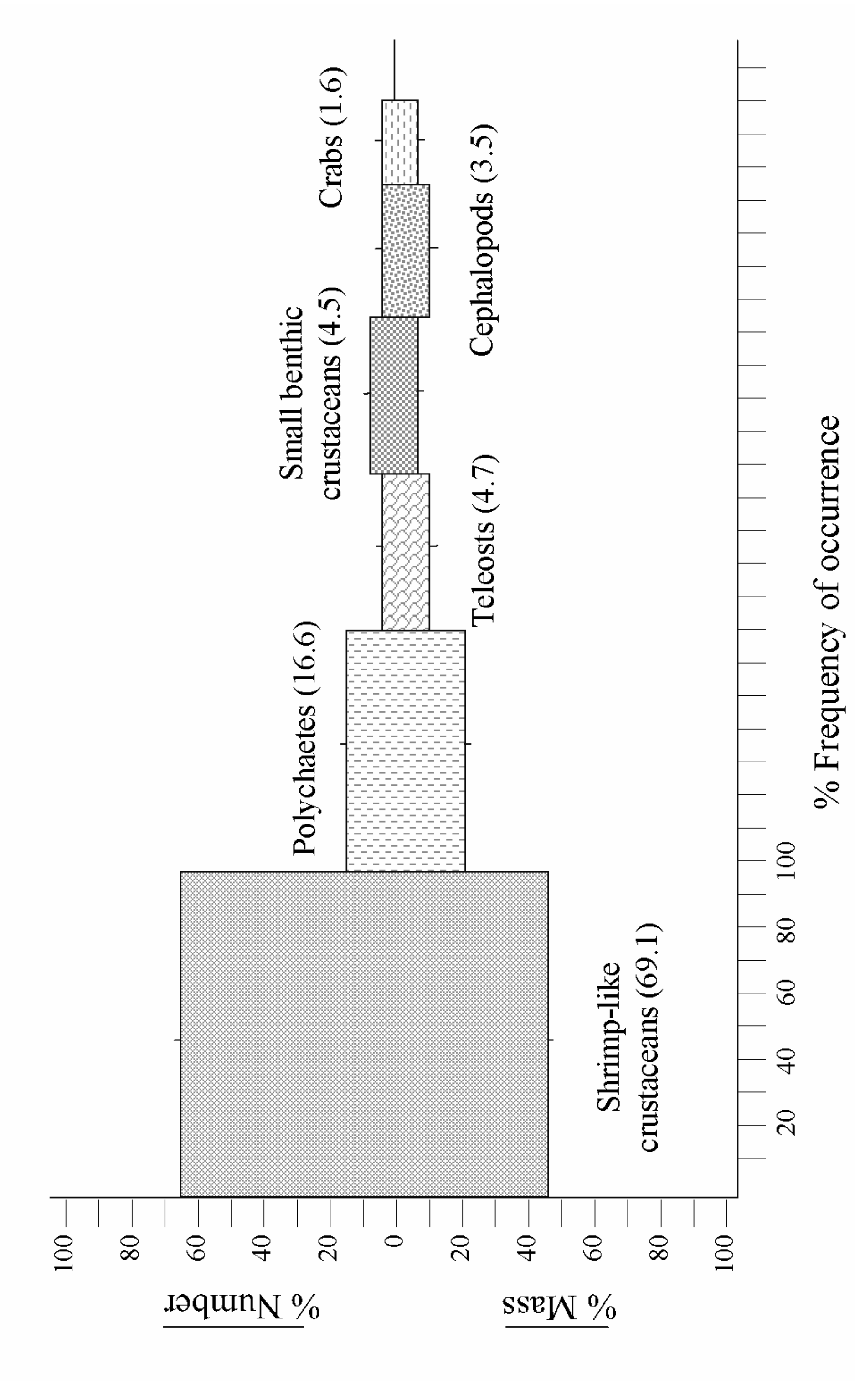

% Number
% Mass
100
80
60
40
20
0
20
40
60
80
100
Shrimp-like crustaceans (69.1)
Polychaetes (16.6)
Teleosts (4.7)
Small benthic crustaceans (4.5)
Cephalopods (3.5)
Crabs (1.6)
20
40
60
80
100
% Frequency of occurrence

Figure 8. Graphical representation of the component indices of importance for major prey categories in the diet of *Bathyraja kincaidii* from SCL samples. Numbers in parentheses indicate %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.

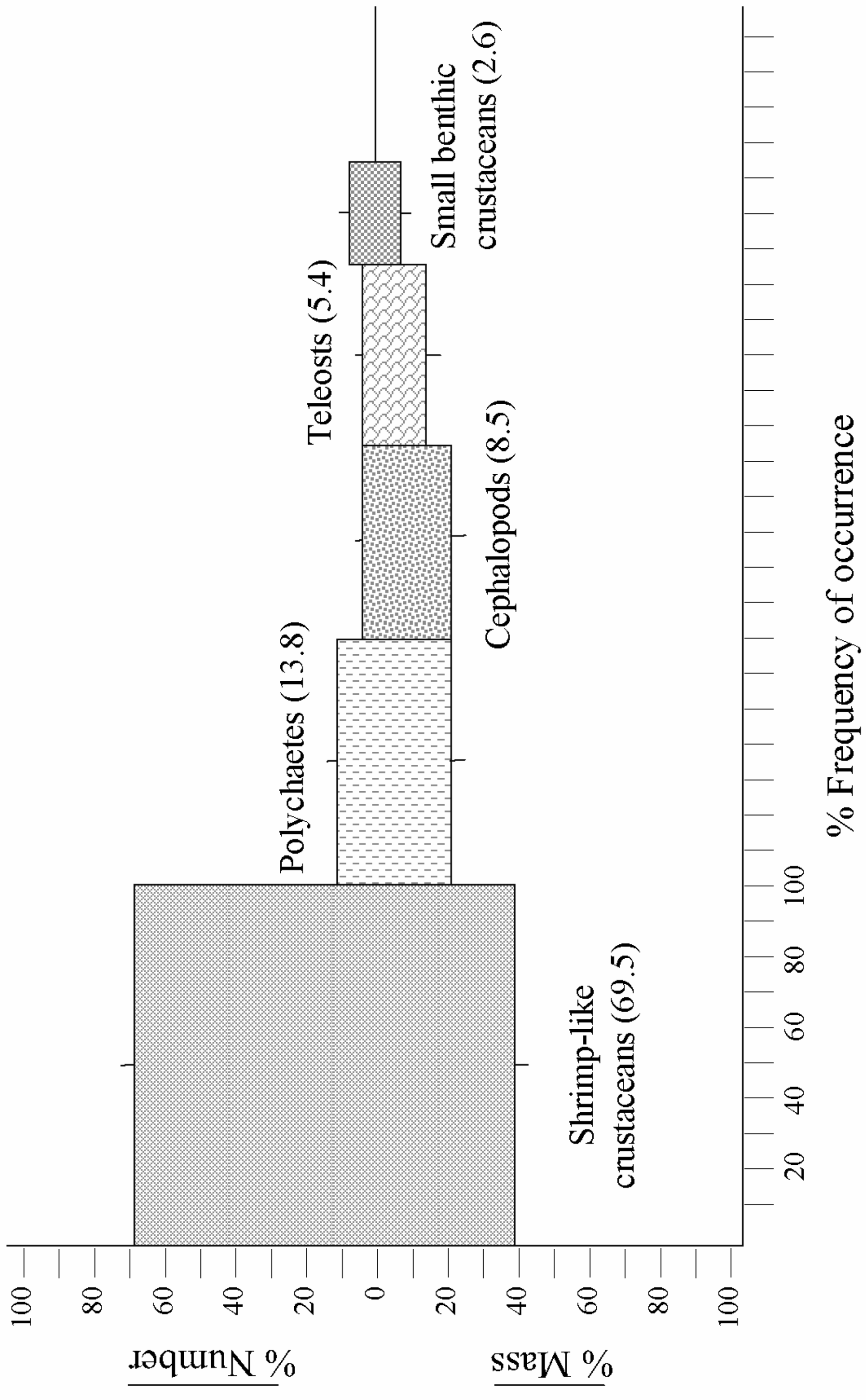

% Number
% Mass
100
80
60
40
20
0
20
40
60
80
100
20
40
60
80
100
% Frequency of occurrence
Shrimp-like crustaceans (69.5)
Polychaetes (13.8)
Cephalopods (8.5)
Teleosts (5.4)
Small benthic crustaceans (2.6)

Figure 9. Graphical representation of the component indices of importance for major prey categories in the diet of *Bathyraja kincaidii* from WCGS samples. Numbers in parentheses indicate %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.

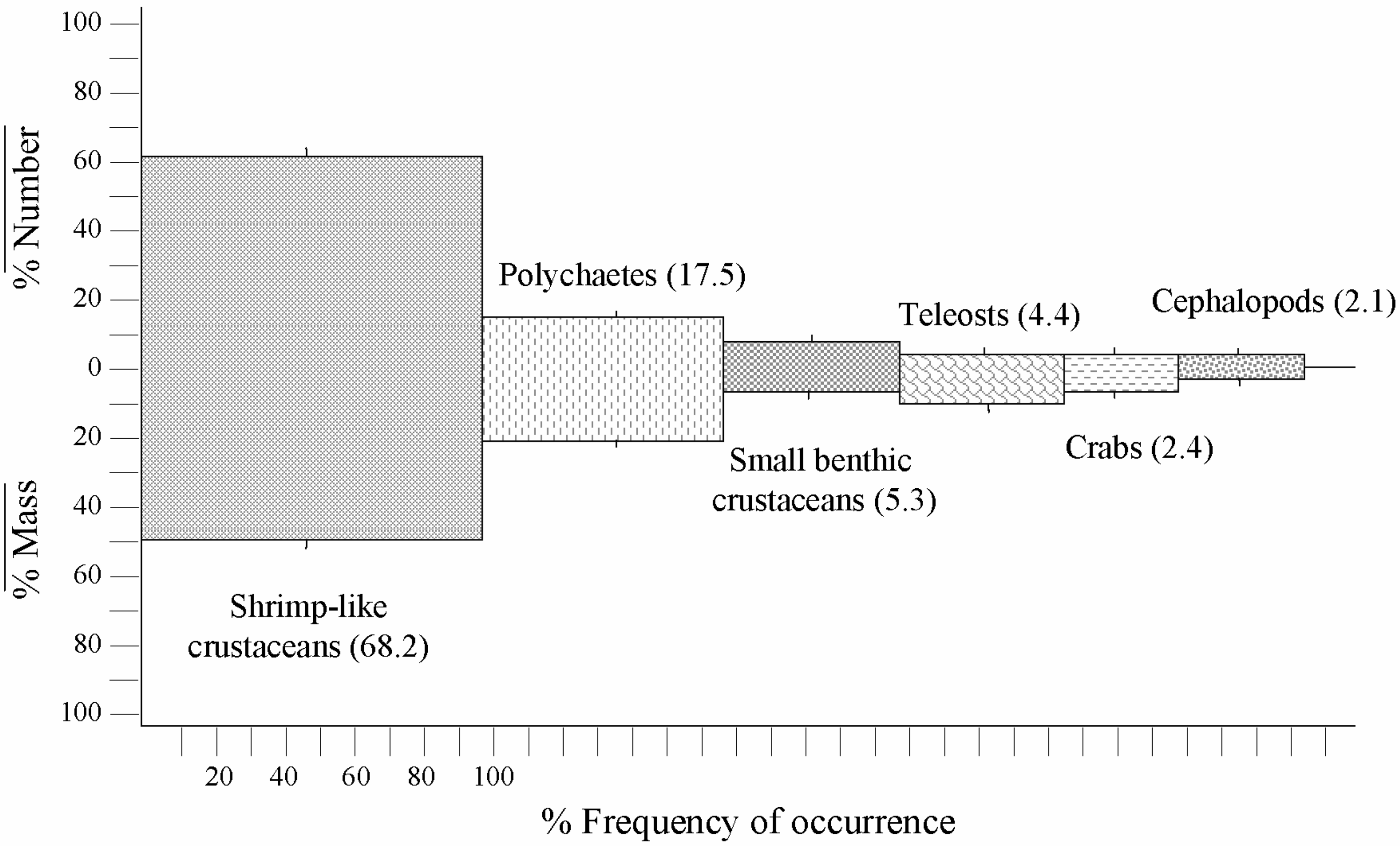

% Number
% Mass
100
80
60
40
20
0
20
40
60
80
100
Polychaetes (17.5)
Teleosts (4.4)
Cephalopods (2.1)
Small benthic crustaceans (5.3)
Crabs (2.4)
Shrimp-like crustaceans (68.2)
20
40
60
80
100
% Frequency of occurrence

Figure 10. Cumulative prey curves of the major prey categories for each combined factor grouping used in the analysis of the diet of *Bathyraja kincaidii* from SCL samples. Error bars represent the standard deviation of the plotted mean generated from 100 resamplings. For the following sex-maturity-season combinations, F0= immature female, F1= mature female M0= immature male, M1=mature male, UPS= Upwelling season, OCS= Oceanic season, DCS= Davidson Current season.

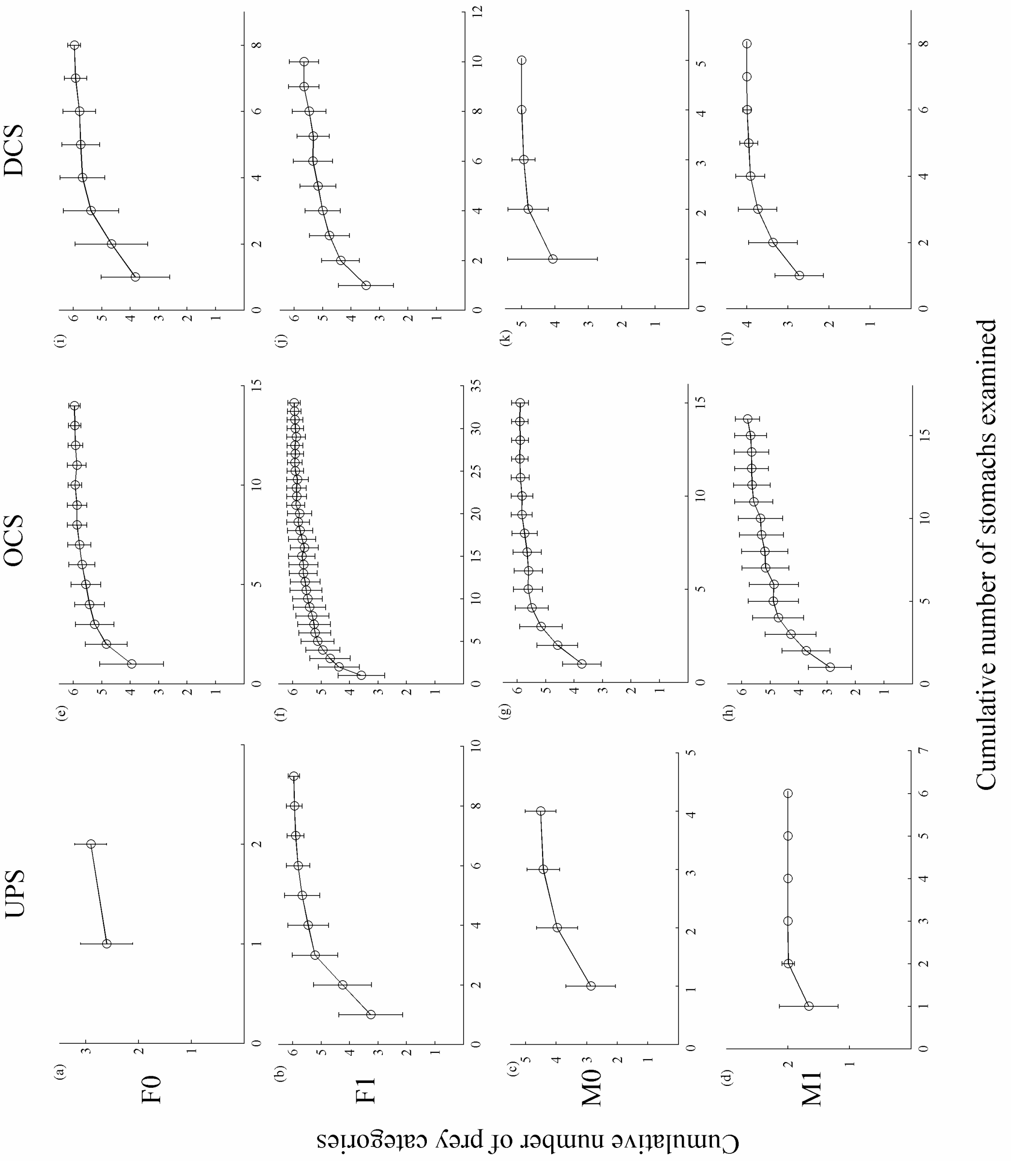

UPS
OCS
DCS
F0
F1
M0
M1
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
(i)
(j)
(k)
(l)
Cumulative number of prey categories
Cumulative number of stomachs examined

Figure 11. Cumulative prey curves of the major prey categories for each combined factor grouping used in the analysis of the diet of *Bathyraja kincaidii* from WCGS samples. Error bars represent the standard deviation of the plotted mean generated from 100 resamplings. For the following sex-maturity-zone combinations, F0= immature female, F1= mature female M0= immature male, M1=mature male.

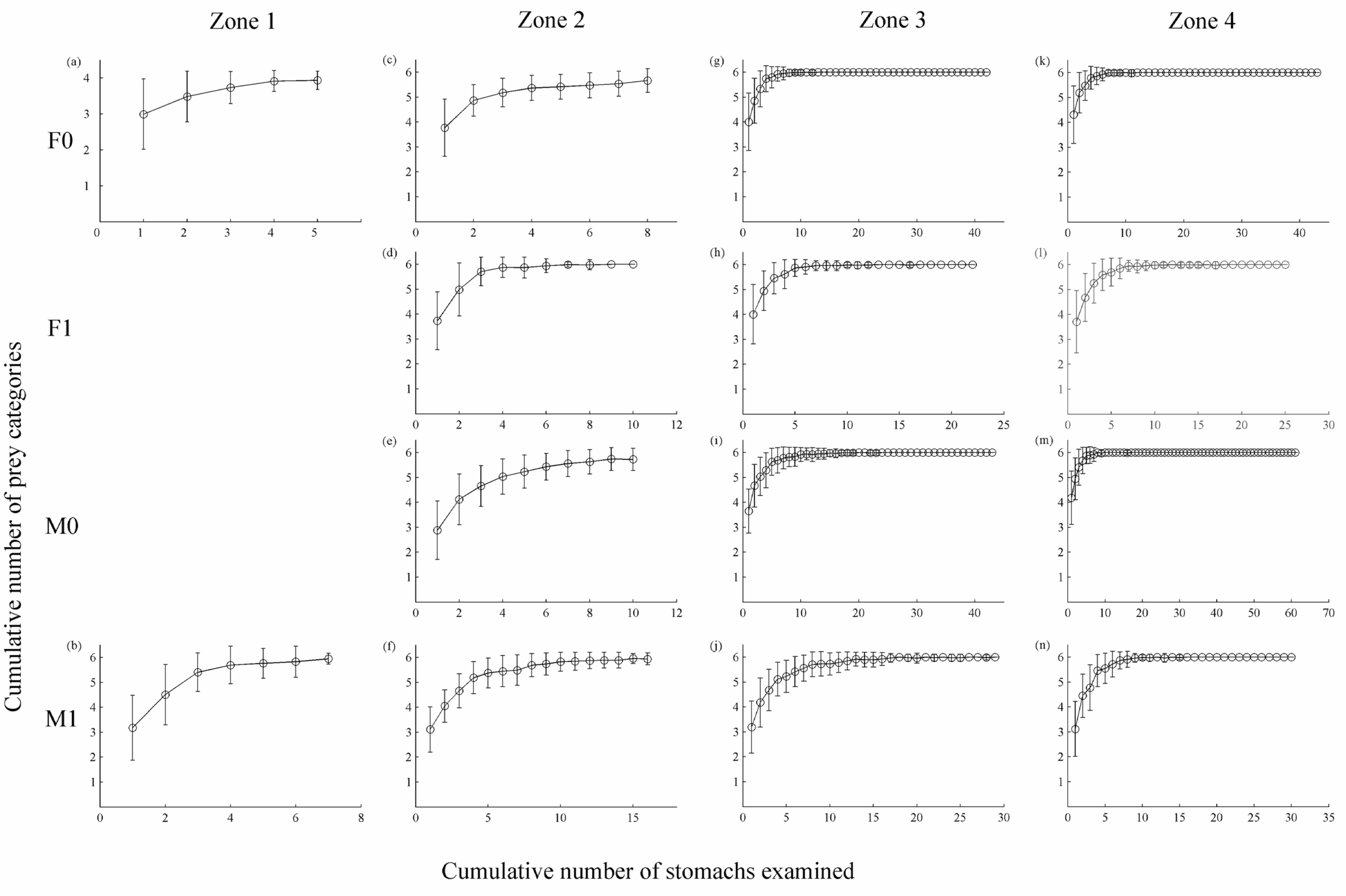

Zone 1
Zone 2
Zone 3
Zone 4
F0
F1
M0
M1
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
(i)
(j)
(k)
(l)
(m)
(n)
Cumulative number of prey categories
Cumulative number of stomachs examined

Figure 12. Mean values and 95% confidence intervals of the gravimetric proportion of the six prey categories in the diet of *Bathyraja kincaidii* from SCL samples. a) maturity*season interaction, ▲= immature skates, ♦= mature skates. b) sex*maturity interaction, IMM= immature, MAT= mature, ■= female skates, ●= male skates. * significant ($p<0.05$) for the interaction

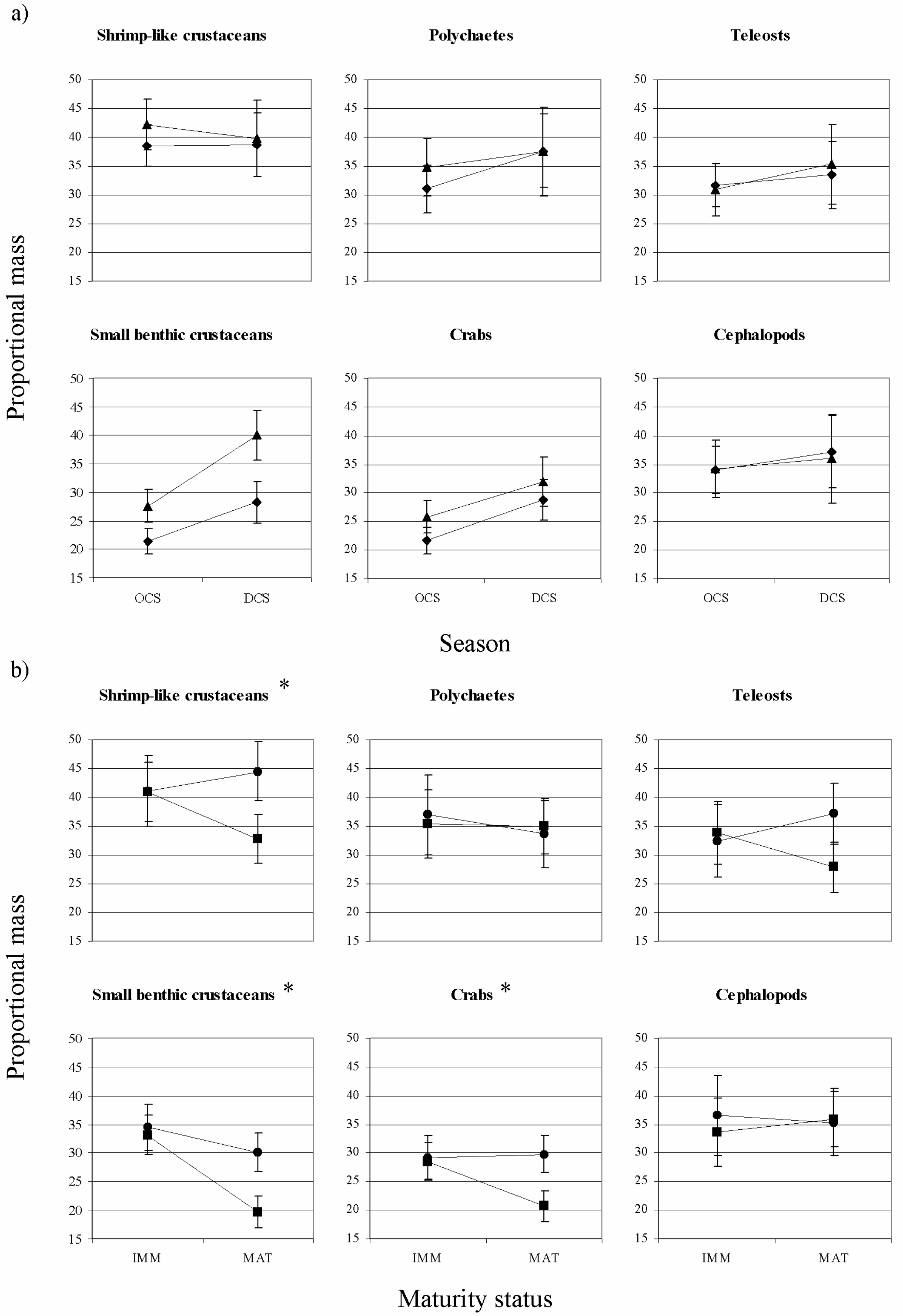

a)
Shrimp-like crustaceans
Polychaetes
Teleosts
Small benthic crustaceans
Crabs
Cephalopods
Proportional mass
50
45
40
35
30
25
20
15
OCS
DCS
Season
b)
Shrimp-like crustaceans *
Polychaetes
Teleosts
Small benthic crustaceans *
Crabs *
Cephalopods
Proportional mass
IMM
MAT
Maturity status

Figure 13. Mean values and 95% confidence intervals of the numeric proportion of the six prey categories in the diet of *Bathyraja kincaidii* from SCL samples. a) sex*season interaction, ■= female skates, ●= male skates. b) maturity*season, ▲= immature skates, ♦= mature skates. * significant ($p<0.05$) for the interaction

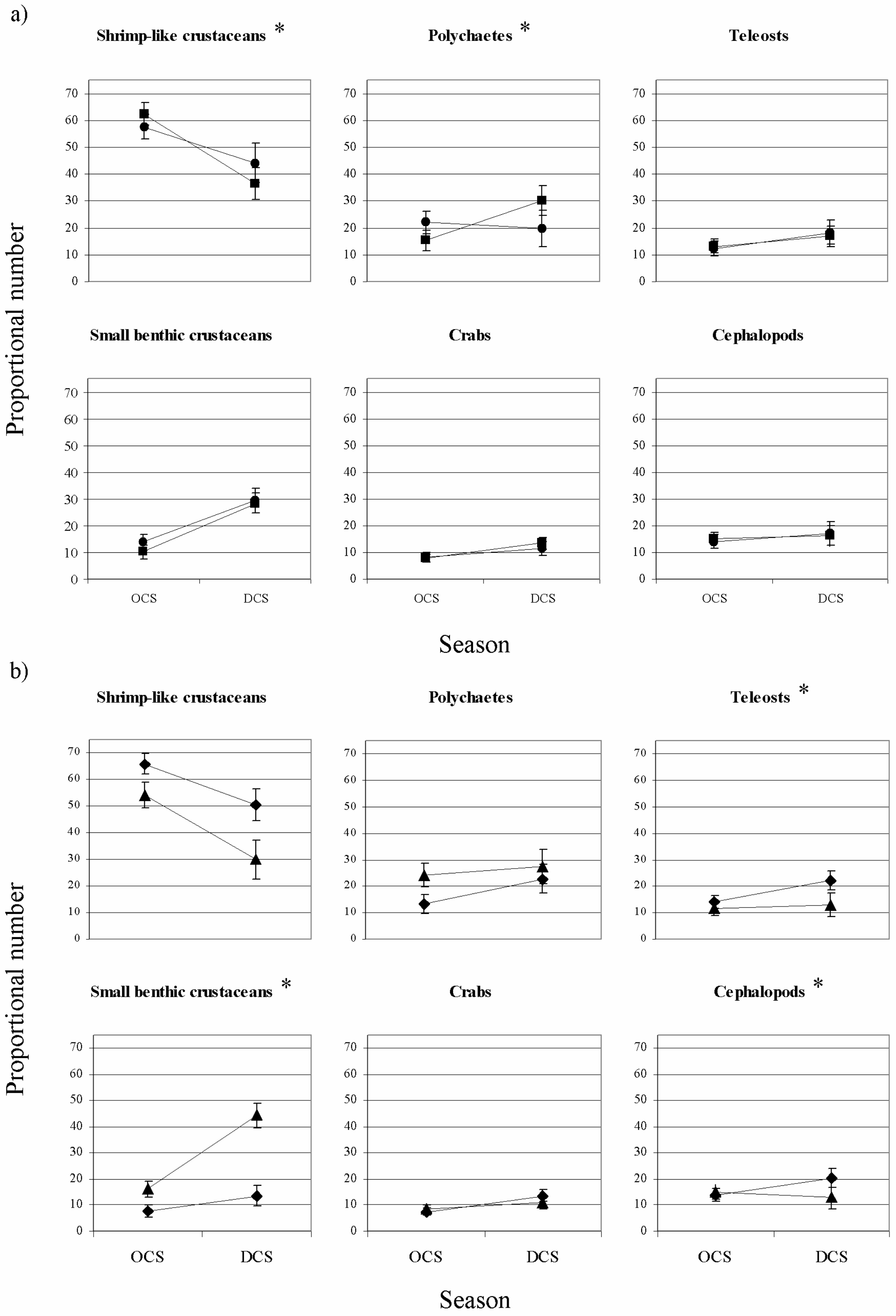
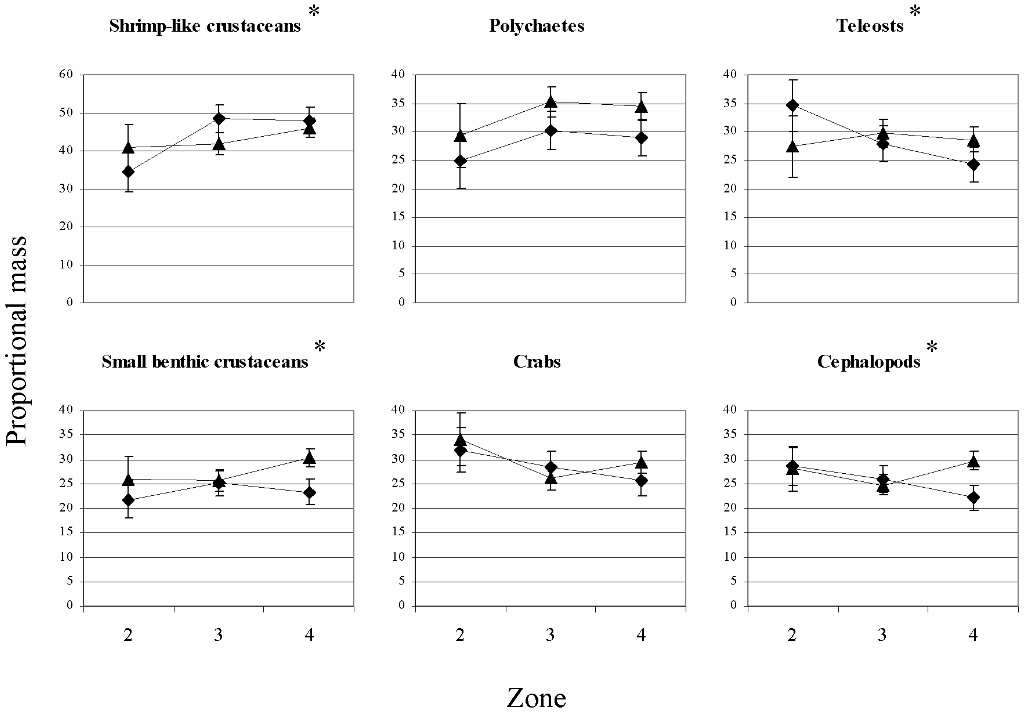

a)
Shrimp-like crustaceans *
Polychaetes *
Teleosts
Small benthic crustaceans
Crabs
Cephalopods
Proportional number
0
10
20
30
40
50
60
70
OCS
DCS
Season
b)
Shrimp-like crustaceans
Polychaetes
Teleosts *
Small benthic crustaceans *
Crabs
Cephalopods *
Proportional number
OCS
DCS
Season

Figure 14. Mean values and 95% confidence intervals of the gravimetric proportion of the six prey categories in the diet of *Bathyraja kincaidii* from WCGS samples. a) maturity*zone interaction, ▲= immature skates, ♦= mature skates. b) sex*maturity interaction, IMM= immature, MAT= mature, ■= female skates, ●= male skates. Note the difference in scale between the shrimp-like crustacean figure and the remaining plots for both interactions. * significant ($p<0.05$) for the interaction

a)


Shrimp-like crustaceans *
Polychaetes
Teleosts *
Small benthic crustaceans *
Crabs
Cephalopods *
Proportional mass
0
10
20
30
40
50
60
5
15
25
35
2
3
4
Zone

b)

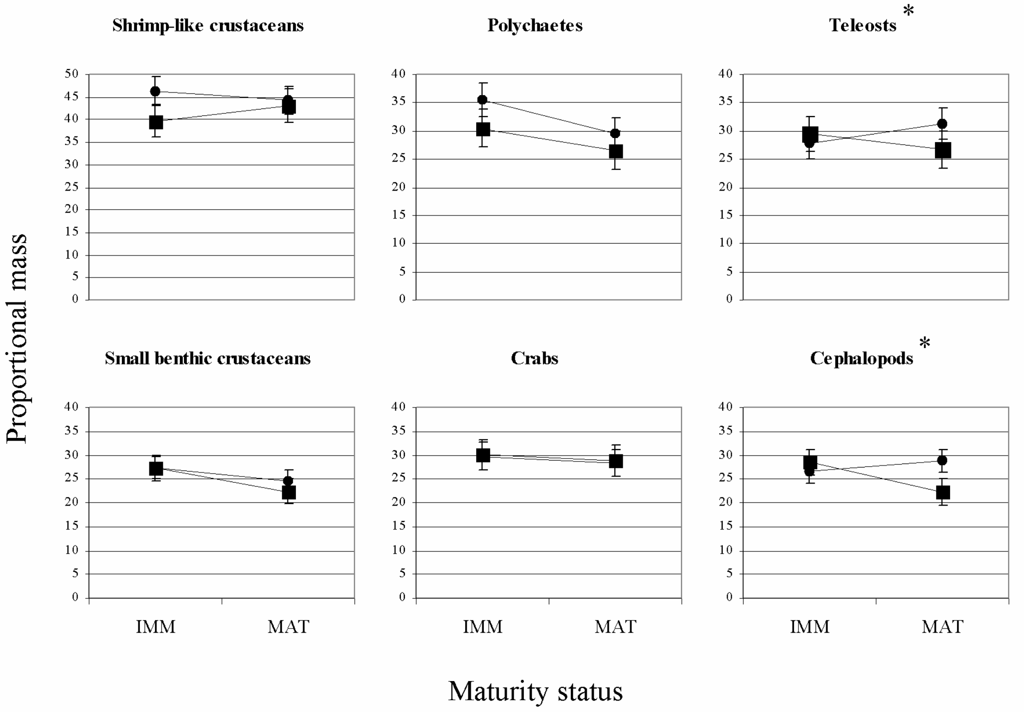

Shrimp-like crustaceans
Polychaetes
Teleosts *
Small benthic crustaceans
Crabs
Cephalopods *
Proportional mass
0
5
10
15
20
25
30
35
40
45
50
IMM
MAT
Maturity status

Figure 15. Mean values and 95% confidence intervals of the numeric proportion of the six prey categories in the diet of *Bathyraja kincaidii* from WCGS samples. a) maturity*zone interaction, ■= female skates, ●= male skates. b) sex*maturity, ▲= immature skates, ♦= mature skates. Note the difference in scale between the shrimp-like crustacean figure and the remaining plots for both interactions. * significant ($p<0.05$) for the interaction

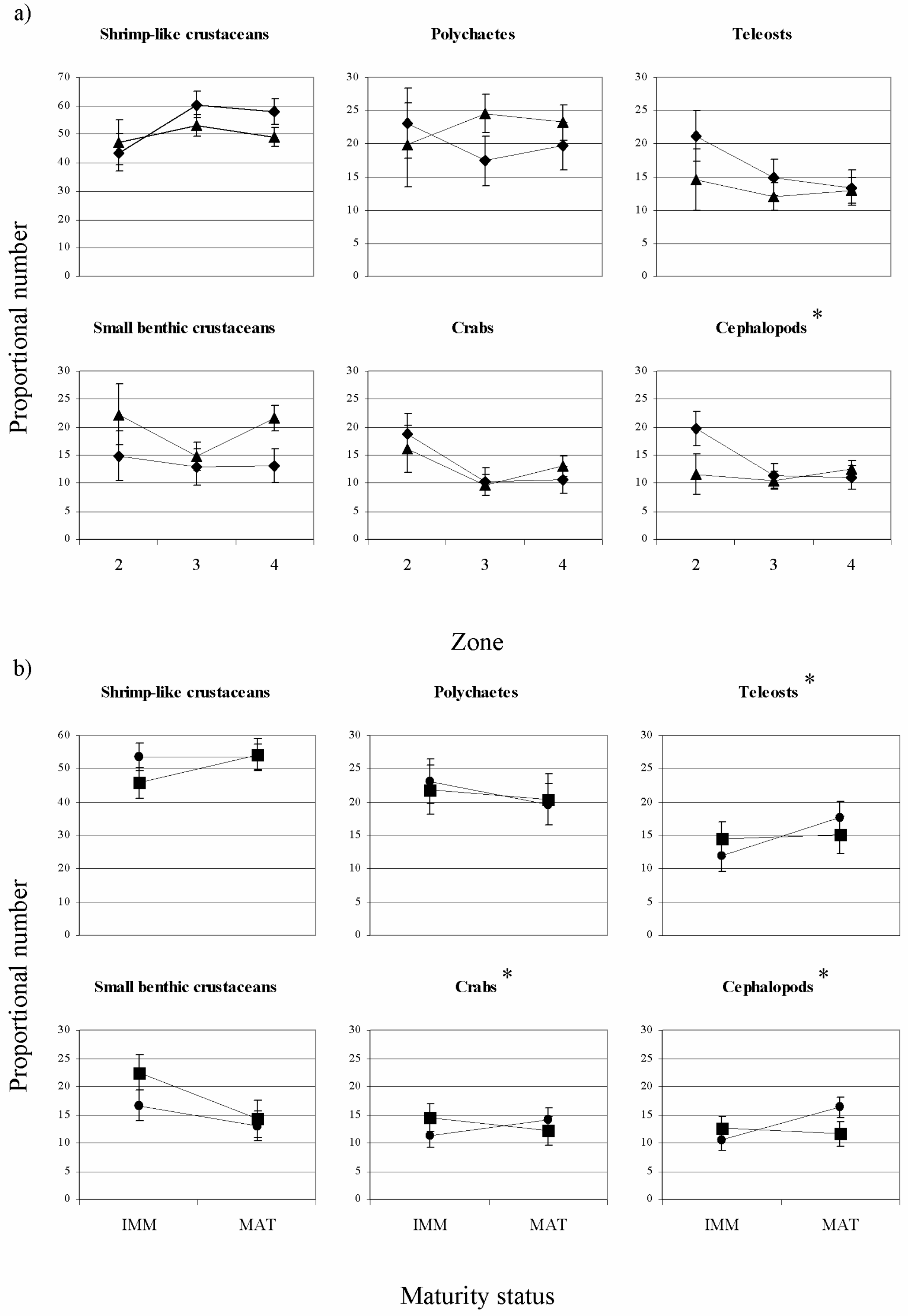

a)
Shrimp-like crustaceans
Polychaetes
Teleosts
Small benthic crustaceans
Crabs
Cephalopods *
Proportional number
0
10
20
30
40
50
60
70
0
5
10
15
20
25
30
2
3
4
Zone
b)
Shrimp-like crustaceans
Polychaetes
Teleosts *
Small benthic crustaceans
Crabs *
Cephalopods *
Proportional number
0
10
20
30
40
50
60
0
5
10
15
20
25
30
IMM
MAT
Maturity status

Figure 16. Mean upwelling index and standard error from the 36º N 122º W station for the month/ year combinations encompassing the dates of collection of SCL samples. The more positive the value of the index, the more likely upwelling is to occur. For those months when no stomach samples were collected (April, May and August), the mean plotted is from each of those months from the entire study period, 2002-2005.

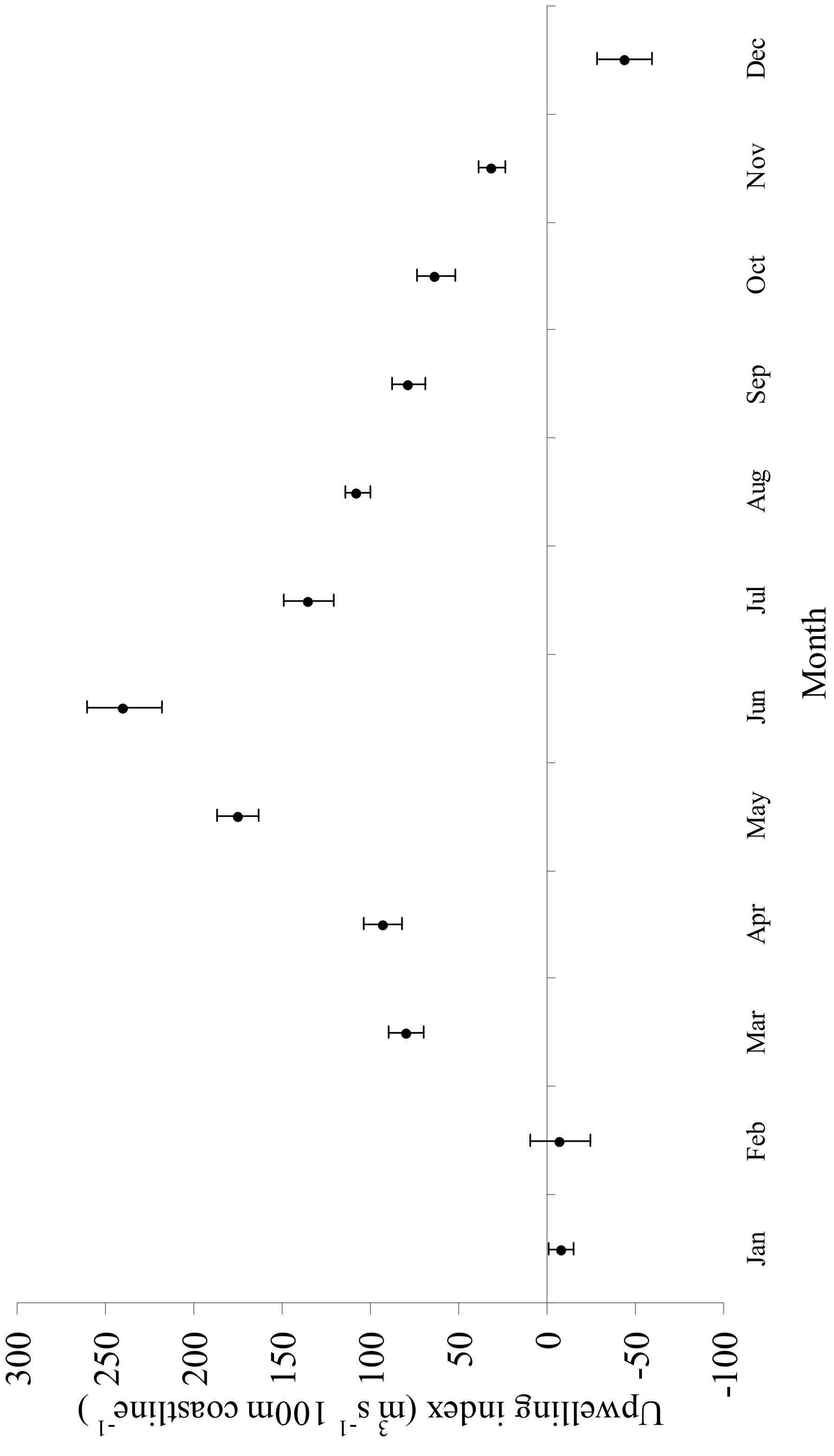
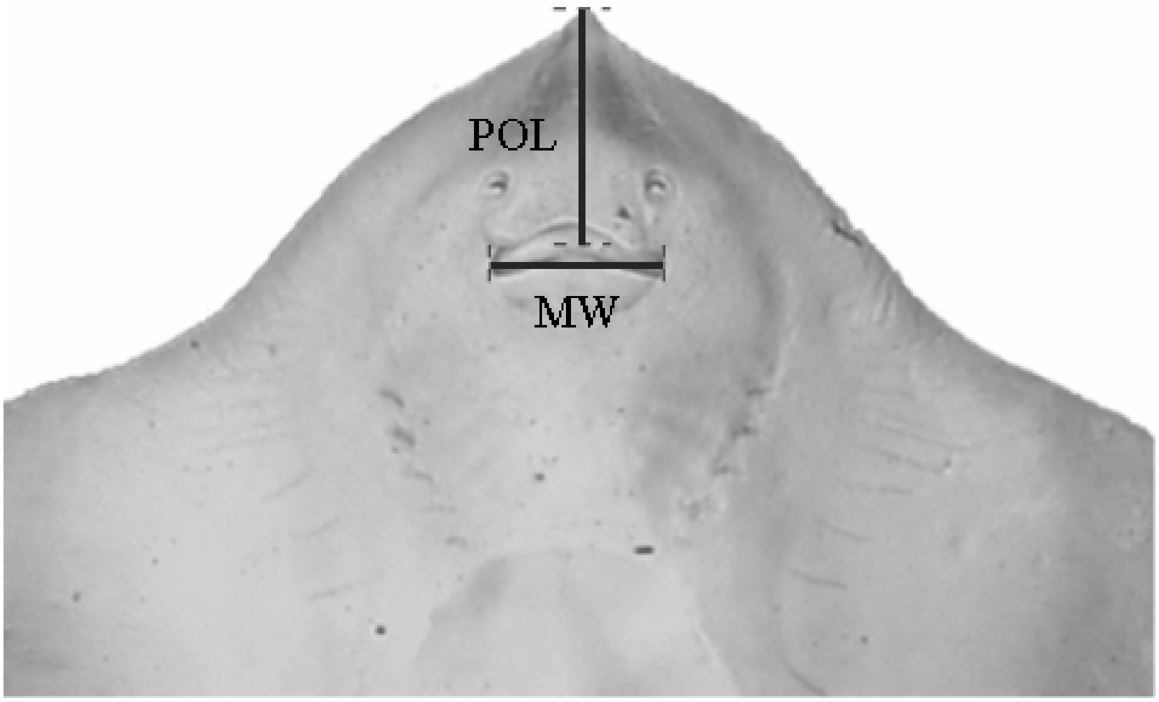

Upwelling index (m^3 s^{-1} 100m coastline^{-1})
300
250
200
150
100
50
0
-50
-100
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Month

Figure 17. An anterior view of *Bathyraja kincaidii* indicating the oral measurements used in the ecomorphological analysis. The upper photograph is a frontal view of the ventrum, POL= pre-oral length, MW= mouth width. The bottom photograph is a sagittal view of the ventrum, PROT= protrusion distance.


POL
MW

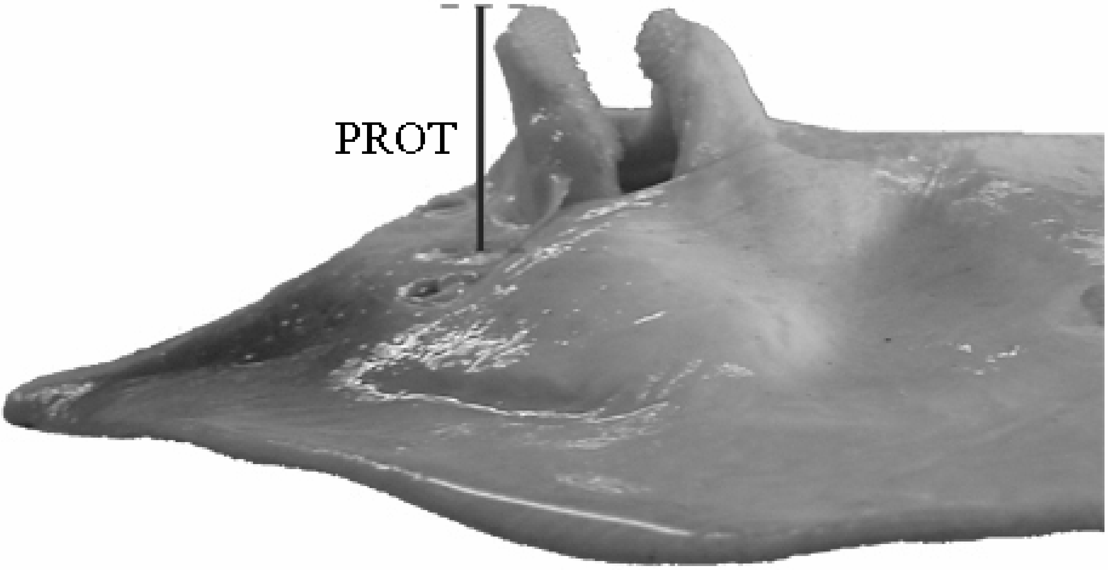

PROT

Figure 18. A representative tooth from *Bathyraja kincaidii* indicating the dental measurements used in the ecomorphological analysis. The upper photograph is an overhead transverse view, CW= crown width, CL= crown length. The bottom photograph is a sagittal view, CuH= cusp height, CuL= cusp length. The cusp is posteriorly directed.

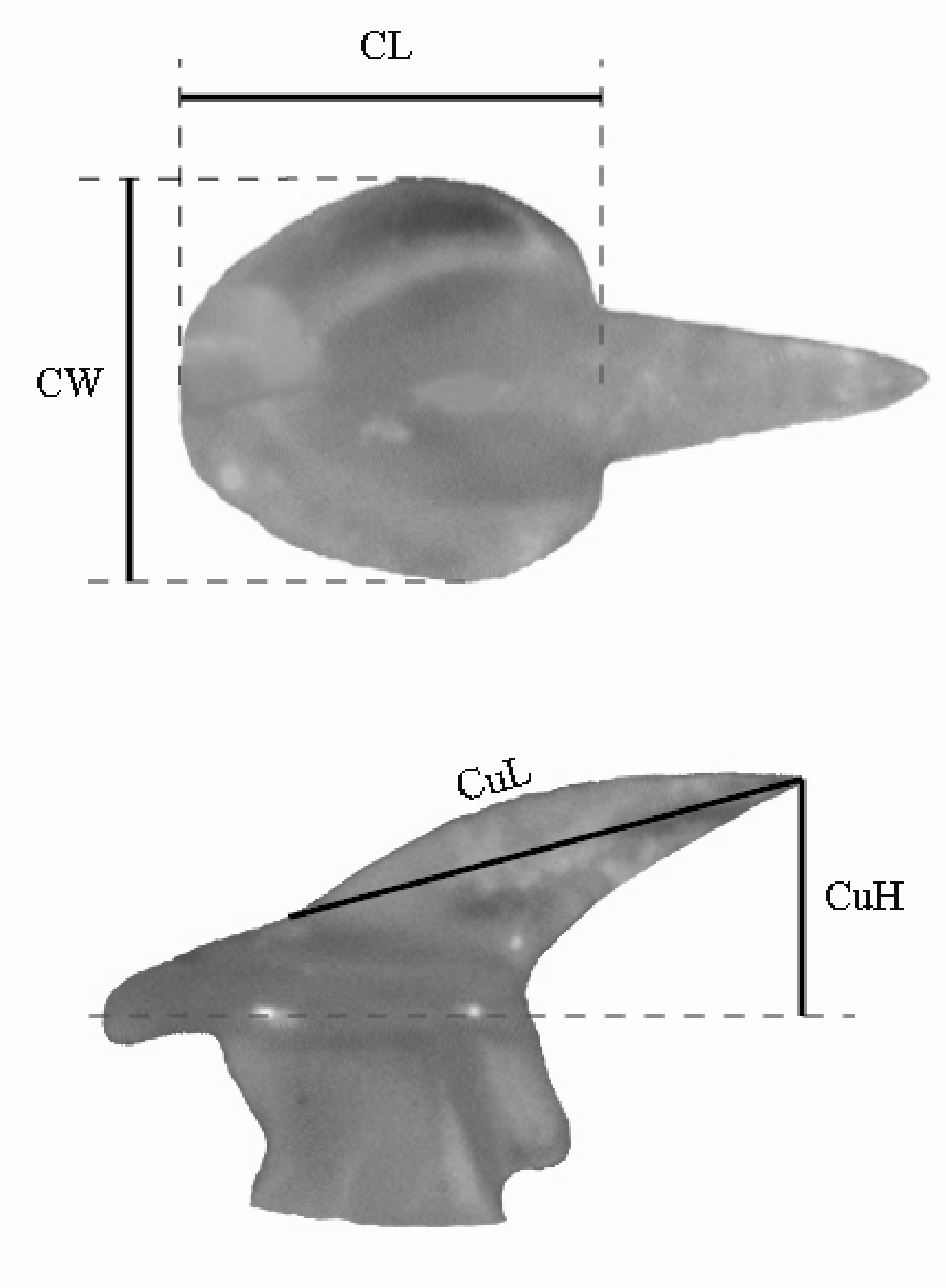

CL
CW
CuL
CuH

Figure 19. Area map of the eastern North Pacific indicating locations and number of *Bathyraja kincaidii* captured in West Coast Groundfish Survey trawls whose measurements were used in the morphological analysis.

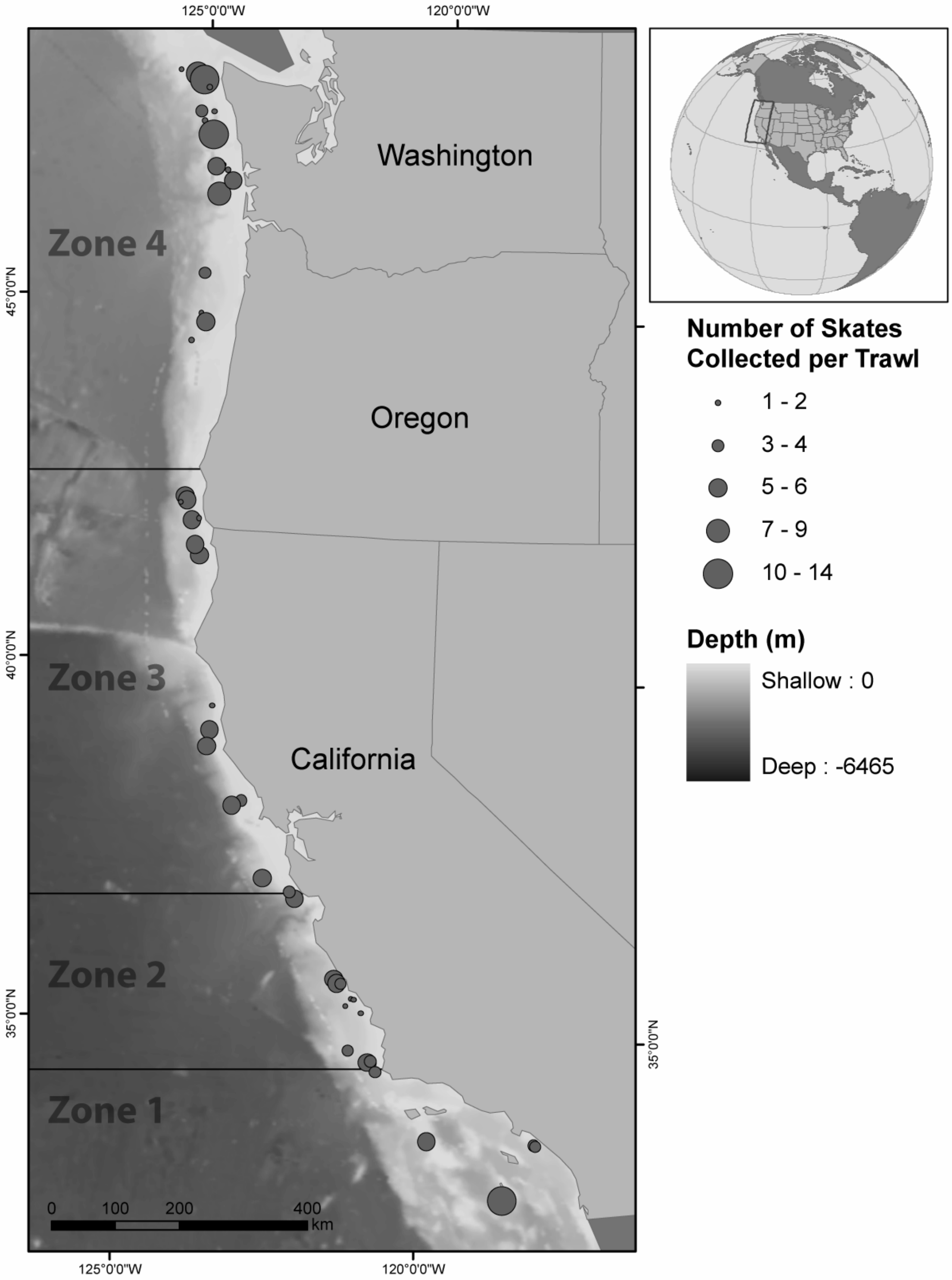

125°0'0"W
120°0'0"W
Washington
Oregon
California
Zone 4
Zone 3
Zone 2
Zone 1
45°0'0"N
40°0'0"N
35°0'0"N
Number of Skates Collected per Trawl
1 - 2
3 - 4
5 - 6
7 - 9
10 - 14
Depth (m)
Shallow : 0
Deep : -6465
0
100
200
400
km

Figure 20. Histogram of the total lengths of male and female *Bathyraja kincaidii* used in the morphological analysis.

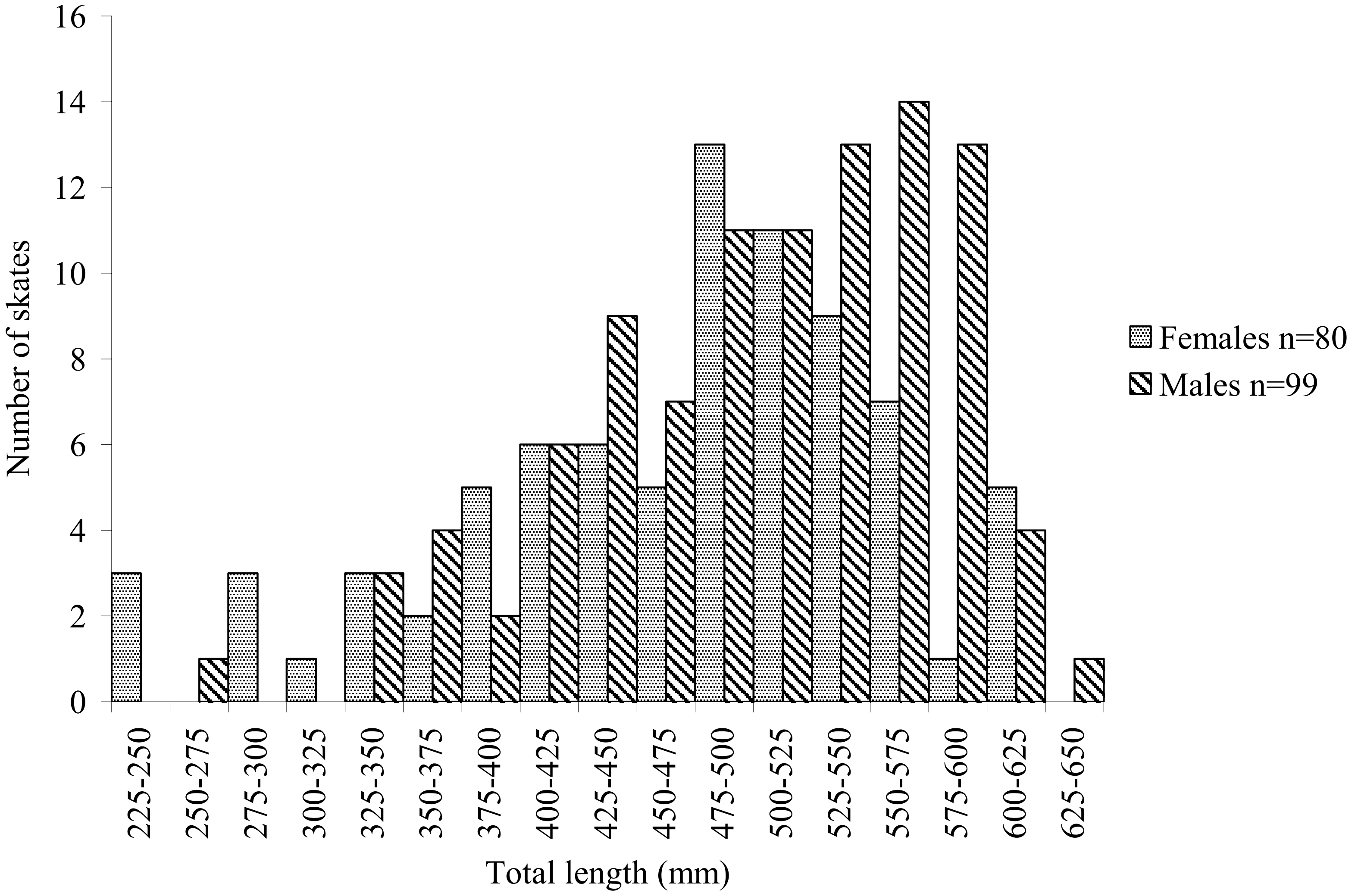

16
14
12
10
8
6
4
2
0
Number of skates
225-250
250-275
275-300
300-325
325-350
350-375
375-400
400-425
425-450
450-475
475-500
500-525
525-550
550-575
575-600
600-625
625-650
Total length (mm)
▨ Females n=80
▧ Males n=99

Figure 21. Log-log plots of the oral measurements used in the study. Δ = immature skates, ♦= mature skates. The regression line and equation are for both maturities combined. The dashed line with a slope of 1 indicates isometric growth.

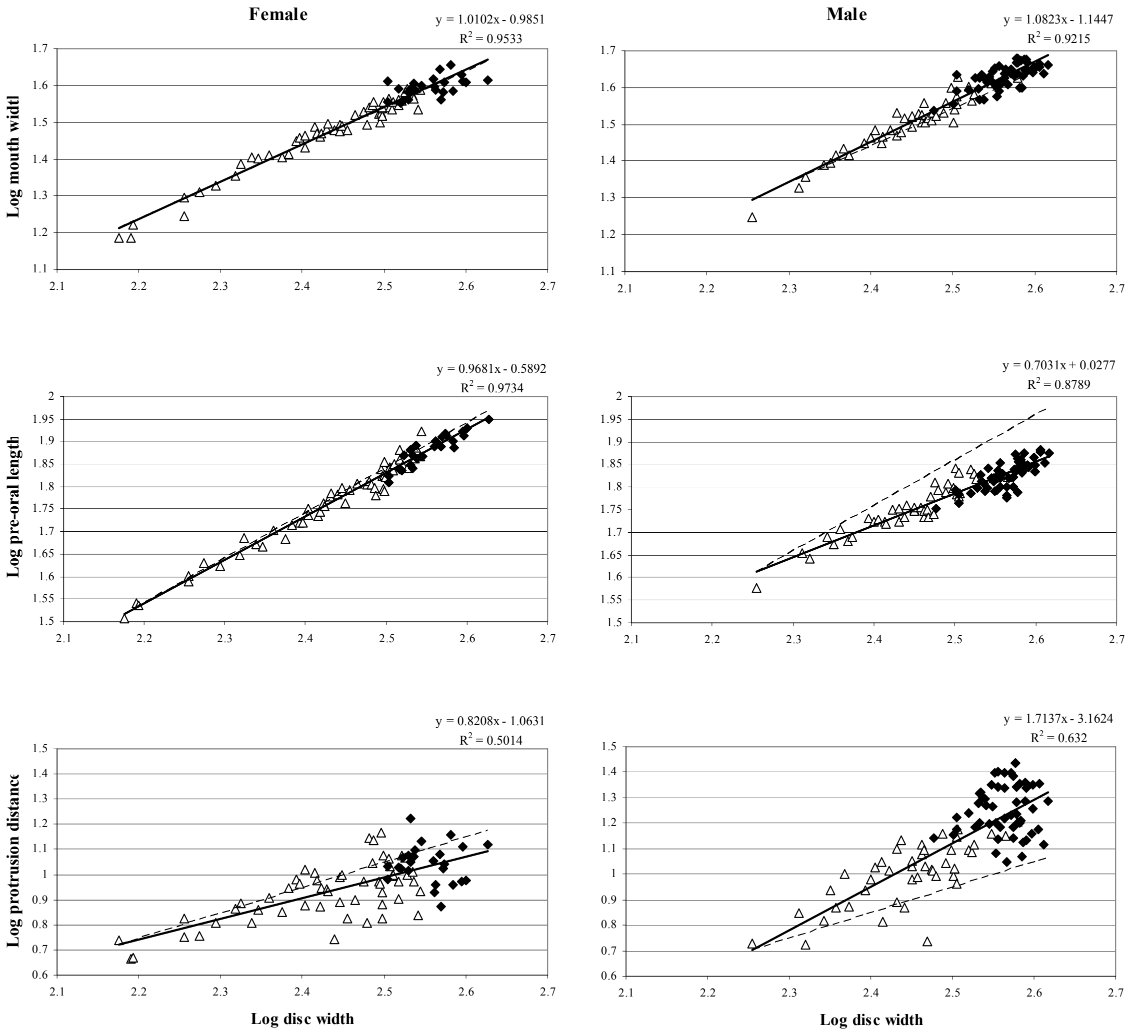
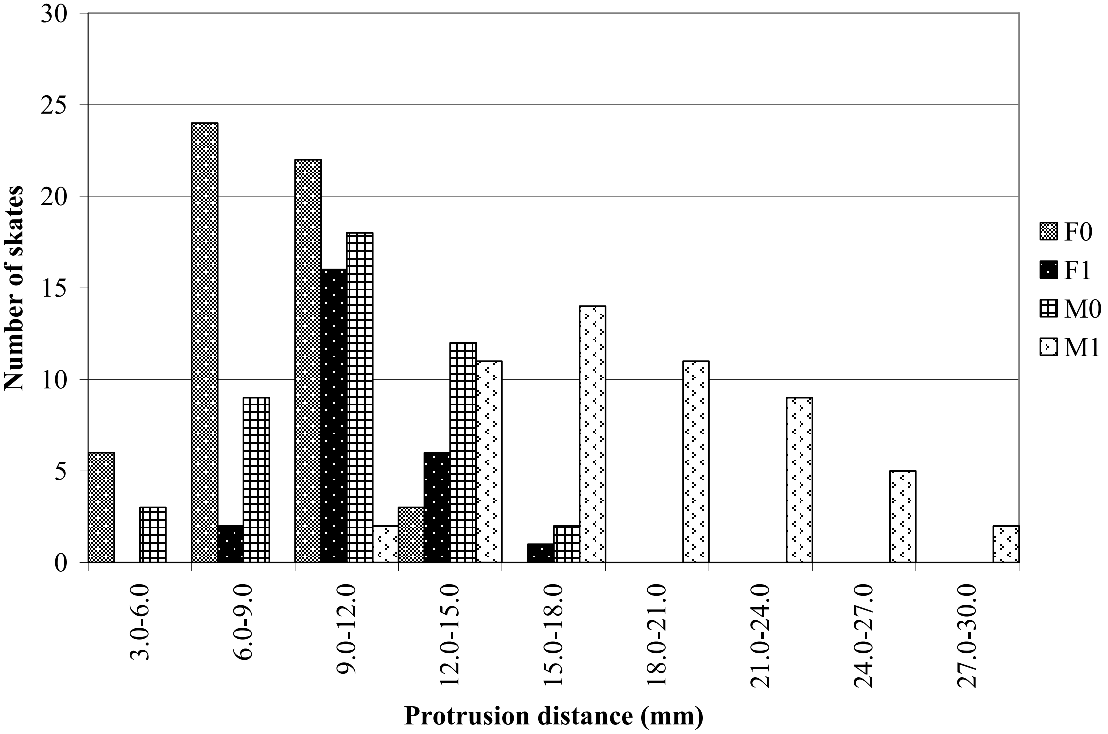

Female
Male
y = 1.0102x - 0.9851
R² = 0.9533
y = 1.0823x - 1.1447
R² = 0.9215
Log mouth widtl
y = 0.9681x - 0.5892
R² = 0.9734
y = 0.7031x + 0.0277
R² = 0.8789
Log pre-oral length
y = 0.8208x - 1.0631
R² = 0.5014
y = 1.7137x - 3.1624
R² = 0.632
Log protrusion distance
Log disc width
Log disc width
2.1
2.2
2.3
2.4
2.5
2.6
2.7

Figure 22. Distribution histogram of protrusion distance for the sex-maturity groupings indicating a non-normal distribution. F0=immature female, F1=mature female, M0=immature male, M1=mature male.



30
25
20
15
10
5
0
Number of skates
F0
F1
M0
M1
3.0-6.0
6.0-9.0
9.0-12.0
12.0-15.0
15.0-18.0
18.0-21.0
21.0-24.0
24.0-27.0
27.0-30.0
Protrusion distance (mm)

Figure 23. Mean values and 95% confidence intervals of the three oral measurements taken from *Bathyraja kincaidii*. a) sex*maturity interaction, IMM= immature, MAT= mature, ■= female skates, ●= male skates b) maturity*zone interaction, ▲= immature skates, ♦= mature skates c) sex*zone interaction, ■= female skates, ●= male skates. * significant ($p<0.05$) for the interaction

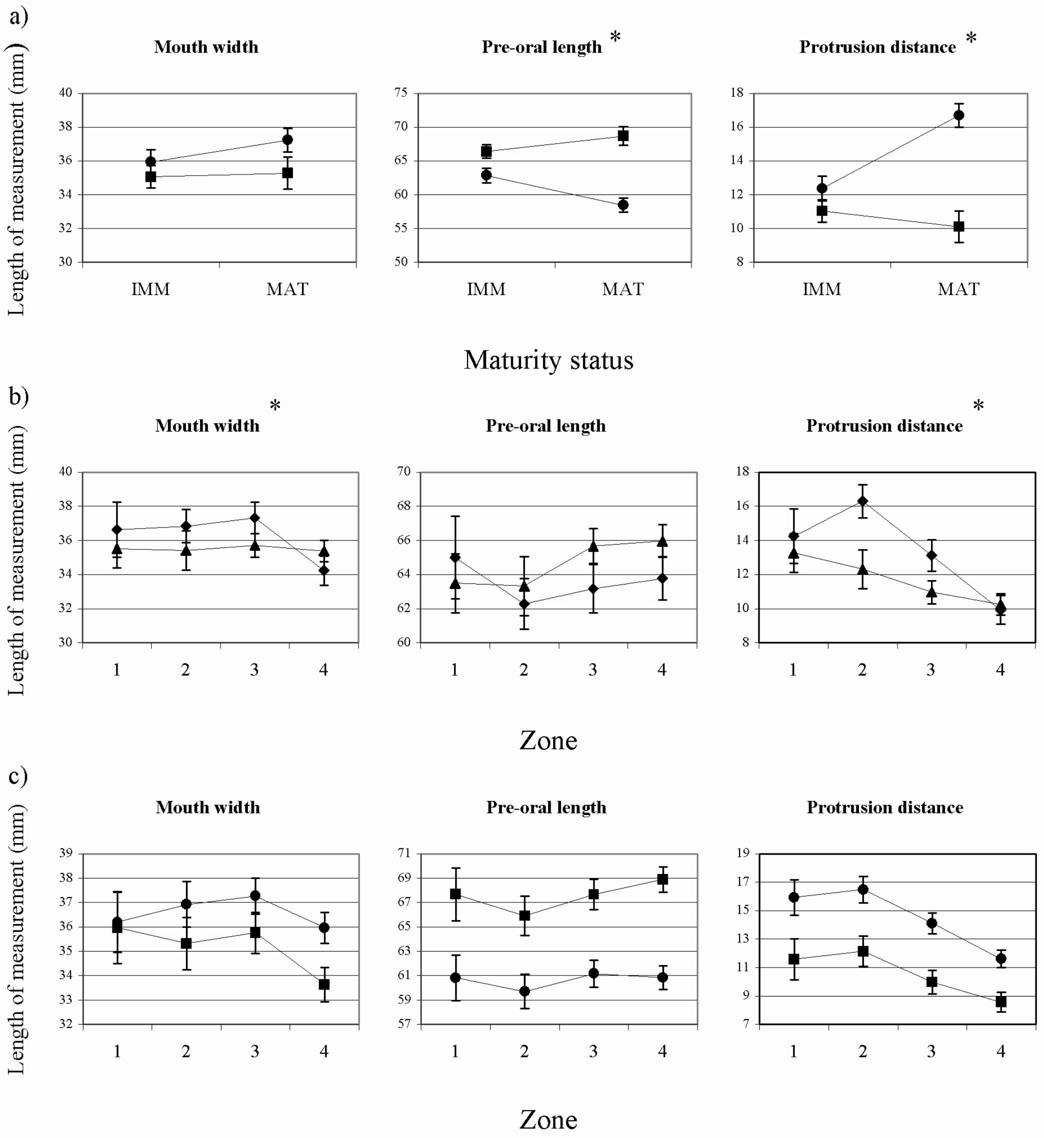

a)
Mouth width
Pre-oral length *
Protrusion distance *
Length of measurement (mm)
IMM
MAT
Maturity status
b)
Mouth width *
Pre-oral length
Protrusion distance *
Length of measurement (mm)
1
2
3
4
Zone
c)
Mouth width
Pre-oral length
Protrusion distance
Length of measurement (mm)
1
2
3
4
Zone

Figure 24. Mean values and 95% confidence intervals for the sex*maturity*zone interaction of the protrusion distance of *Bathyraja kincaidii*. IMM= immature, MAT= mature, ■= female skates, ●= male skates.

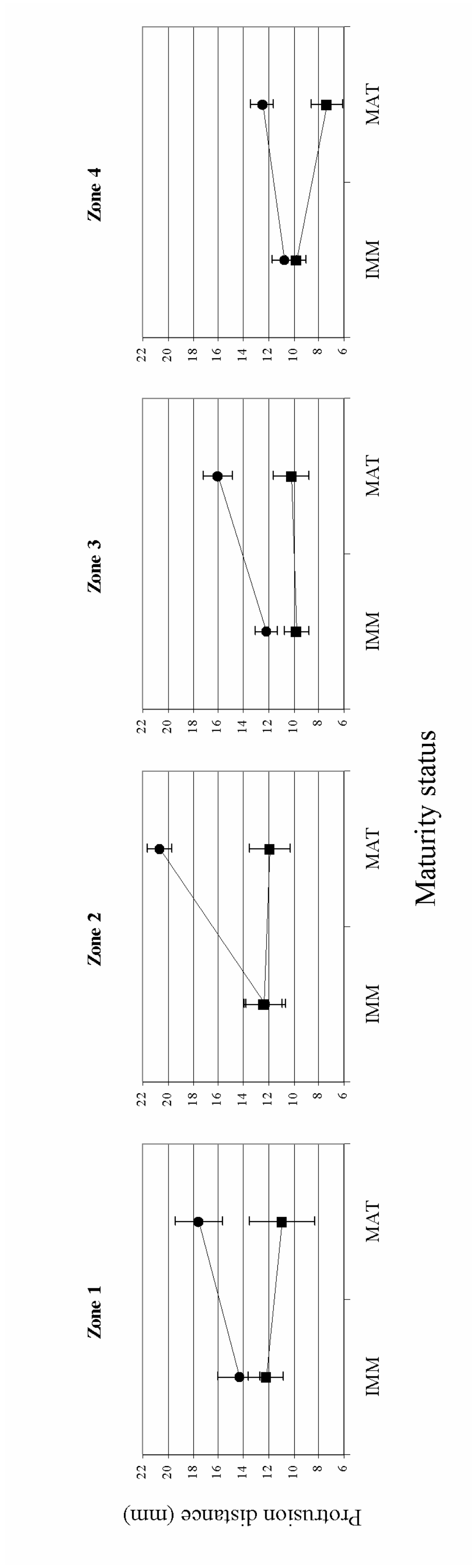

Protrusion distance (mm)
22
20
18
16
14
12
10
8
6
Zone 1
Zone 2
Zone 3
Zone 4
IMM
MAT
Maturity status

Figure 25. Log-log plots of the dental measurements used in the study. Δ = immature skates, ♦= mature skates. The regression line and equation are for both maturities combined. The dashed line with a slope of 1 indicates isometric growth.

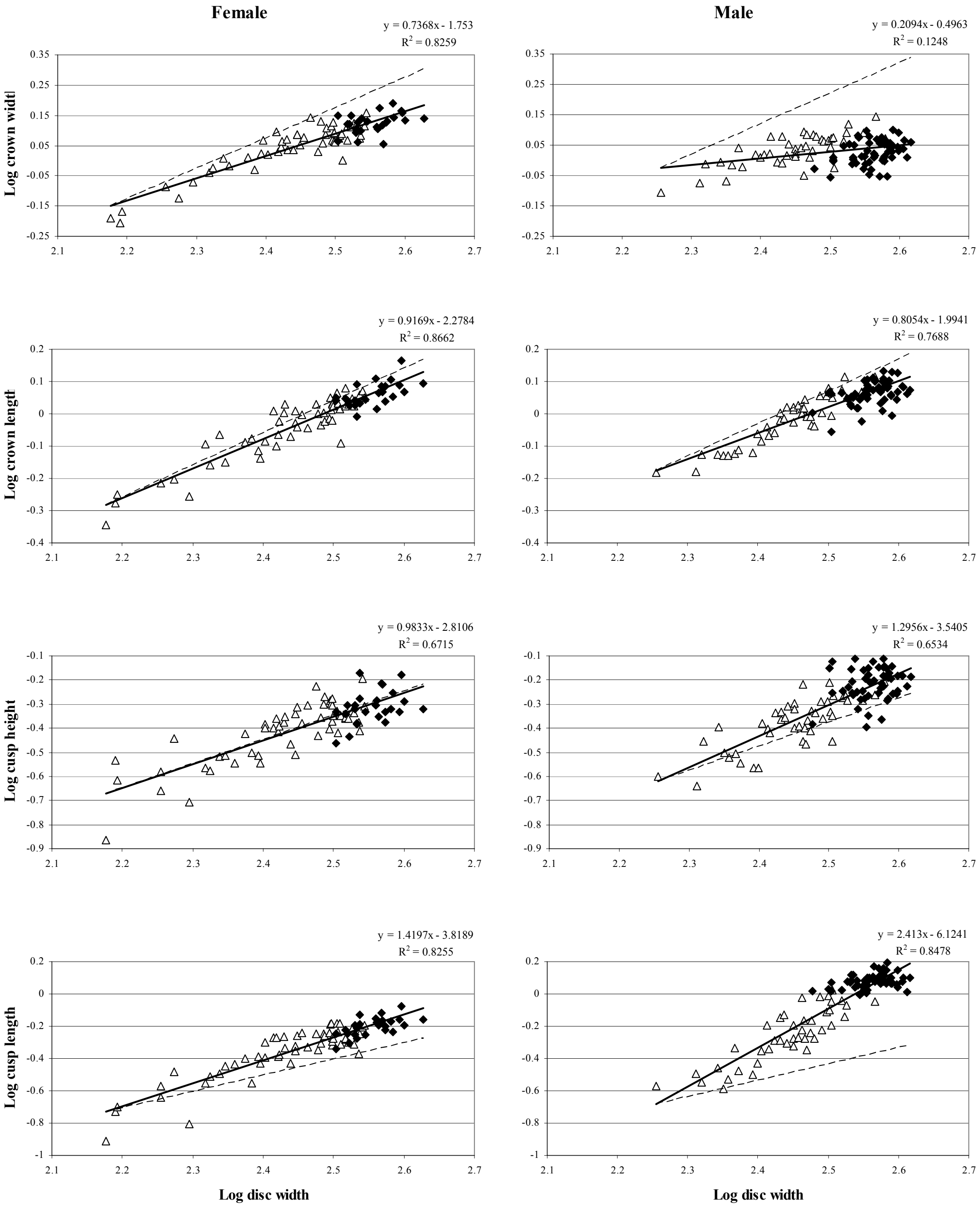
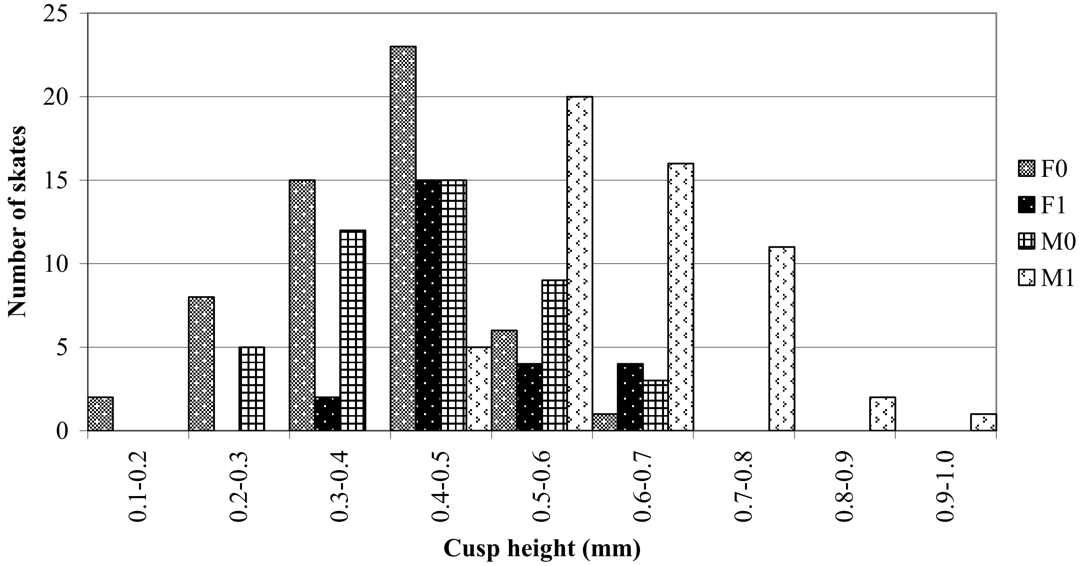

Female
Male
y = 0.7368x - 1.753
R² = 0.8259
y = 0.2094x - 0.4963
R² = 0.1248
Log crown width
0.35
0.25
0.15
0.05
-0.05
-0.15
-0.25
y = 0.9169x - 2.2784
R² = 0.8662
y = 0.8054x - 1.9941
R² = 0.7688
Log crown length
0.2
0.1
0
-0.1
-0.2
-0.3
-0.4
y = 0.9833x - 2.8106
R² = 0.6715
y = 1.2956x - 3.5405
R² = 0.6534
Log cusp height
-0.1
-0.2
-0.3
-0.4
-0.5
-0.6
-0.7
-0.8
-0.9
y = 1.4197x - 3.8189
R² = 0.8255
y = 2.413x - 6.1241
R² = 0.8478
Log cusp length
0.2
0
-0.2
-0.4
-0.6
-0.8
-1
2.1
2.2
2.3
2.4
2.5
2.6
2.7
Log disc width
Log disc width

Figure 26. Distribution histograms of cusp height and cusp length for the sex-maturity groupings indicating a non-normal distribution. F0=immature female, F1=mature female, M0=immature male, M1=mature male.


25
20
15
10
5
0
Number of skates
0.1-0.2
0.2-0.3
0.3-0.4
0.4-0.5
0.5-0.6
0.6-0.7
0.7-0.8
0.8-0.9
0.9-1.0
Cusp height (mm)
F0
F1
M0
M1

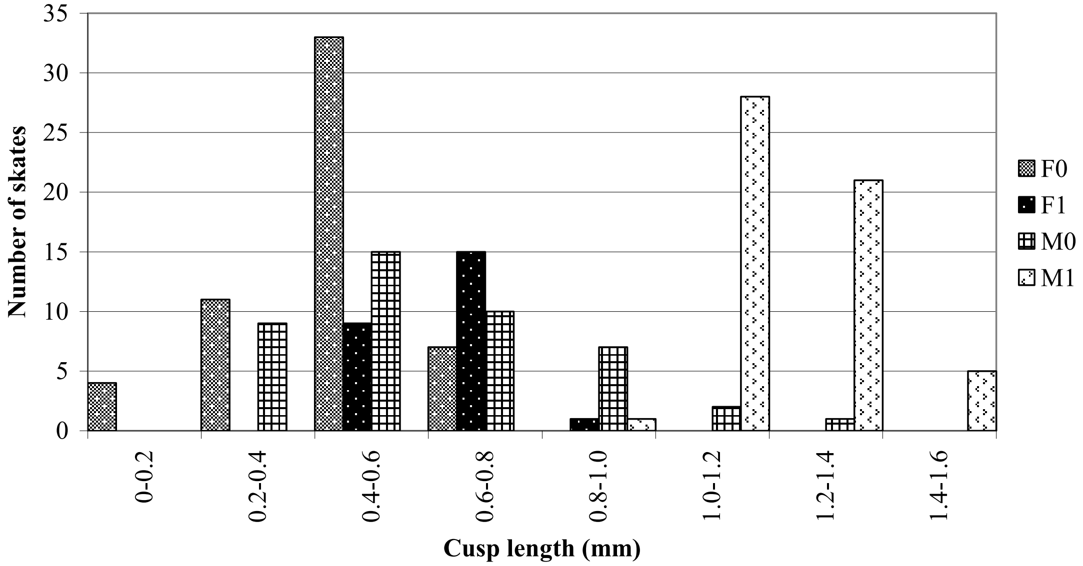

35
30
25
20
15
10
5
0
Number of skates
0-0.2
0.2-0.4
0.4-0.6
0.6-0.8
0.8-1.0
1.0-1.2
1.2-1.4
1.4-1.6
Cusp length (mm)
F0
F1
M0
M1

Figure 27. Mean values and 95% confidence intervals of the four dental measurements taken from *Bathyraja kincaidii*. a) sex*maturity interaction, IMM= immature, MAT= mature, ■= female skates, ●= male skates b) maturity*zone interaction, ▲= immature skates, ♦= mature skates * significant ($p<0.05$) for the interaction

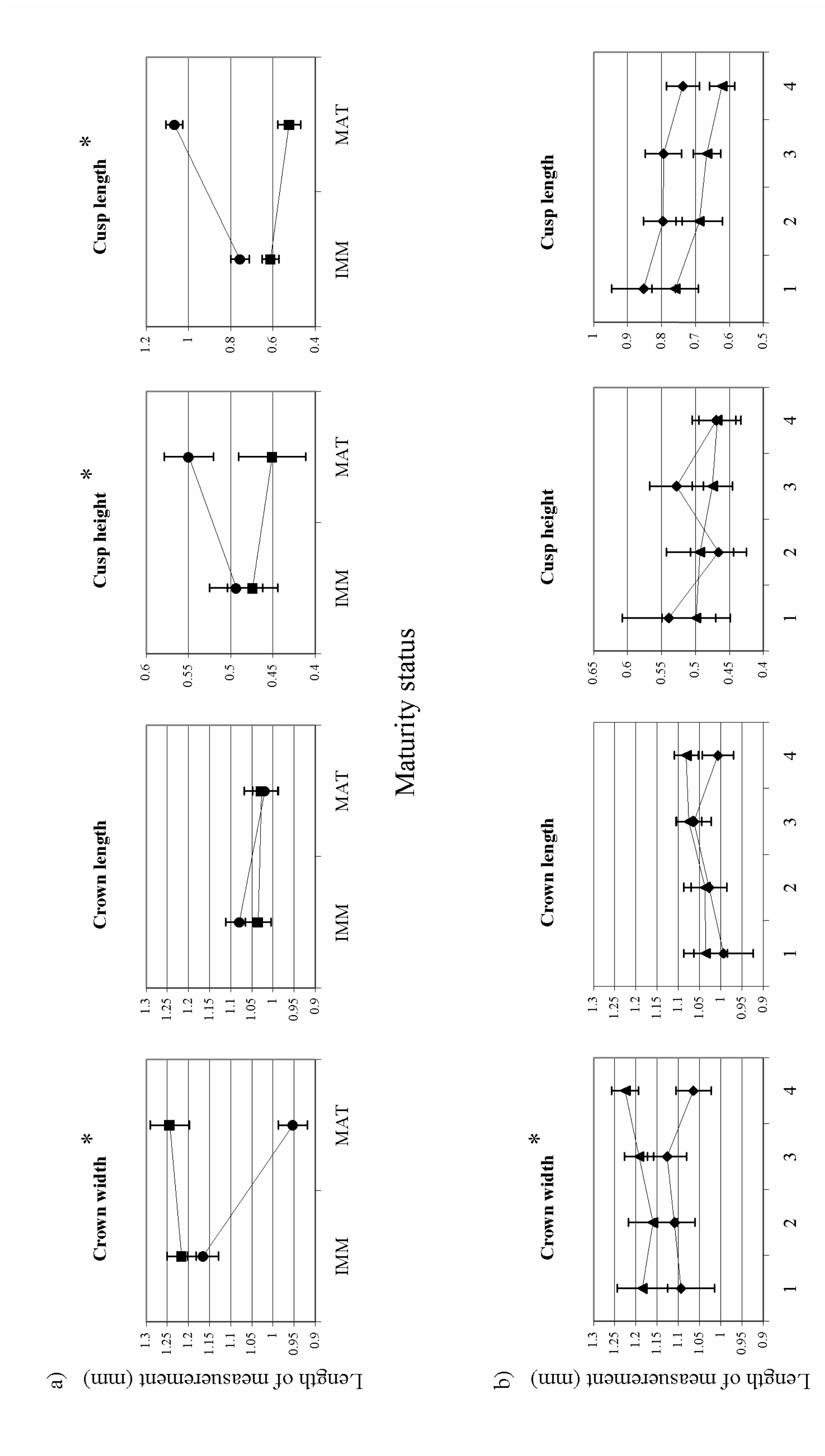
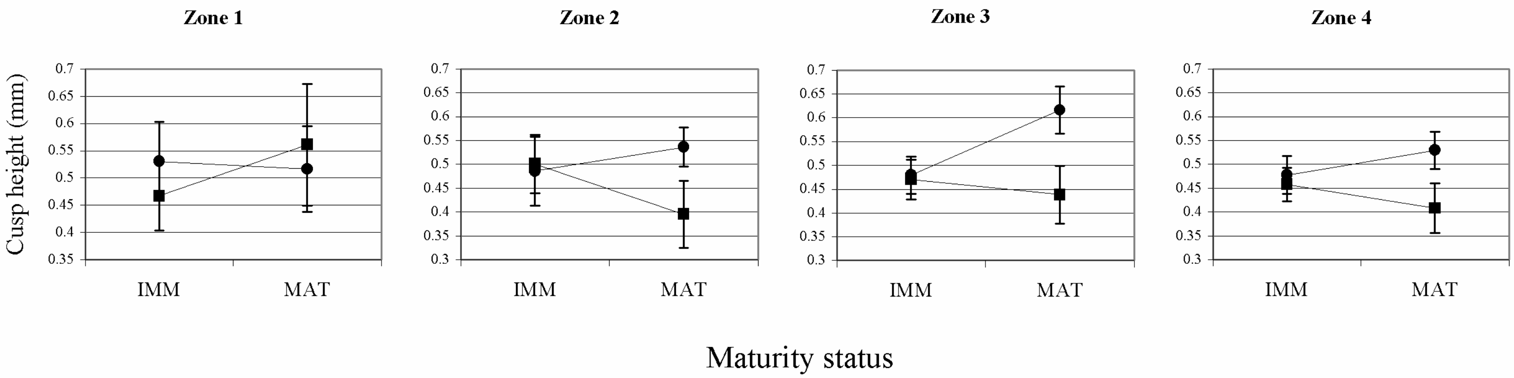

a)
Length of measurement (mm)
Crown width *
Crown length
Cusp height *
Cusp length *
1.3
1.25
1.2
1.15
1.1
1.05
1
0.95
0.9
0.6
0.55
0.5
0.45
0.4
0.8
0.6
IMM
MAT
Maturity status
b)
Length of measurement (mm)
Crown width *
Crown length
Cusp height
Cusp length
0.65
0.7
1
2
3
4
Zone

Figure 28. Mean values and 95% confidence intervals for the sex*maturity*zone interaction of the cusp height measurement of *Bathyraja kincaidii*. IMM= immature, MAT= mature, ■= female skates, ●= male skates.


Zone 1
Zone 2
Zone 3
Zone 4
Cusp height (mm)
0.7
0.65
0.6
0.55
0.5
0.45
0.4
0.35
0.3
IMM
MAT
Maturity status

APPENDIX I. IDENTIFICATION REFERENCES

Polychaetes

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Blake JA, P.H. Scott (eds) (1997) Taxonomic atlas of the benthic fauna of the Santa Maria Basin and western Santa Barbara Channel. Vol. 10. The Arthropoda- The Pycnogonida. The Crustacea Part 1- The Decapoda and Mysidacea. Santa Barbara Museum of Natural History, Santa Barbara, 151p

Kathman RD, Austin WC, Saltman JC, Fulton JD (1986) Identification manual to the Mysidacea and Euphausiacea of the northeastern Pacific. Can Spec Publ Fish Aquat Sci 93:1-411.

Shrimps

Butler TH (1980) Shrimps of the Pacific coast of Canada. Can B Fish Aquat Sci 202: 1-280

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