2006

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Recommended Citation

Robinson, Heather Joan, "Food habits of the Longnose Skate, Raja rhina (Jordan and Gilbert, 1880), in central California waters" (2006). *Capstone Projects and Master's Theses*. 85.
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FOOD HABITS OF THE LONGNOSE SKATE, *RAJA RHINA* (JORDAN AND GILBERT, 1880), IN CENTRAL CALIFORNIA WATERS

A Thesis
Presented to
The Faculty of
Moss Landing Marine Laboratories
and the College of Science
California State University, Monterey Bay

In Partial Fulfillment
of the Requirements for the Degree
Masters of Science

by
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September 2006

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ABSTRACT

FOOD HABITS OF THE LONGNOSE SKATE, *RAJA RHINA* (JORDAN AND GILBERT, 1880), IN CENTRAL CALIFORNIA WATERS

by Heather Joan Robinson

Feeding studies can provide researchers with important insights for understanding potential fishery impacts on marine systems. Knowing what a species eats can provide information about possible distribution and its position in food webs. *Raja rhina* is one of the most common elasmobranch species landed in central and northern California demersal fisheries, yet life history information is extremely limited for this species and aspects of its diet are unknown. Specimens of *R. rhina* were collected between September 2002 and August 2003 from fishery-independent trawl surveys. Values of Percent Index of Relative Importance (IRI) indicated that the most important prey items in 618 stomachs of *R. rhina* were unidentified teleosts (31.6% IRI), unidentified shrimps (19.6%IRI), unidentified euphausiids (10.9% IRI), Crangonidae (7.4% IRI), and *Neocrangon resima* (6.0% IRI). Smaller skates generally ate crustaceans and larger skates ate fishes and cephalopods. With increasing depths, diet included deeper-living fish species and more cephalopods and euphausiids. The findings of this study were consistent with previous researchers that reported similar diet shifts in skate species with size and depth.

ACKNOWLEDGEMENTS

Funding for this research was provided by NOAA/NMFS to the National Shark Research Consortium and Pacific Shark Research Center, and in part by the National Sea Grant College Program of the U.S. Department of Commerce's National Oceanic and Atmospheric Administration under NOAA Grant no. NA04OAR4170038, project number R/F-199, through the California Sea Grant College Program, and in part by the American Elasmobranch Society and the Western Groundfish Conference.

I would like to start off by thanking my committee members. Dr. Gregor M. Cailliet was incredibly supportive during my entire term here at MLML and provided me with a great deal of advice. I could not have done so well without his guidance. To Dr. David A. Ebert I owe many thanks for continued support to this project, both with his elasmobranch expertise and with providing me with a steady job. Dr. Lara Ferry-Graham has made huge contributions to this project and without her amazing mind for statistics I may have been her for another few years! And Dr. James Harvey, without whom my project would be lacking some details that he made me explore further.

I owe a great deal of gratitude to the many members of the Pacific Shark Research Center who have been there from the beginning to the end of this project. They have helped process skate specimens, read snippets of this manuscript, and listened to many practice talks throughout these past four years.

Mainly I would like to thank Shaara Ainsley, Daniele Ardizzone, Lewis Barnett, Simon Brown, Aaron Carlisle, Chante Davis, Brooke Flammang, Diane Haas, Ashley Neway, Chris Rinewalt, Tonatiuh Trejo.

I would like to thank Don Pearson and his crew from the National Marine Fisheries Service, Santa Cruz Lab, for providing me with the samples that were used for this project.

I would especially like to thank Wade Smith and Joe Bizzarro. Without these two individuals my experience here at MLML would have been a much harder ordeal. They truly paved the way for future generations here in the Ichthyology Lab and I have benefited from their knowledge in more ways than I can count. Wade was always willing to listen to my problems and try to help me figure out solutions and for that I cannot thank him enough. Joe, what can I say about Joe? When I got to MLML I knew nothing about feeding studies and within a matter of months Joe had taken me under his wing and had taught me all he knew. From there he encouraged me to grow by treating me as an equal. We often spent time conversing about ideas and techniques. Those conversations were probably the most significant events to the development of not only this project but to my own self as a scientist. So thank you Joe for never giving me the answers, but working things through with me!

The many staff members of MLML deserve a big round of applause for all the help they have given me. Donna Kline, Ashley Vizurraga, Jane Schuytema, Toni Fitzwater, Jeff Arlt, Brandon Rose, Lynne McMasters, Joan Parker, Barry

Giles, James and Billy Cochran, Ralph Dzuro. All of these individuals have meant so much to me and have all aided in this process immensely!

To all of my friends and family, thank you for the continued love and support.

And finally I would like to dedicate this project to my father, Richard John Robinson. Without this amazing man not only would I not be alive, but I would in no way be the woman that I am today. He taught me so much about who I wanted to be and he always encouraged me to follow my heart. Throughout this entire adventure at MLML I have had him by my side encouraging me. It is only with his love and memory that I had the courage to return to California three years ago, and I feel it is only appropriate to dedicate my work to him!

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INTRODUCTION

Diet is an important component of the life history of a species. Knowing what a species eats can provide information about possible distribution and its position in food webs (Ebert et al. 1991, Barry et al. 1996, Ellis et al. 1996, Cortés 1999). Understanding a predator's trophic interactions also can be crucial for developing proper management strategies.

Skates (families Anacanthobatidae, Arhynchobatidae, and Rajidae) comprise a large portion of bottom fishes caught off California. Although, not specifically targeted from 1916 to 1990, skate landings were 90% of all elasmobranch catch, and the most recent estimates indicated that these landings have increased tenfold for a net profit of greater than $340,000/yr. (Zorzi et al. 2001). In comparison with many teleost fishes, skates, generally, are slow growing, late maturing, and have low fecundity, making them potentially more susceptible to overfishing (Zorzi et al. 2001). Although skates are widespread and speciose (with more than 280 species from temperate and sub-polar waters) minimal research has been conducted on the life history traits of these fishes. The limited amount of specific life history information for most skate species in the eastern North Pacific Ocean, along with poor fisheries statistics, due to an inability to properly identify species, makes it difficult to determine exactly what impacts fisheries are having on skate populations. Although the diets of several skates have been examined (McEachran et al. 1976, Berestovskiy 1989, Pedersen 1995, Morato et al. 2003), the majority of these studies were conducted in the Atlantic Ocean, and few researchers have analyzed diet of Pacific skate species (Orlov 1998, 2003, Yeon et al. 1999). The community-level effects of population changes, therefore, cannot be easily predicted for this region.

Raja rhina (Jordan & Gilbert 1880), the longnose skate, is one of eleven skate species off California (Ebert 2003), and with *R. binoculata* and *R. inornata*, it is one of the most commercially important skates caught in central and northern California fisheries (Zorzi et al. 2001). It is easily distinguished from the other four members of the family Rajidae by its extremely long, acutely pointed snout. This skate occurs from southeast Bering Sea southward to Cedros Island, Baja California and the Gulf of California (Mecklenburg et al. 2002). *Raja rhina* occurs in areas of mud-cobble bottoms with some vertical relief, nearshore to depths of 1,000 m (Ebert 2003), making it easily captured by bottom trawlers working on the Pacific continental shelf. The only life history research on *R. rhina* is an unvalidated age and growth study by Zeiner & Wolf (1993).

Other than anecdotal reports, the diet of *R. rhina* is unknown. The first objective of this study was to characterize the diet of *R. rhina*. I, therefore, provide information that helps elucidate the integral role of *R. rhina* in the surrounding community and the potential impacts of its removal on the central California benthic food web.

Shifts in diet have been studied for many other skate species by several researchers. Diet has been observed to change as skates reach larger sizes;

with shrimp and small crustaceans dominating the diet in small juveniles and teleosts, large crustaceans, and polychaetes being more common in larger adults (Ajayi 1982, Yeon et al. 1999, Koen Alonso et al. 2001). Templeman (1982) found that in deeper water, teleosts and cephalopods were more important in the diets of *Raja radiata* than they were to those skates inhabiting shallower waters. Some researchers have examined dietary differences between sexes and found no difference (Koen Alonso et al. 2001, Dolgov 2005). It is the second objective of this study to compare the diet of *R. rhina* between the sexes, size classes, and among depth categories. I will, thereby, determine if the population of *R. rhina* from central California exhibits similar diet shifts as other skate species.

MATERIALS AND METHODS

Sample Collection

Raja rhina were collected between September 2002 and August 2003 by the National Marine Fisheries Service, Southwest Fisheries Science Center (NMFS-SWFSC). Fishing vessels were contracted by NMFS-SWFSC to make a series of five otter trawls every month, weather permitting. Each of the five hauls was at a different depth, ranging from 15 to 532 m, along the continental shelf and upper slope, over soft bottom habitats. The majority of hauls was off Davenport, California (n=27), with the rest in Monterey Bay (n=17). This method of sample collection presents a potential bias in that samples used to characterize this population's diet may be caught in various amounts by individual hauls. For instance, one haul may land over a hundred specimens while another haul may only land a few individuals. The resulting diet analysis would then be biased towards the stomach contents of the individuals in the larger haul, while stomach contents of the individuals from the smaller haul would be greatly underrepresented in the overall analysis. This collection methods also limited the sampling spatially, therefore data collected from these samples provides information about food habits of*Raja rhina* from central California only, not from the entire range of this species.

All skate specimens were transported to Moss Landing Marine Laboratories (MLML) for dissection. Whole skates were frozen within 2-12 hours from initial capture, and at later dates (usually within several days after freezing) specimens were thawed and sorted by species. Skates were weighed to the nearest 0.1 kg using a hanging scale, however, extremely small individuals were weighed on a top-loading balance. Measurements of total length (TL, tip of snout to tip of tail), disk length (DL, tip of snout to posterior edge of pectoral fins), and disk width (DW, widest span of pectoral fins) were made to the nearest millimeter (mm) for each specimen (Ebert 2003). Sex and maturity were determined following Ebert (2005). Stomachs of all skates were removed, placed in individual bags, and re-frozen. The time intervals between freezing, thawing, and re-freezing were not thought to be long enough to cause any further degradation of stomach contents.

Overall Diet Characterization

For months in which more than 100 *R. rhina* were collected, a random sub-sample of 100 stomachs was chosen for processing. In months when fewer than 100 *R. rhina* were collected, all samples were processed. By processing these random sub-samples I have lessened the effect of any sampling biases (explained above) due to collection efforts. All stomachs were thawed and contents retained on a 500 μm sieve were sorted into prey categories. Once sorted, prey items were blotted on paper towels, wet-weighed to the nearest 0.1 milligram (mg), enumerated, and identified to lowest possible taxa using a dissection microscope and local taxonomic guides and museum specimens. When prey were greatly digested and only body fragments remained, the greatest number of individuals potentially represented by those remains was recorded (Skjaeraasen & Bergstad 2000). Prey items that were unfamiliar at the time of stomach dissection were preserved in 10% buffered formalin and stored in 70% ethyl alcohol until they could be identified to lowest possible taxonomic level, as described above.

Cumulative prey species and prey diversity curves were plotted to determine if enough stomach samples had been processed to assess the species richness and diversity of *R. rhina* diet. The prey species curves were generated using a MATLAB computer program (Adams, 2004), that randomized and resampled the data 100 times to estimate mean, and standard deviation (SD), numbers of new prey for each stomach analyzed. Prey diversity curves, using the Shannon – Weiner diversity index, were generated in the same randomized manner with a modified version of the MATLAB program that calculated mean diversity and standard error (SE). This technique relies upon the assumption that as sample size increases, variation in the estimate of species richness and diversity should decrease and the curve should reach an asymptote as the number of new species in samples approaches zero or the diversity does not change because new prey items are introduced only rarely (Ferry & Cailliet 1996, Cortés 1997).

Prey items were quantified using measures discussed by Hyslop (1980). The percentage by number (%N) was calculated by dividing the number of individuals in one prey category by the total number of individuals from all prey categories in that stomach. The percentage by weight (%W) was determined in the same manner as %N. These two measures were generated for each stomach containing food, and means were calculated to obtain average values for %N and %W across a sample group (Cailliet et al. 1986). Frequency of occurrence (%FO) was obtained by dividing the total number of stomachs containing prey of one category by the total number of stomachs containing prey of any categories. The values of these three measures were combined into the Index of Relative Importance (IRI) to alleviate the biases of using any one measure alone, and to provide a more complete description of a prey item's importance in the diet of *R. rhina*. IRI was calculated by adding %N to %W and multiplying the sum by %FO (Pinkas et al. 1971). To facilitate comparisons with previous research, IRI values were standardized by converting them to percent IRIs (Cortés 1997, 1998, Hansson 1998). Diet also was described using the following resource indices: prey diversity, $H' = |(\Sigma p_i * \ln p_i)|$; prey evenness, $J = H'/H'_{max}$; and prey dominance, $D = \Sigma p_i^2$, where p_i = proportion of species i in diet (Cailliet et al. 1986, Krebs 1999).

Intraspecific Dietary Comparisons

Shifts in the diet of *R. rhina* were assessed using the following intraspecific variables: sex (male/female), size classes, and depth. Ontogenetic shifts in diet were determined by analyzing the following size classes: small (<60 cm TL) and large (>60 cm TL). Size categories were chosen based on reports that *R. rhina* reaches maturity at 62-74 cm TL for males and 70-100 cm TL for females (Zeiner & Wolf 1993, Ebert 2003). Depth categories were: shelf (<200 m), shallow slope (200-450 m), and deep slope (>450 m). These depth categories were chosen to reflect the local bathymetry of the sampling area (Wright & King 2002).

To facilitate comparisons among intraspecific variables, all prey items were pooled into six higher taxonomic groupings: fishes, shrimps, Euphausiidae, other crustaceans, Cephalopoda, and Gastropoda. Using %IRI values for these six groupings the diets were initially compared in a pair-wise fashion with 5 separate tests of Morisita's Simplified Index of Similarity (Krebs 1999). Morisita's Simplified Index of Similarity was calculated as follows:

$$C_\lambda = \frac{2(\Sigma p_{ij} p_{ik})}{\Sigma (p_{ij})^2 + \Sigma (p_{ik})^2}$$

where: p_{ij} = proportion that resource *i* is of the total resources used by species *j*, and

p_{ik} = proportion that resource *i* is of the total resources used by species *k*.

To further examine possible dietary patterns, and to provide support for the Morisita's tests, a Principal Components Analysis (PCA) was conducted with the six prey groupings as dependant variables (McGarigal et al. 2000). Bi-plots were generated for each intraspecific variable using the PC scores, and vector plots were created with eigenvectors. The resulting component variables from the PCA were then tested with a Multivariate Analysis of Variance (MANOVA) to determine if the patterns indicated by the PCA were statistically significant (Paukert & Wittig 2002). Conducting the MANOVA on the component variables rather than on the original %IRI measures for the six prey groupings ensured the variables would not violate the assumptions of covariance and multivariate normality (Crow 1979). Within the MANOVA, significance of main effect was tested using Wilk's Lambda, Pillai's Trace Criterion, and Hotelling's Trace Criterion. Probability values were considered significant with a value less than $\alpha = 0.05$. When multivariate tests were significant, post-hoc 3-way Analysis of Variance (ANOVA) tests were conducted to determine which Principal Component (PC) was the cause for the difference in diets. The main factors (all fixed) for the ANOVAs were sex, size, and depth. Interactions were tested among all factors (sex*size, sex*depth, size*depth, and sex*size*depth), however, only significant interaction terms among factors were considered in the results.

RESULTS

Sample Collection

A total of 1,193 *R. rhina* (527 female, 666 male) was collected in NMFS-SWFSC otter trawl sampling at depths ranging from 29-532 m (Figure 1). No *R. rhina* were collected shallower than 29 m. No samples were collected in April, May, or August due to cruise cancellation.

Overall Diet Characterization

A total of 618 samples was randomly selected for analysis of stomach contents, of which 55 stomachs were empty and excluded, therefore 563 samples were analyzed. The cumulative species curve (Figure 2a) and the cumulative diversity curve (Figure 3a) for all 563 samples reached asymptotes near450 samples for species, and 75 for diversity, indicating that enough stomachs were processed to adequately describe the number of prey species in the diet and the overall diversity of *R. rhina* diet.

Sixty-seven prey items were identified to lowest taxonomic level, containing at least 23 fishes, 10 shrimps, 4 cephalopods, 1 euphausiid, 3 gastropods, and 6 other crustaceans (Table 1). Those prey items having a percent Index of Relative Importance (%IRI) value greater than 5% were: teleost (unidentified), shrimp (unidentified), Euphausiidae (unidentified), Crangonidae, *Neocrangon resima*, and *Sebastes* spp. (Figure 4a). The other 61 prey items collectively only had a %IRI value of 18.9. Of the top eight prey items identified to species level (Figure 4b), five were fishes; *Sebastes* spp., *Sebastes jordani, Citharichthys sordidus, Merluccius productus,* and *Chilara taylori*, two were cephalopods; *Octopus rubescens* and *Loligo opalescens*, and one was a shrimp; *Neocrangon resima*. Results of the resource indices indicate a diverse diet: prey diversity, H' = 3.176; prey evenness, J = 0.755; prey dominance, D = 0.060.

Intraspecific Dietary Comparisons

Cumulative species curves for each category of all intraspecific variables (sex, size, and depth) reached asymptotes (male ~ 250, female ~ 225, small ~ 200, large ~200, shelf ~ 250, shallow slope ~ 100, and deep slope ~ 70), indicating that enough samples were processed from each category to adequately describe and compare the prey species in the diets (Figure 2 b-h). Cumulative diversity curves for all intraspecific variables (Figure 3 b-h) also reached asymptotes indicating enough samples were processed to assess the diversity of each category. The diversity of prey items was less for small *R. rhina* (Figure 3d) than for large *R. rhina* (Figure 3e), and the diversity of prey items was less for skates feeding at the deepest depth (Figure 3h) than for skates feeding at either of the two shallower depths (Figure 3 f & g). Sixteen samples lacked any depth information so they were excluded from the Morisita's Index comparing depth classes. These samples also were excluded from PCA and MANOVA testing, therefore 547 samples were analyzed.

The five separate Morisita's Index of Overlap tests demonstrated a low level of similarity between the size classes (Table 2). Diets of males and females almost completely overlapped (99.4%), as did the diets of skates caught at the two shallower depths (94.3%). When the diet of skates from the deeper depths (>450 m) was compared with either of the shallower depths (76.2% and 64.4%) overlap was considered great based upon standards set forth in Cailliet and Barry (1978), however, the values were much less than the comparison of the two shallow depths, indicating a possibility that different prey items were eaten at deeper depths.

Examination of the PCA bi-plots and vector plots revealed several dietary patterns among the intraspecific variables compared (Figure 5). PC 4 explained less than 10% of the total variance; therefore, only the first three PCs were considered. In combination, the first three PCs explained 71% of the total variation in *R. rhina* diet. Prey categories that loaded heavily on PC 1 were shrimps (positive) and fishes (negative). Cephalopods, euphausiids (both positive) and shrimps (negative) loaded heavily on PC 2. Other crustaceans and gastropods (both positive) loaded heavily on PC 3. When the data were coded for sex (Figure 5 a,e) no pattern was observed, indicating there was no difference in the diets of males and females. When the data were coded for size (Figure 5 b,f) a pattern emerged, however, in which the large individuals were trending towards the lower left quadrant (Figure 5b) and to the left of the x-axis (Figure 5f), whereas the small individuals were interspersed with a slight trend to the lower right quadrant (Figure 5b). When these patterns were examined in conjunction with the vector plots (Figure 5 d,h) it appeared that diet of large individuals was dominated by fishes and diet of small individuals by shrimps. When the data were coded for depth (Figure 5 c,g), the individuals caught on the deep slope trended towards the left hand side of the group of points (Figure 5c), and below the y-axis (Figure 5g), hence this dietary pattern appeared to be driven by the presence of fishes, euphausiids, and cephalopods (Figure 5 d,h). There was no apparent pattern in diet between the two shallower depths (shelf and shallow slope).

Multivariate Analysis of Variance (MANOVA) supported the dietary patterns observed in the PCA bi-plots. All three tests for main effect (Wilks' Lambda, Pillai's Trace, and Hotelling's Trace) provided consistent values; therefore, only the results for Wilks' Lambda will be presented and discussed further. A low value of Wilks' Lambda indicated no statistical significance between diets of male and female *R. rhina*. Significant differences were detected, however, when testing for effects of size and depth (Table 3). Size-based effects on diet were the strongest and were significant on all three PCs. Although depth-based effects were significant, they were less so than size-based effects, and they were significant for PC 2. It is important to point out, however, that the prey categories that loaded heavily on PC 2 were cephalopods and euphausiids that were more commonly observed in samples from the deep slope category.

The outcome of the post-hoc ANOVA tests indicated a significant interaction between size and depth for PC 1 and PC 2 (Table 3). The resulting plots of these interactions for each PC (Figure 6) demonstrated that fish and shrimp prey that loaded heavily on PC 1 were consumed by small and large skates, respectively, such that size-effects were less extreme in skates from the deeper depths (Figure 6 a-c). The opposite trend was observed for PC 2. Cephalopods and euphausiids, which loaded heavily on PC 2, were more abundant in small *R. rhina* from deeper depths. Size effects were not extreme in skates from shallower depths (Figure 6 d-f). There was no difference in the consumption of prey items that loaded heavily on PC 3 (other crustaceans & gastropods) for either size class at any depth (Figure 6 g-i).

DISCUSSION

Overall Diet Characterization

Intermittent feeding, bouts of feeding followed by longer periods of resting or non-feeding, occurs for several shark species (Wetherbee et al. 1990, Joyce et al. 2002, Braccini et al. 2005); however skates use a more constant feeding strategy (Abd El-Aziz 1986, Ezzat et al. 1987, Muto et al. 2001). I found only 8.9% of stomachs were empty. This value is less than other rajid feeding studies that used similar collection methods (Pedersen 1995, Skjaeraasen & Bergstad 2000). State of digestion among all stomachs containing prey items was fairly consistent. Within each stomach, however, it was common to find similar prey items in various states of decomposition. The low occurrence of empty stomachs and the lack of homogeneous digestion demonstrates that *R. rhina* have no periodicity of feeding. This study, therefore, supports the idea that skates exhibit continuous feeding activity.

The ecological role of skates in terms of their dietary relationships is not easily generalized. Many researchers have classified skates as specialist feeders (Ebert et al. 1991, Orlov 1998, Mabragaña et al. 2005, Braccini & Perez 2005) whereas several others have found skate species to be generalist feeders (Holden & Tucker 1974, Smale & Cowley 1992, Koen Alonso et al. 2001). The diet of *R. rhina* consisted of 67 prey items from a wide array of biological groups (i.e. fishes, shrimps, gastropods). Washington (1984) reported that in most biological communities the value of diversity (H') does not exceed 5.0, and within this population of *R. rhina* the maximum diversity (H'_{max}) was only 4.21. Therefore, the value of prey diversity measured for *R. rhina*, 3.18, indicates that the probability of finding any one of the 67 prey items within this skate's diet was highly uncertain. Although only six prey items had a %IRI value greater than 5%, the overall diet was not dominated by any one prey species, and the remaining 61 prey items caused the diet to remain fairly even. These factors; a large number of prey items, high diversity of prey species, and an even diet, lead to the conclusion that *R. rhina* should be classified as a generalist feeder.

Although there are only two anecdotal reports of *R. rhina* diet (Wakefield 1984, Ebert 2003), neither of which had a large sample size, the findings of this study are generally consistent with those of previous researchers. Ebert (2003) described diet items as mainly benthic crustaceans and bony fishes. Wakefield (1984) found mostly fishes and decapod crustaceans, but only had four stomachs to analyze. The overall diet of *R. rhina* from my current study consisted of mostly teleost fishes (~23 species) and shrimps (~10 species). The major fish groups were the families Scorpaenidae, Myctophidae, and the order Pleuronectiformes, and the major shrimp groups were the families Crangonidae, Hippolytidae, and Pandalidae. In his recent book chapter, Allen (2006), mentions that *R. rhina* is an important member of the outer shelf (100-200 m) and mesobenthal (200-500 m) slope habitats from northern California through northern Baja California. My study in central California supports these claims, indicating that *R. rhina* is an upper lever predator feeding on other important fish species in these habitats;

Pacific hake *(Merluccius productus*), spotted cusk-eel (*Chilara taylori*), rex sole (*Glyptocephalus zachirus*) and splitnose (*Sebastes diploproa*), stripetail (*S. saxicola*) and shortbelly (*S. jordani*) rockfishes.

Cephalopods were the third most important prey group in the diet of *R. rhina*. Several other skate species have been shown to feed on cephalopods (McEachran et al. 1976, Pedersen 1995, Kabasakal 2002, Morato et al. 2003), however, this has not been previously reported for *R. rhina*. The main species eaten by *R. rhina* were *Octopus rubescens* and *Loligo opalescens*. Both of these cephalopods are common in central California with *O. rubescens* being mainly a benthic inhabitant and *L. opalescens* occupying pelagic habitats.

The use of pelagic food sources by demersal elasmobranchs has been well documented by several authors (Holden & Tucker 1974, Mauchline & Gordon 1983, Smale & Cowley 1992, Koen Alonso et al. 2001, Braccini et al. 2005). Although the actual mechanism how these prey items are ingested remains unknown there are two possible explanations. The first is simply that demersal predators are consuming fishery discards or prey that have died of other natural causes. Berestovskiy (1989) argued that the relative body shape and lie-and-wait feeding behavior of skates prevented them from successfully hunting large pelagic species, therefore, large pelagic species in skate diets can only be explained by scavenging on dead fishes.

The second explanation is that demersal predators swim off the substrate to actively hunt pelagic species that vertically migrate. Kabasakal (2002) provided evidence that demersal predators consumed several semi-pelagic cephalopod species because during daylight hours the cephalopods lived in close proximity to the bottom. Orlov (2003) speculated that due to the relative shape of the continental slope and the migratory patterns of mesopelagic fishes these prey species could be eaten by demersal skate species. Morato et al. (2003) also reported active hunting was why pelagic species were in the diet of *Raja clavata*. Pelagic species also were apparent in the diet of *R. rhina* as evidenced by the presence of *Loligo opalescens*, *Thysanoessa spinifera*, juvenile *Sebastes jordani*, and several myctophid fishes. Although I did not investigate how these pelagic prey items were ingested, the relative frequency that they were eaten by *R. rhina* indicated they were actively preyed upon rather than opportunistically scavenged. These findings are consistent with the notion that many skates may have a more benthopelagic feeding strategy.

Intraspecific Dietary Comparisons

Several investigators have compared the diet of skates between sexes (Orlov 1998, Koen Alonso et al. 2001, Morato et al. 2003, Braccini & Perez 2005, Dolgov 2005). In the majority of species examined, males and females fed on similar prey items. Only Orlov (1998, 2003) found different diets between sexes of several species of bathyrajid skates; males consumed more crab and cephalopod species whereas females ate more fish species. Orlov (1998) attributed these differences to a size dimorphism between male and female skates. Although size dimorphism does occur in other rajid species, no other researcher found dietary segregation. My results are consistent with previous papers, diets of male and female *R. rhina* overlapped by 99.4%, despite the fact that females are larger than males.

Ontogenetic shifts in diet are common phenomena among rajid species. Many researchers have reported a general trend whereby younger, smaller skates tended to feed on smaller prey such as gammarid amphipods and small shrimps, whereas older, larger typically consumed larger shrimps, polychaetes, and fishes (Ajayi 1982, Yeon et al. 1999, Muto et al. 2001, Brickle et al. 2003). Lucifora et al. (2000) provided evidence that large and small *Dipturus chilensis* fed on the same prey species but the relative size of the fish consumed increased with larger predator size. These general patterns were clearly observed in the diet of *R. rhina*. Smaller *R. rhina* had a diet consisting more of shrimps, whereas larger *R. rhina* consumed a greater amount of fishes. Although there was some degree of overlap between the two size classes, due to similar prey species being consumed by both size classes, the relative sizes of those prey species increased with increasing size of *R. rhina.* The reason for these patterns is morphological constraints in which smaller skates are restricted to smaller prey because of gape limitation and less-developed foraging abilities (Smale & Cowley 1992, Lucifora et al. 2000, Braccini & Perez 2005). It is commonly thought that these shifts in diet are a mechanism to reduce intraspecific competition among members of a community. The central

Californian population of *R. rhina* exhibited ontogenetic shifts in diet that are common within this group of fishes.

Changes in diet with increasing depth has been a highly understudied aspect of skate feeding, and only a few authors have included it into their research. Hacunda (1981) reported that in the Gulf of Maine, demersal fishes selected prey from different depth strata as a means of food resource partitioning. Templeman (1982) determined that in the diet of *Raja radiata* certain fish species and cephalopods were more important in deeper water whereas crabs and other fishes were consumed more often in shallower water. Ebert et al. (1991) concluded that off the west coast of southern Africa there were two distinct skate communities, one shallower and one deeper than 380 m. Although these two communities were determined to be distinct, both groups had members that filled similar niches (i.e. crustacean specialists). Although all three of these studies concluded there were depth-based dietary differences not one of them performed any analyses to determine if these differences were statistically significant, therefore, these conclusions have to be accepted with caution. In the present study, the diet of *R. rhina* changed with increasing depth. Cephalopods, euphausiids, and certain fishes (mainly rockfishes) were all more important in the diets of skates living deeper than 450 m. Unlike previous studies, these results were significant by means of multivariate analyses. Although prey abundance was not measured, it seems likely that these shifts with depth were a function of prey species availability in the deeper sections of *R. rhina* range. Therefore, it is possible that *R. rhina* has incorporated these prey species into its diet as a way to further reduce intraspecific competition.

Importance of Statistical Methodology

Compound measures of importance (IRI, etc.), while being used more commonly, are still highly underutilized in diet and feeding studies. The importance of measuring more than one individual parameter (i.e. number, weight/volume, or frequency of occurrence) and incorporating these measures into one encompassing index has been discussed by several authors (Hyslop 1980, Ferry & Cailliet 1996, Cortés 1997, Braccini et al. 2005). The major reasoning behind using a compound index is that each measure alone has an amount of inherent bias, therefore, using any one measure will provide different conclusions than if another measure was chosen for analysis. For instance, in the current study, if only data for %W were examined, *Sebastes* species would have had greater importance in *R. rhina* diet whereas, if only %FO was examined, the importance of cephalopod species in *R. rhina* diet would have been over accentuated. Only by combining all three measures into the %IRI was I able to remove the bias of numerically abundant prey items, heavier prey items, and frequently consumed prey items to provide a complete comprehensive description of the overall diet of *R. rhina*. This study thereby provides evidence to support and to endorse the use of compound measures of importance in any future feeding studies.

There is an overwhelming lack of any statistical support for results presented in the majority of published literature of feeding studies. Most authors use common overlap or similarity measures to compare diets within and among species. Although there is nothing inherently wrong with using these measures, the problem arises in that researchers try to classify the resulting data as significant. Ferry & Cailliet (1996) indicated that, in spite of an index's power, they are not probability-based statistics, therefore, you cannot infer any significance. The only means for a researcher to make these claims is to follow a similarity index with some sort of parametric or non-parametric statistical test. Crow (1979) stated, that when testing for differences in two or more groups of fish with more than one prey species, multivariate tests are mandatory, and although this was published more than 25 years ago researchers continue to publish these types of comparisons without the proper statistics.

Another problem with simply using an index is that sometimes patterns in data are not fully realized until a more complex statistic is employed. The results of this current study make this point very clearly. If *R. rhina* diet was only compared with the Morisita's Index of Overlap, then it would have been thought that the diet of skates at any depth were greatly overlapped and were similar. The diets of small and large skates also would have been considered only marginally dissimilar. However, by also using a Principal Components Analysis and a Multivariate Analysis of Variance, some significant patterns were observed between the size classes and among the depth categories. These are patterns that can yield important differences in any management models, yet they would have remained unnoticed without the use of parametric statistics. By clearly describing significant patterns in *R. rhina* diet I have supported previous reports that complex statistical methods are mandatory to completely characterize diet.

CONCLUSION

Despite obvious regional differences in species composition, the diet of *Raja rhina* is consistent with other skate species (Orlov 1998, Yeon et al. 1999, Lucifora et al. 2000, Koen Alonso et al. 2001). The main prey groups used by *R. rhina* are fishes (mainly *Sebastes* spp., *Citharichthys sordidus, and Merluccius productus*), crustaceans (mainly Crangonidae, *Pasiphaea pacifica*, and Euphausiidae), and cephalopods (*Octopus rubescens* and *Loligo opalescens*). No difference was detected between males and females. There was a significant dietary shift, however, from small shrimps to large teleosts with increasing skate total length. Along the central California coast, *R. rhina* ate more cephalopods, euphausiids, and certain fishes became more important at deeper depths. These details of *R. rhina* feeding are crucial in understanding how this species fits into the demersal food web of this region. When other life history parameters are determined, and combined with my research, we can infer how this skate may be impacted by commercial fisheries and how this impact will translate to the larger community. Such findings will be essential for developing models for ecosystem-based management.

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Table 1: Percent Index of Relative Importance (%IRI) values calculated for all prey items (n=67) for all *R. rhina* stomach samples (n=563) with sexes, sizes, and depths combined. Values in bold are those for the 6 prey categories of higher taxonomic grouping.

Prey Category		%N	%W	%FO	%IRI
Fishes		**41.13**	**51.75**	**71.05**	**63.47**
	Teleost (unidentified)	13.29	13.81	33.39	31.66
	Sebastes spp.	4.60	6.22	14.39	5.45
	Sebastes jordani	4.53	6.01	6.75	2.49
	Citharichthys sordidus	3.26	4.22	6.75	1.77
	Merluccius productus	2.63	3.79	6.22	1.40
	Chilara taylori	2.81	3.39	5.15	1.12
	Stenobrachius leucopsarus	1.44	2.50	5.51	0.76
	Glyptocephalus zachirus	1.22	2.14	2.66	0.31
	Lycodes diapterus	0.68	1.36	1.78	0.13
	Pleuronectidae	0.64	0.90	2.31	0.12
	Sebastes saxicola	0.91	1.27	1.42	0.11
	Genyonemus lineatus	1.01	1.01	1.24	0.09
	Diaphus theta	0.52	0.58	1.60	0.06
	Sebastes diploproa	0.75	0.81	0.89	0.05
	Parophrys vetulus	0.42	0.60	0.89	0.03
	Myctophidae	0.41	0.19	1.42	0.03
	Microstomus pacificus	0.43	0.46	0.89	0.03
	Lyopsetta exilis	0.28	0.50	0.89	0.02
	Zoarcidae	0.20	0.35	0.53	0.01
	Citharichthys spp.	0.22	0.23	0.53	0.01
	Icelinus spp.	0.10	0.19	0.36	0.00
	Citharichthys stigmaeus	0.09	0.20	0.36	0.00
	Porichthys notatus	0.12	0.09	0.36	0.00
	Tarletonbeania crenularis	0.02	0.17	0.36	0.00
	Lycodes cortezianus	0.18	0.18	0.18	0.00
	Xeneretmus spp.	0.09	0.18	0.18	0.00
	Engraulis mordax	0.09	0.16	0.18	0.00

TABLE 1 CONTINUED

Prey Category		%N	%W	%FO	%IRI
	Zalembius rosaceus	0.09	0.16	0.18	0.00
	Apristurus brunneus	0.09	0.08	0.18	0.00
	Agonidae	0.01	0.01	0.18	0.00
Shrimps		**31.55**	**26.57**	**47.96**	**26.81**
	Shrimp (unidentified)	13.93	8.93	24.51	19.61
	Crangonidae	7.78	6.72	14.56	7.39
	Neocrangon resima	7.10	7.37	11.90	6.03
	Pasiphaea pacifica	1.05	0.89	3.02	0.20
	Pandalidae	0.34	0.89	1.24	0.05
	Spirontocaris spp.	0.35	0.36	0.89	0.02
	Spriontocaris sica	0.13	0.28	0.89	0.01
	Crangon alaskensis	0.23	0.24	0.71	0.01
	Spirontocaris holmesi	0.13	0.30	0.71	0.01
	Sergestes similis	0.24	0.16	0.53	0.01
	Spirontocaris snyderi	0.06	0.14	1.07	0.01
	Pandalopsis spp.	0.18	0.18	0.18	0.00
	Pandalus jordani	0.04	0.10	0.18	0.00
	Heptacarpus spp.	0.01	0.02	0.18	0.00
Cephalopoda		**6.94**	**11.05**	**27.00**	**4.67**
	Octopus rubescens	3.15	5.54	12.61	3.83
	Loligo opalescens	2.19	4.53	8.70	2.05
	Cephalopoda (unidentified)	1.43	0.84	6.75	0.53
	Octopoda	0.09	0.06	0.36	0.00
	Gonatus spp.	0.07	0.00	0.36	0.00
	Histioteuthis spp.	0.01	0.08	0.18	0.00
Euphausiidae		**11.59**	**5.61**	**18.83**	**3.11**
	Euphausiidae (unidentified)	11.43	5.48	18.47	10.93
	Thysanoessa spinifera	0.16	0.13	0.71	0.01
Other Crustaceans		**8.06**	**4.83**	**15.28**	**1.89**
	Eucarida	6.50	3.00	10.48	3.48
	Brachyura	0.33	0.40	1.07	0.03

TABLE 1 CONTINUED

Prey Category		%N	%W	%FO	%IRI
	Schmittius politus	0.31	0.50	0.89	0.03
	Mursia gaudichaudii	0.34	0.46	0.89	0.02
	Crustacean (unidentified)	0.27	0.24	0.89	0.02
	Euphilomedes carcharodonta	0.15	0.01	1.07	0.01
	Chionoecetes tanneri	0.06	0.16	0.18	0.00
	Stomatopoda	0.04	0.02	0.18	0.00
	Chirostylidae	0.03	0.02	0.18	0.00
	Galathaidae	0.01	0.02	0.18	0.00
	Cumacea	0.03	0.00	0.18	0.00
Gastropoda		**0.72**	**0.20**	**4.09**	**0.04**
	Amphissa bicolor	0.30	0.11	1.95	0.03
	Gastropoda (unidentified)	0.29	0.08	1.24	0.02
	Astyris gausapata	0.07	0.01	0.71	0.00
	Amphissa spp.	0.06	0.00	0.53	0.00

Table 2: Results of five separate Morisita's Index of Overlap tests that were calculated to compare the intraspecific variables of sex, size, and depth. Asterisks indicate values of low similarity when using a significance level of 0.53 (Cailliet and Barry 1978). Values in parentheses are the number of samples within each variable.

Intraspecific Variables Compared	Morisita's Index of Similarity
Females/Males (264/299)	0.994
Small/Large (327/236)	0.491*
Shelf/Shallow Slope (348/117)	0.943
Shelf/Deep Slope (348/82)	0.762
Shallow Slope/Deep Slope (117/82)	0.646

Table 3: Multivariate Analysis of Variance (MANOVA) results for all intraspecific variables tested (sexes, sizes, and depths) using %IRI values. Wilks' Lambda values are presented. Univariate F-tests are presented for size and depth as the MANOVA was significant for these effects. Only size*depth yielded a significant interaction in the ANOVA tests and is included here.

Variable Tested	Multivariate Test Statistics			Univariate Test Statistics								
	Wilks' Lambda			Principal Component 1			Principal Component 2			Principal Component 3		
	df	*F*	*p*	*df*	*F*	*p*	*df*	*F*	*p*	*df*	*F*	*p*
Sex	3, 540	1.709	0.164	-	-	-	-	-	-	-	-	-
Size	3, 540	77.473	<0.0001*	1	105.471	<0.0001*	1	8.156	0.004*	1	5.115	0.024*
Depth	6, 1080	16.025	<0.0001*	2	1.836	0.160	2	40.260	<0.0001*	2	1.189	0.305
Size*Depth	-	-	-	2	8.662	<0.0001*	2	3.639	0.027*	2	0.952	0.387

* Indicates significant result at $\alpha = 0.05$.

Figure 1: Sample locations in central California where *R. rhina* were collected by National Marine Fisheries Service–Southwest Fisheries Science Center (NMFS-SWFSC) otter trawls. Each white circle is an individual trawl and size of white circle indicates the relative number of *R. rhina* collected in each trawl.

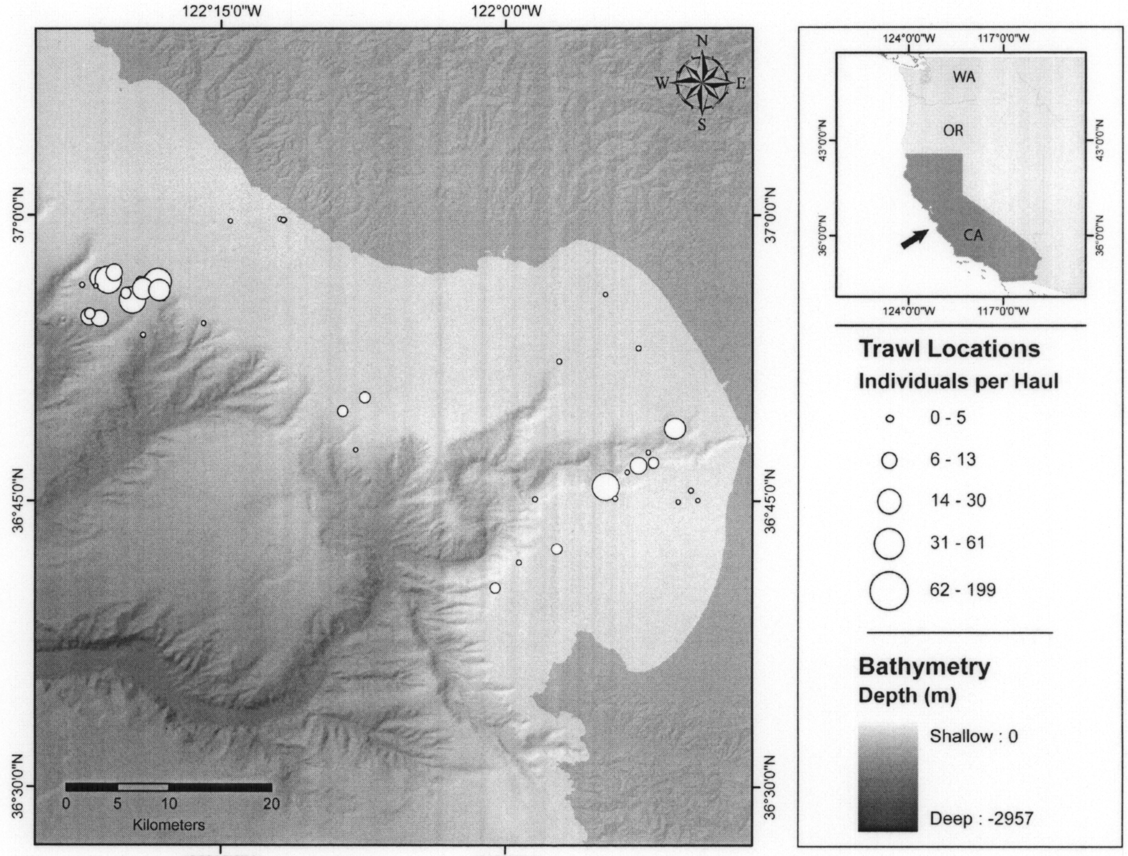

122°15'0"W
122°0'0"W
37°0'0"N
36°45'0"N
36°30'0"N
N
S
E
W
0
5
10
20
Kilometers
124°0'0"W
117°0'0"W
43°0'0"N
36°0'0"N
WA
OR
CA
Trawl Locations
Individuals per Haul
0 - 5
6 - 13
14 - 30
31 - 61
62 - 199
Bathymetry
Depth (m)
Shallow : 0
Deep : -2957

Figure 2: Cumulative prey species curves for all *R. rhina* samples processed (a) to lowest possible taxonomic level (n=67), and for all intraspecific variable categories (b-h). Variable categories are male, female, small (<60 cm), large (>60 cm), shelf (<200 m), shallow slope (200-450 m), and deep slope (>450 m). The numbers of samples processed within each category are given with the corresponding curves. Error bars represent standard deviation (SD).

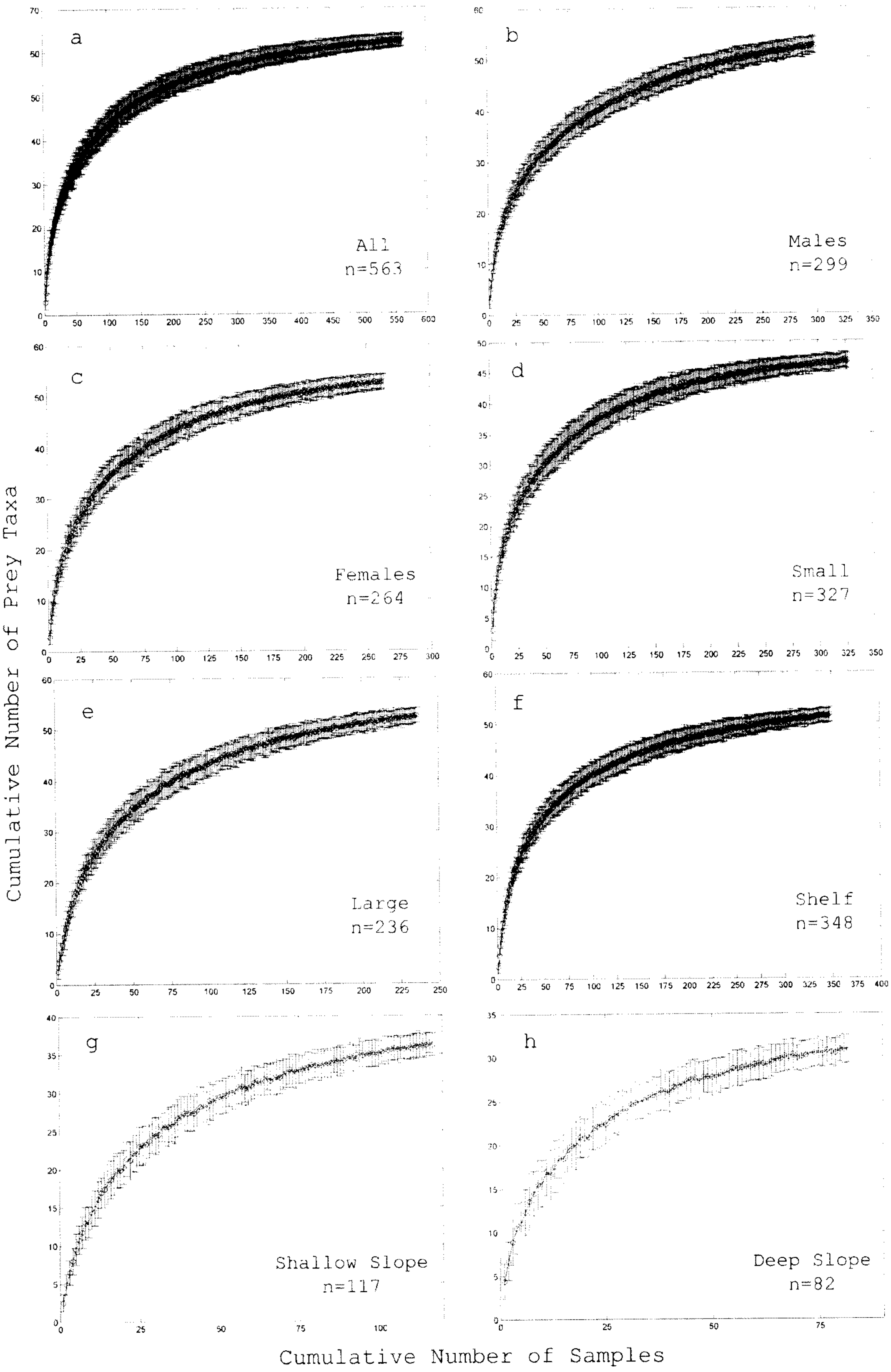
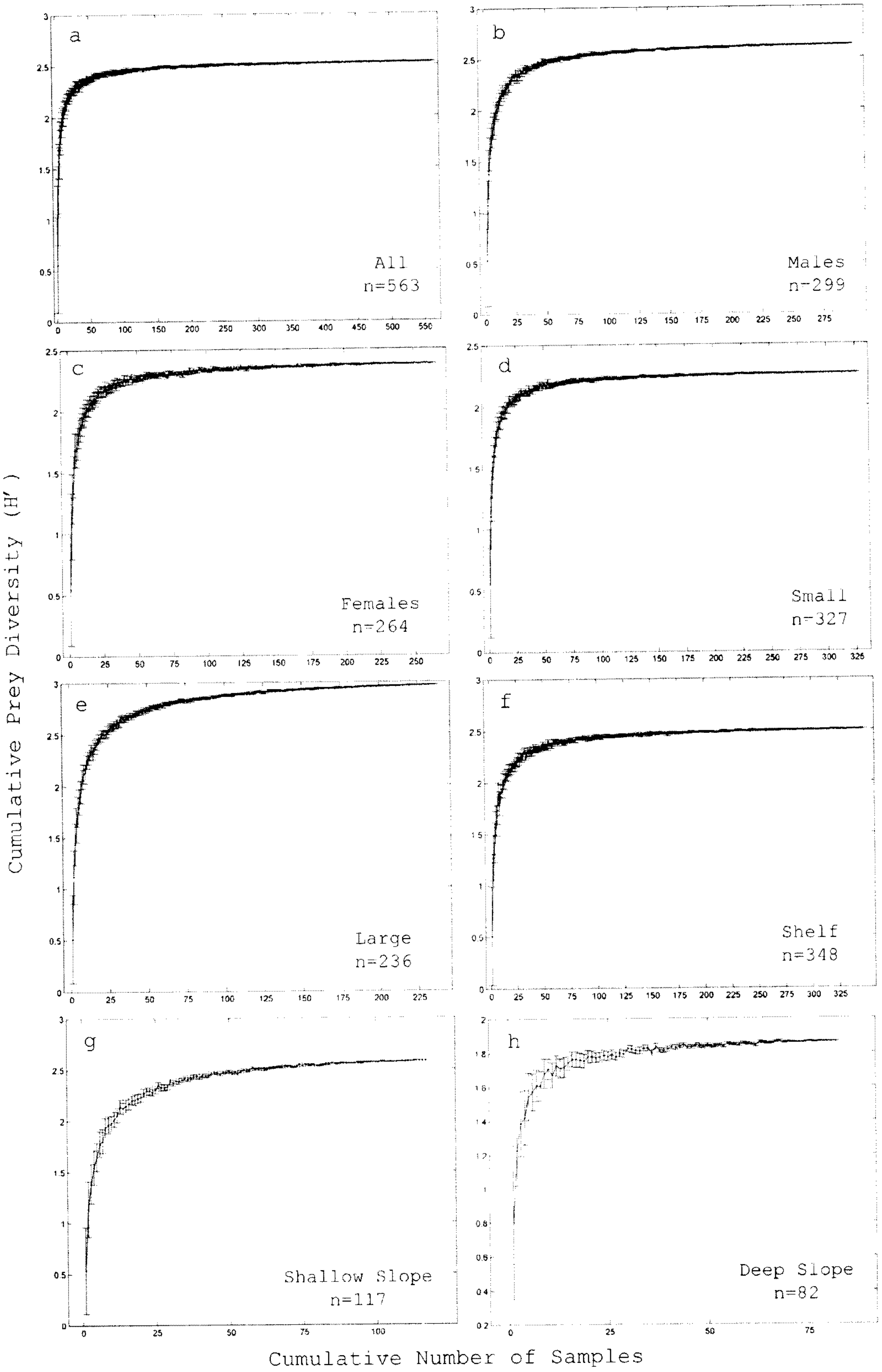
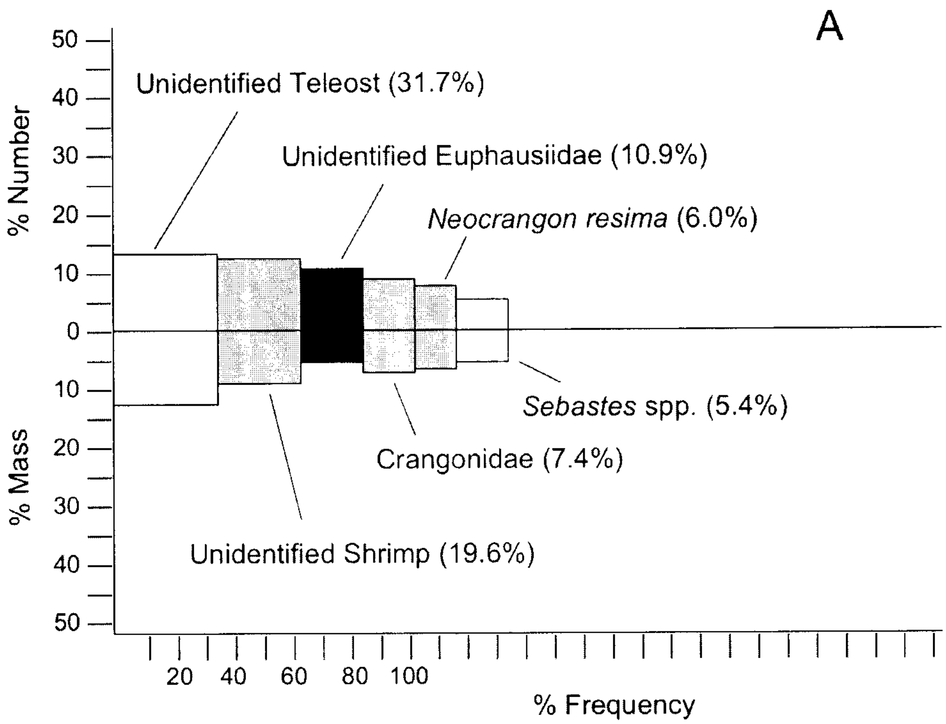

Cumulative Number of Prey Taxa
a
All
n=563
b
Males
n=299
c
Females
n=264
d
Small
n=327
e
Large
n=236
f
Shelf
n=348
g
Shallow Slope
n=117
h
Deep Slope
n=82
Cumulative Number of Samples

Figure 3: Cumulative prey diversity curves for all *R. rhina* samples processed (a) to lowest possible taxonomic level (n=67), and for all intraspecific variable categories (b-h). Variable categories are male, female, small (<60 cm), large (>60 cm), shelf (<200 m), shallow slope (200-450 m), and deep slope (>450 m). The numbers of samples processed within each category are given with the corresponding curves. Error bars represent standard error (SE).



Cumulative Prey Diversity (H')
a
All
n=563
0 50 100 150 200 250 300 350 400 450 500 550
b
Males
n=299
0 25 50 75 100 125 150 175 200 225 250 275
c
Females
n=264
0 25 50 75 100 125 150 175 200 225 250
d
Small
n=327
0 25 50 75 100 125 150 175 200 225 250 275 300 325
e
Large
n=236
0 25 50 75 100 125 150 175 200 225
f
Shelf
n=348
0 25 50 75 100 125 150 175 200 225 250 275 300 325
g
Shallow Slope
n=117
0 25 50 75 100
h
Deep Slope
n=82
0 25 50 75
Cumulative Number of Samples

Figure 4: *Raja rhina* prey items that have %IRI values (in parentheses) greater than 5% (A), and top eight prey items that were identified to species level (B). Total number of prey items was 67 and total number of stomach samples in this analysis was 563.


A
% Number
% Mass
50
40
30
20
10
0
10
20
30
40
50
Unidentified Teleost (31.7%)
Unidentified Euphausiidae (10.9%)
Neocrangon resima (6.0%)
Sebastes spp. (5.4%)
Crangonidae (7.4%)
Unidentified Shrimp (19.6%)
20 40 60 80 100
% Frequency

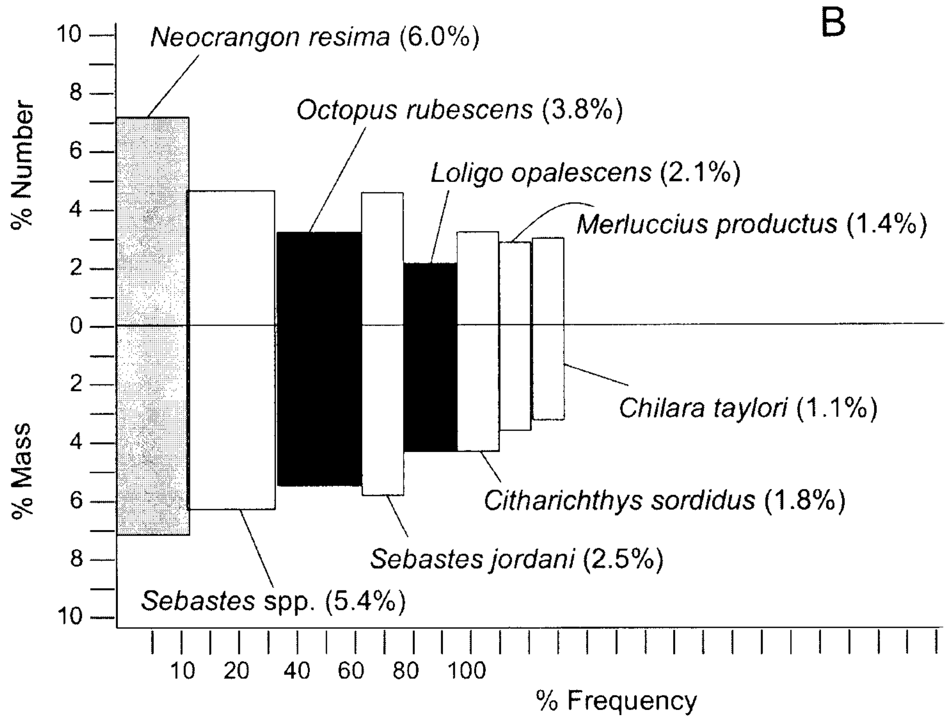

B
% Number
% Mass
10
8
6
4
2
0
2
4
6
8
10
Neocrangon resima (6.0%)
Octopus rubescens (3.8%)
Loligo opalescens (2.1%)
Merluccius productus (1.4%)
Chilara taylori (1.1%)
Citharichthys sordidus (1.8%)
Sebastes jordani (2.5%)
Sebastes spp. (5.4%)
10 20 40 60 80 100
% Frequency

Figure 5: Principal Components Analysis (PCA) bi-plots (a-c, e-g) and vector plots (d, h) for sex (triangles), size classes (squares) and depths (circles). Together, the three Principal Components explain 71% of the variance in *R. rhina* diet. The six bi-plots (a-c, e-g) depict patterns in *R. rhina* diet, while the vector plots (d, h) help explain which prey categories are driving the bi-plot patterns.

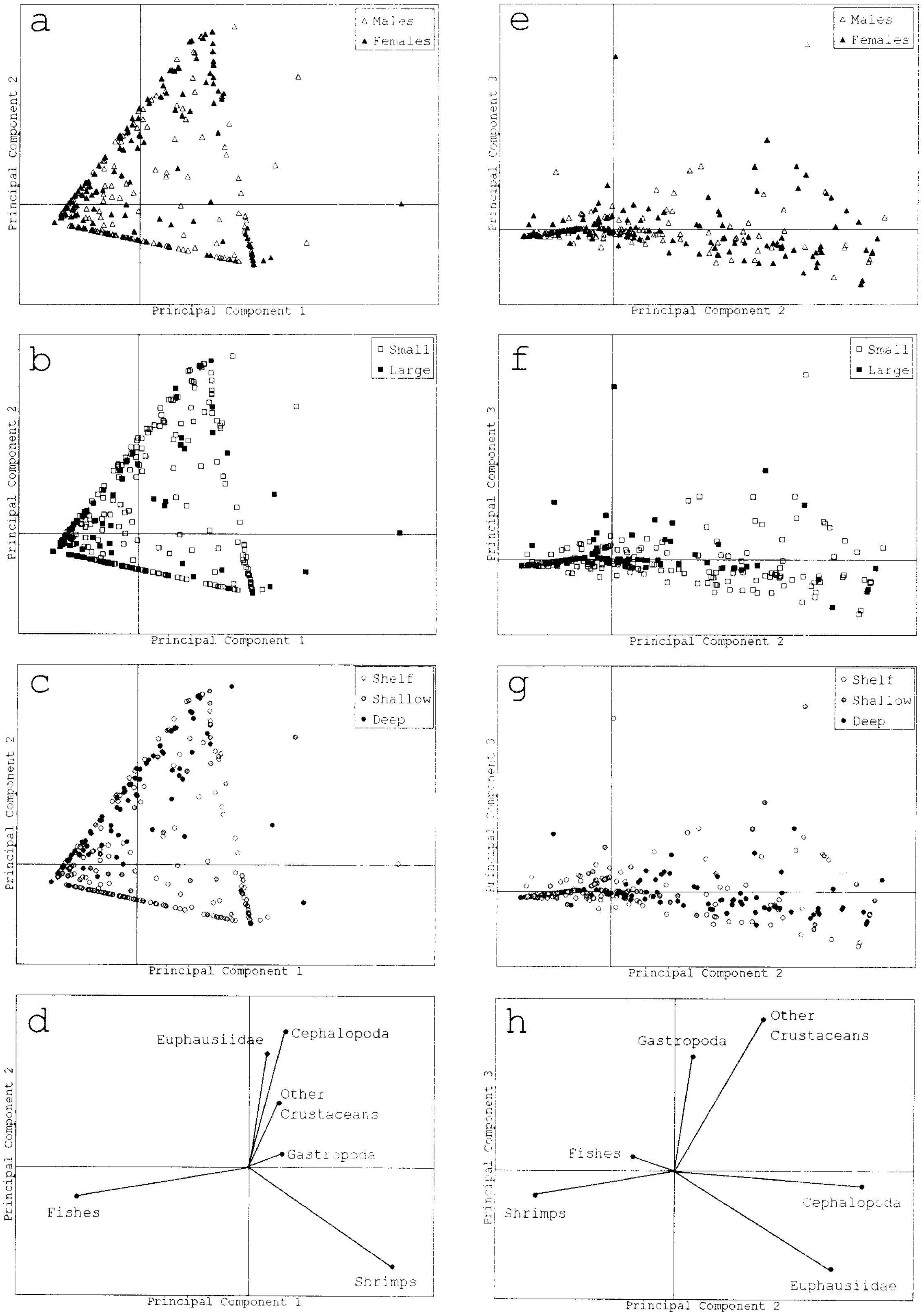
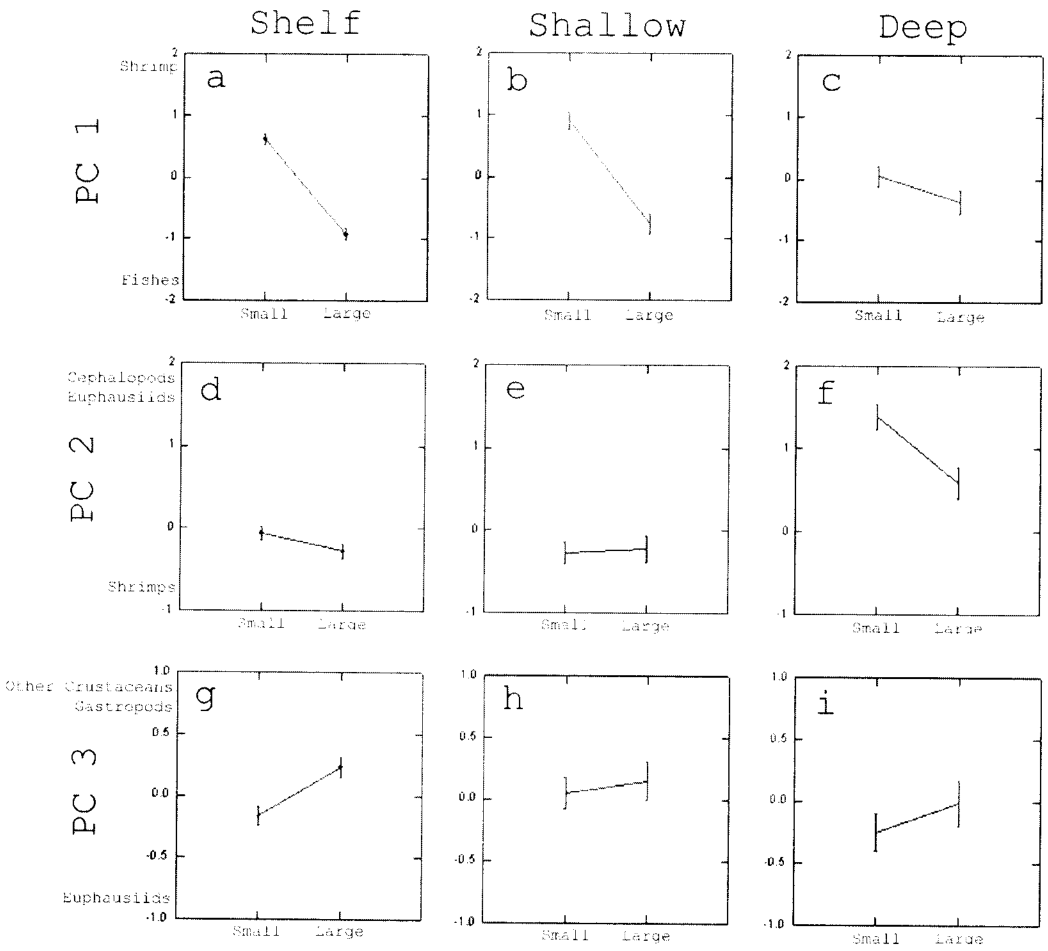

a
Males
Females
Principal Component 1
Principal Component 2
b
Small
Large
Principal Component 1
Principal Component 2
c
Shelf
Shallow
Deep
Principal Component 1
Principal Component 2
d
Euphausiidae
Cephalopoda
Other Crustaceans
Gastropoda
Fishes
Shrimps
Principal Component 1
Principal Component 2
e
Males
Females
Principal Component 2
Principal Component 3
f
Small
Large
Principal Component 2
Principal Component 3
g
Shelf
Shallow
Deep
Principal Component 2
Principal Component 3
h
Gastropoda
Other Crustaceans
Fishes
Shrimps
Cephalopoda
Euphausiidae
Principal Component 2
Principal Component 3

Figure 6: Plots of Analysis of Variance (ANOVA) interaction terms between size and depth for all three Principal Components (PC). Prey categories that loaded heavily on each PC are presented on the y-axes. This interaction term was significant for PC 1 (a-c) and PC 2 (d-f) due to diet differences between size classes being different at deeper depths (c,f) from either of the shallower depths (a,b & d,e). There was no significant interaction for PC 3 (g-i) between size and depth because dietary differences between size classes were similar at all three depth categories.


Shelf
Shallow
Deep
PC 1
PC 2
PC 3
a
b
c
d
e
f
g
h
i
Shrimp
Fishes
Cephalopods
Euphausiids
Shrimps
Other Crustaceans
Gastropods
Euphausiids
2
1
0
-1
-2
1.0
0.5
0.0
-0.5
-1.0
Small
Large