RESOURCE PARTITIONING IN AN ASSEMBLAGE OF DEEP-WATER, DEMERSAL ROCKFISH (*SEBASTES* SPP.) ON THE NORTHEAST PACIFIC CONTINENTAL SHELF

By

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To the Faculty of Washington State University:

The members of the Committee appointed to examine the thesis of KERI JANE YORK find it satisfactory and recommend that it be accepted.

Chair

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RESOURCE PARTITIONING IN AN ASSEMBLAGE OF DEEP-WATER, DEMERSAL ROCKFISH (*SEBASTES* SPP.) ON THE NORTHEAST PACIFIC CONTINENTAL SHELF

Abstract

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Identifying resource utilization patterns within marine communities can indicate potential competitive interactions and provide information relevant to ecosystem management and descriptions of essential fish habitat for overfished species. Aspects of resource partitioning have been shown to occur in many communities, including shallow-water rockfish assemblages. This paper explores the possibility that competitive interactions have influenced present distribution patterns among Northeast Pacific deep-water, demersal rockfish.

Habitat use patterns of continental shelf fishes inhabiting the submerged rocky reef of Heceta Bank, Oregon, have been assessed using the *Delta* submersible between 1988 and 2002. Using fish abundance, area of distinct habitat types, and invertebrate abundance, ecological communities on Heceta Bank were described using canonical correlation analyses. In all years, distinct but overlapping habitat use patterns were apparent among six demersal rockfish: canary (*S. pinniger*), yelloweye (*S. ruberrimus*), pygmy / Puget Sound (*S. wilsoni / S. emphaeus*), rosethorn (*S. helvomaculatus*), greenstriped (*S. elongatus*), and sharpchin (*S. zacentrus*). In

2002, each rockfish species was found to highly overlap in distribution with only one other, creating three distinct pairs of rockfish with similar distribution patterns.

Feeding habits were analyzed using stomach contents and morphology of fish collected from a wide geographic range on the Northeast Pacific continental shelf. For two of the three co-occurring rockfish pairs, stomach content analysis indicated that those species with similar distribution did not overlap in prey utilization. The third co-occurring pair of rockfish, *S. elongatus* and *S. zacentrus,* was unique because some degree of dietary overlap existed. In addition, all species overlapping in distribution were morphologically distinct, reflecting patterns in prey use.

Differential use of space and prey items appeared to allow this assemblage of deep-water rockfish to coexist in rocky areas on the continental shelf. Because these six species appeared to partition resources, changes in the distribution or abundance of one in response to altered habitat or prey availability may affect all others. This possibility is especially important in this assemblage because of the inclusion of two overfished species, *S. pinniger* and *S. ruberrimus*, and the present efforts to define essential fish habitat for these species.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Efforts to manage and conserve all species, especially those that are endangered, threatened, or overfished are improved when the ecological interactions and resource needs of entire communities are understood. One important ecological interaction in communities is competition, which may result in resource partitioning. The resources most commonly partitioned among sympatric species are space, food, and time of activity (Schoener 1974, Werner 1977, Hallacher and Roberts 1985). On ecological time scales, patterns of resource utilization within entire communities may change when the distribution of one species or its food resources is altered (Connell 1980). Such changes can occur seasonally or gradually over time. With current exploitation of many fisheries and recent calls for ecosystem-based management (Pikitch et al. 2004), studies that provide community level information about overfished species are of critical importance. The U.S. west coast groundfish fisheries are cases where ecological information is needed for improved management.

The outer continental shelf off Oregon, Washington, and California has supported a number of productive groundfish fisheries in the past. Rockfishes (genus *Sebastes*) constitute a significant portion of this assemblage, and a number of species have been commercially and recreationally exploited, resulting in substantial population declines in recent decades (Bloeser 1999). Recently, canary (*Sebastes pinniger*), yelloweye (*S. ruberrimus*), widow (*S. entomelas*), Pacific ocean perch (*S. alutus*), darkblotched (*S. crameri*), cowcod (*S. levis*), and boccacio (*S. paucispinis*) rockfish, along with lingcod (*Ophiodon elongatus*) were declared overfished (PFMC 2004). Because conventional management has generally failed to sustain these species effectively, this situation has created a need for ecologically-based management principles (Schmitten 1999, Pikitch et al. 2004).

In addition to developing management plans for overfished stocks, defining and protecting essential fish habitats are required by the Magnuson-Stevens Fishery Conservation and Management Act of 1976. Essential fish habitat is defined as “the waters and substrate necessary to fish for spawning, breeding, feeding, or growth to maturity” (U.S.C. § 1802 (10)). Essential fish habitats for one or more life stage of many rockfish species have been described (PFMC 2003). However, these descriptions only focus on depth, latitudinal, and large-scale habitat distributions.

There is great potential for improvement of essential fish habitat descriptions and rockfish stock assessments by using ecological and community-based habitat information, such as the distribution of and fishing impacts on, potential competitors and prey. Competition within and among species is one of the most influential factors affecting population abundance and distribution in West Coast rockfishes (review by Hixon *in press*). Currently, this information is not incorporated into ecosystem-based management, and stock assessments focus on single, commercially important species, while non-commercially important species and whole communities may also be at risk (Pikitch et al. 2004).

Resource use and ecological interactions within assemblages have been studied in a number of systems. A common pattern in communities with multiple shared resources is resource partitioning, which was reviewed by Schoener (1974). If a resource is shared and limited, species will compete and ultimately adapt to a certain range (size, prey, depth strata, etc.) to minimize overlap. As the number of species and shared resources increases, specialization may occur. The degree of overlap may also change through time or seasonally depending on prey availability (Zaret and Rand 1971, Tyler 1972). The first studies on resource partitioning in fish assemblages investigated fresh-water stream fishes (Zaret and Rand 1971, Werner 1971), and a number of studies since then have focused on demersal fish assemblages (Ross 1986). Coexisting fishes have been found to segregate along gradients of depth (MacPherson 1981, Wakefield 1984), prey use (Adams 1980), and diel use of habitat (Moulton 1977, Hart 2004). Closely related organisms are likely to have similar resource utilization patterns (Ross 1986), making rockfish good candidates for such studies.

There are approximately sixty-nine rockfish species occurring in the Northeast Pacific and many inherently overlap in latitudinal and depth range (Love et al. 2002), creating the potential for competition and resource partitioning. Rockfish are also known to be habitat specific (O'Connell and Carlisle 1993, Hixon et al. 1991, Yoklavich et al. 2000), and there are many instances of multiple species utilizing shared space. Some assemblages of rockfish exhibit characteristics of resource partitioning (Hallacher 1973, Roberts 1979, Larson 1980, Brodeur and Pearcy 1984, Hallacher and Roberts 1985). Partitioning of prey type and/or microhabitat has been demonstrated both observationally and experimentally in a shallow-water assemblage of rockfish inhabiting a kelp forest. Six rockfish species occurred in overlapping habitat patterns, and those most similar in habitat use utilized different prey resources (Hallacher and Roberts 1985). This example of resource partitioning is a likely result of competition for food among all species within the assemblage (Hallacher 1973). Experimental studies between two species from a similar kelp forest assemblage, *S. carnatus* and *S. chrysolemas*, indicate that territoriality and competition influence their distribution patterns (Larson 1980). Competitive exclusion has had a strong impact on community structure and resource partitioning among these kelp forest rockfishes. It is possible that similar interactions take place among other rockfish assemblages with overlapping habitat use patterns if resources are limited; however, this is not known.

Deep-water rockfish aggregate around geographic features offering complex habitats such as rocky banks (Issacs and Schwartlose 1965, Pearcy et al. 1989, Stein et al. 1992, O'Connell and Carlisle 1993), submarine canyons (Pereyra et al. 1969, Yoklavich et al. 2000, Bosley et al. 2004), coastal fjords (Murie et al. 1994), and in areas with structure-forming invertebrates, such as sea pens (Brodeur 2001). Here, the term deep-water is used to operationally distinguish rockfish generally living at depths > 60 m (Pearcy et al. 1989, Karpov et al. 1995) from shallow-water species, generally living 0 – 60 m.

One area that has been a site of historic commercial fishing and more recent intensive fish and habitat studies is Heceta Bank, the largest rocky submarine bank on the Oregon continental shelf. Beginning in 1987, manned submersible and remotely operated vehicle (ROV) work has been conducted to assess habitat of demersal fishes and evaluate non-invasive sampling techniques (Pearcy et al. 1989, Hixon et al. 1991 and 1992, Stein et al. 1992). Exploratory submersible dives in 1987 found rockfishes occurring in species-specific spatial patterns in habitats of shallow rock (67-76 and 104-149 m), shallow cobble (122-145 m), deep mud-cobble (185 – 220 and 140-148 m), and deep mud (164-300 m) (Pearcy et al. 1989). Subsequent dives from 1988-1990 further investigated fish and invertebrate communities that occur in these habitats. Although most groundfish appear in one of several broad habitat types, most are distributed over a range of depths and subhabitats, co-occurring with other fish and invertebrate species (Hixon et al. 1991, Stein et al. 1992, Tissot et al. *in review 1*).

Within the Heceta Bank groundfish assemblage, six demersal species of rockfish use habitats in an overlapping fashion similar to the kelp forest rockfish assemblage studied by Hallacher (1973), Roberts (1979), Larson (1980), and Hallacher and Roberts (1974). Although all Heceta Bank rockfish species occur in rocky habitats, each displays a unique habitat utilization pattern (Hixon et al. 1991, Stein et al. 1992, Tissot et al. *in review 1).* Canary and yelloweye rockfish tend to be associated with ridges, boulders, and cobbles, greenstriped (*S. elongatus*) and sharpchin (*S. zacentrus*) rockfish are associated with mud and cobble, pygmy (*S. wilsoni*) rockfish with mud and boulder, while rosethorn (*S. helvomaculatus*) rockfish are considered habitat generalists, but are most abundant on boulders (Stein et al. 1992). Tissot et al. (*in review 1*) also highlights the mid-depth boulder-cobble (100-150 m) and deep cobble (150 - 200 m) habitats because pygmy/Puget Sound rockfish, rosethorn, greenstriped, and sharpchin rockfish coexist in this specific depth range and may partition habitat and food resources similarly to the kelp forest rockfish assemblage.

Utilization of prey resources is commonly indicated through diet and morphology analyses. There have been numerous studies that used feeding habits to indicate community interactions and resource use in coexisting fish communities, including Werner (1971), Moulton (1977), MacPherson (1981), and Wakefield (1984). In addition to indicating community interactions, diet can reflect habitat disturbance (Tyler 1972), the effects of introduced species (Crowder 1986), or changes in prey behavior or availability (Pereyra et al. 1969, Brodeur and Pearcy 1984). Diet studies have been conducted for a number of rockfish species, but only a few have used feeding habits to suggest resource partitioning within rockfish assemblages. Roberts (1979) and Hallacher and Roberts (1985) found that, within a kelp rockfish assemblage, those species that occur in similar habitats have different feeding habits. Brodeur and Pearcy (1984) investigated overlap of prey among five co-occurring commercially important Northeast Pacific rockfish. Some degree of prey overlap occurred among all species, and two species with high overlap in prey utilization and temporal feeding patterns may co-occur by utilizing different depths in the water column. This current study investigated the possibility that an assemblage of deep-water, demersal rockfish partitioned resources similarly.

In addition to diet analyses, morphology can indicate feeding mode and potential for competition for food, as physical characteristics associated with sensing, capturing, and digesting of prey can be the result of natural selection on feeding habits (Allen 1982). Morphology has been used solely or in conjunction with stomach contents to describe interspecific relationships in fish communities, and is practical for resource partitioning studies of deep-water rockfish. Stomach contents are often difficult to obtain for deep-water rockfish because many live in areas that cannot be sampled with a trawl, and stomach regurgitation upon capture is common. In addition, the existing small population sizes of overfished species decreases catchability. General body characteristics, such as length, scale type, and body shape (Allen 1982) and those directly related to feeding, such as jaw, orbit, and head size (Roberts 1979, Hallacher and Roberts 1985) indicate potential prey items while stomach contents indicate the actual prey utilized. Morphology has been used to indicate prey utilization and relationships among 37 rockfish species (Pequeño 1983) and similarity of feeding habits among seven commercially important, spatially segregated rockfish species (Adams 1980).

The goal of this project is to investigate patterns of resource use within a deep-water rockfish assemblage of the Pacific Northwest continental shelf. Through analysis of habitat data collected via submersible video and the examination of feeding habits through stomach contents and morphology, I have evaluated resource use patterns and the potential for competitive interactions. I conclude that resource partitioning does occur within this assemblage through the differential use of space and prey.

METHODS

Submersible data collection

The *Delta* submersible was used to collect data on habitat and distribution of demersal fishes and invertebrates on Heceta Bank, OR. Heceta Bank is a submerged rocky bank on the Oregon continental shelf, located approximately 55 km off the central Oregon coast. Although most of the bank is untrawlable, areas surrounding the bank have been intensely fished historically. Eighteen dives were made on Heceta Bank at depths of 68 - 379 meters during September 2002 (Fig. 1, Table 1). Submersible transect methodology was identical to that described in Stein et al. (1992). A brief description and modifications to the previous method follows. The same three observers who participated in historical work (Hixon, Stein, and Barss) each made one dive at each of six predetermined stations, the same used in Stein et al. (1992). All dives were conducted during daylight hours and consisted of two, 30-minute transects with a 10-15 minute "quiet period" between transects, where the submersible rested on the substrate while the observer assessed fish behavior and response to the submersible. Based on these observations, the effects of submersible presence on fish behavior appeared to be minimal, as in previous studies (Carlson and Straty 1981, Hixon et al. 1991, Stein et al. 1992, Hart 2004). However, these studies note that some groundfish occasionally follow or hide from submersibles.

Transects were recorded through an externally-mounted, high resolution, color video camera onto miniDV tapes using a digital video cassette recorder. Two sets of lasers were mounted on the submersible to estimate the size of objects and to provide an accurate measure of transect width. One set of parallel lasers, spaced 20 cm apart, was mounted near the video camera, and a second set was mounted 10 cm apart with the outermost laser 115 cm starboard of the center line of the video transect. Lights were used at all times during transects, and a digital still camera with a flash was used to take pictures for identification purposes when the submersible was not conducting quantitative transects. During each transect, fish species identification, abundance, and size estimates were verbally recorded on separate video and audio tapes. The *Delta* traveled approximately 2 m off the bottom, providing forward-looking transects of approximately 2.3 m wide. The latitude and longitude of each transect was recorded with Winfrog™ Navigational Software (GeoPacific) Solutions, integrating ORE Trackpoint II ultrastart baseline (USBL) fixes for *Delta* with the support ship's GPS navigation and heading data. Before each dive, a Horita titler (KCT-50) was synchronized to the ship's GPS and an overlay of time, depth, and latitude and longitude was burned on the video.

Fish, invertebrate, and habitat data were later quantified using the recorded miniDV video tapes. Immediately after each *Delta* dive, the observer reviewed the tape and a recorder simultaneously entered the time and size of all fish into a database. All fish identified as pygmy or Puget Sound (*S. emphaeus*) rockfish were called pygmy/Puget Sound (*S. wilsoni* / *S. emphaeus*) because of difficulty in distinguishing between these species. Invertebrate and habitat data were later quantified by subdividing transects into unique habitat patches. Invertebrates were enumerated per habitat patch (Tissot et al. *in review 1*).

Habitat was described by a two-coded system of seven different categories of substrate, the same used in Stein et al. (1992). The substrate categories in order of decreasing particle size and relief were: rock ridge (R, high vertical relief), boulder (B, diameter >25.5 cm.), cobble (C, 6.5 cm. < diameter < 25.5 cm.), pebble (P, diameter <6.5 cm.), flat rock (F), sand (S), and mud (M, noticeable organic material). At each distinct change in substrate, new habitat codes were assigned to the respective patch, with the first code representing primary habitat (at least 50% of the patch) and the second representing secondary habitat (at least 20% of the patch). For example, “PC” represented a habitat patch with at least 50 % cover of pebble and at least 20% cover of cobble, and “MM” represented a habitat patch with only one substratum of mud. Of the 49 habitat combinations possible, 45 were observed. Using the statistical program Primer (PRIMER–E Ltd.), these data were analyzed by a cluster analysis (Euclidean distance, group average method) using the abundance of fish species that equaled the top cumulative 99% in overall abundance. Using the resulting dendrogram and similarity of >40%, the 45 habitat combinations were pooled into the 16 most dominant habitat types.

Data were analyzed using habitat patches as sample units for fishes and invertebrate abundance and associated substrate type. Relationships between station and depth and statistical differences among observers and stations were assumed to be comparable to Stein et al. (1992). A canonical correlation analysis (CCA), using SAS version 8 (SAS Institute, Inc.), was used to describe community associations among fishes (schooling and non-schooling), invertebrates, and habitat. The CCA quantified associations among abundance of fishes that equaled the top cumulative 99% in overall abundance (data set 1) and abundance of invertebrates and area of habitat (data set 2). Invertebrate species that were representative of certain habitat types (Hixon et al. 1991, Tissot et al. *in review 1*) were chosen for this analysis. Habitat types were not pooled and all data were log transformed to obtain the most normal distribution.

Canonical correlation analysis estimates associations among the data sets and helps identify the factors affecting abundance and distribution (Pimentel 1979, Dillon and Goldstein 1984). Orthogonal, independent combinations of correlations among the data sets are calculated. The computed canonical variate scores (transformations of original variables to canonical axes) are used to calculate the overall canonical correlation between the two data sets along each axis. Canonical variate loadings are correlates of the raw variable scores and original canonical variate and indicate which variables are correlated on the different axes. The redundancy coefficient measures the actual overlap of the two data sets and provides a measure of variation in one data set as predicted by the other. This analysis provides a measure of the variables associated together between the two data sets. Kruskal-Wallis and Tukey's multiple range tests were used to describe differences in species distribution patterns along CCA axis 4.

Sample collection for feeding habits

Morphology and stomach content samples were collected during the 2003 and 2004 NOAA Fisheries Northwest Fisheries Science Center's annual West Coast continental shelf and slope bottom trawl survey (Fig. 1, Appendix A). This survey was designed to collect data for stock assessments of selected fish species on the continental shelf and slope of the U.S. West Coast. The survey area was categorized by depth strata and International North Pacific Fisheries Commission (INPFC) area in 2003 and depth strata and placement above or below Point Conception, CA, in 2004. A designated number of cells were then randomly selected within each area and stratum. An Aberdeen style bottom trawl net with a 15 m horizontal opening, a 5 m vertical opening, and a 2" mesh liner in the codend was used on all vessels. Bottom time of all trawls was fixed at a nominal 15 minutes unless aborted early. The exact location of the vessel during each trawl was tracked using a GPS. A Simrad Integrated Trawl Instrumentation (ITI) system and bottom contact sensors were used to assess overall net performance, trawl duration, and whether trawls were satisfactory.

Geographic area, size of fish, season, and year may influence the feeding habits of rockfish. Geographic area was the only factor considered for morphology differences, as variation in size was revealed in analysis and morphology is not likely to vary among season.

Samples were grouped into geographic area based on the latitude strata used in Brodeur and Pearcy (1984) with the addition of a southern strata extending into central California (Table 2). The two seasons that were used in the analysis were summer (June – August) and fall (September – October). These two periods were identified by Huyer (1977) as featuring seasonal shifts in the hydrographic regime on the Oregon continental shelf. Prey utilization may also differ among size range within species, and fish were classified into size classes of 100 mm increments from 100 to 600 mm. Despite potential differences in these environmental factors, all samples were pooled in dietary and morphological analyses. This allowed for species-specific comparisons of feeding habits in relation to species-specific habitat utilization patterns.

Habitat, behavior and feeding habits may change ontogenetically in rockfish (Love et al. 1991), and an effort was made to collect mature individuals whenever possible. Reference size at 50% maturity was used to evaluate the percentage of samples that were mature (Table 3). Reference sizes and lengths from this study were converted to standard length using conversions for blue rockfish (MacGregor 1983). Sharpchin rockfish lengths were not converted because reference length measurement is not stated in Love et al. (2002), and the size at 50% maturity for pygmy rockfish is unknown.

Stomach content analysis

In 2003, stomach samples were taken from all fish that were collected for morphology samples (full and non-full), and in 2004, fish were randomly selected for stomach samples from all those with full stomachs brought up in the net (Appendix A). In both years, fish that showed signs of regurgitation, net feeding, or stomach eversion were discarded. Ventral slits were made in selected fish and internal organs were removed. The stomachs, foregut, and pyloric caeca were placed in mesh bags. Spilled stomach contents were also saved, and care was taken to collect all material from the foregut. All fish with the exception of pygmy rockfish collected in 2003 were preserved in 10% formalin and later transferred to 70% alcohol (2003) or directly preserved in 70% alcohol (2004), because of preservative limitations. In 2003 pygmy rockfish were frozen whole at sea, and the stomachs were later removed and preserved in 70% alcohol.

Prey items were examined in the laboratory and identified to the lowest taxa possible with the aid of multiple guides (Appendix B). Prey were weighed to the nearest 0.01 g and enumerated whenever possible. When whole organisms were not present or could not be deciphered, numbers were not estimated. Those items that did not weigh 0.01 g were given a weight of 0.004 g to account for presence in the stomach. Because stomachs were collected during daylight hours and stomach fullness or ratio of empty/non-empty stomachs was not estimated, these methods assume that rates of consumption, feeding periodicity, and prey availability were equal among demersal rockfish species.

Measures of diet analyses were conducted to assess prey resource use. All stomachs that were non-regurgitated and non-empty were pooled by species. Both prey item frequency of occurrence and weight were used in diet analyses, as the two measures indicate different aspects of an organisms' diet. Frequency of occurrence indicates preference or availability of a prey item, while weight indicates the amount of consumption, or nutritional value of a prey item (Roberts 1979). Percent weight was calculated by dividing the total weight of the prey item by the total weight of all prey items, and percent frequency of occurrence was calculated by dividing the frequency of occurrence of a prey item by the total number of stomachs for a species. Using both measures also helped to eliminate some bias. Prey items that were consumed well before capture may be more digested than those consumed immediately before capture. More digested prey would not contribute as much in weight, but would in frequency of occurrence.

The adequacy of stomach sample collection was evaluated using a cumulative prey species curve for each rockfish species. This method was developed by Hurturbia (1973) and is commonly applied to stomach content analyses using data from each individual study. The cumulative number of unique prey taxa was plotted versus the number of individual stomachs randomly ordered. The number of stomach samples corresponding with the asymptote was considered the minimum necessary to adequately describe diet.

Measures of diet breadth and overlap among species were calculated for all prey items that were identified to at least taxonomic order and weighed $\geq$ 0.1% of the total weight of all prey for each rockfish species. Diet breadth, an indication of prey diversity, was calculated using Levins's (1968) measure:

$$B = \frac{1}{\Sigma p_j^2} \tag{1}$$

where p_j equals the proportion of weight of diet item j. B ranges between 1 to n, where n equals the number of prey items for a particular rockfish species. This measure gives more weight to abundant resources than others (Hurlbert 1978), which allowed for a comparison of principal prey items among rockfish species. A standardized Levins's measure was also used, which gives a measure of breadth if all diet items were in equal proportion, or a measure of the evenness of prey utilization (Hurlbert 1978), using the equation:

$$B_A = \frac{B - 1}{n - 1} \tag{2}$$

This value ranges from 0 (use of prey items in unequal abundance) to 1 (use of prey items in equal abundance). This measure assumes equal prey availability among all predator species (Krebs 1998).

Two different measures of diet overlap were chosen because of low bias and data type (Smith and Zaret 1982, Krebs 1998). Both range from 0 (no overlap in diet) to 1 (complete overlap in diet). Morisita's index of similarity (Morisita 1959) was used to estimate dietary overlap in prey item numerical abundance:

$$C = \frac{2 \Sigma p_{ij} p_{ik}}{\Sigma p_{ij} [(n_{ij} - 1) / (N_j - 1) + \Sigma p_{ik} [(n_{ik} - 1) / (N_k - 1)} \quad (3)$$

where p_{ij} and p_{ik} represent the proportion of prey item i used by species j and k, respectively, n_{ij} and n_{ik} are the numbers of prey item i in the diet of species j and k, and N_j and N_k are the total number of prey items in the diet of species j and k. The index described by Horn (1966) was also used to calculate dietary overlap in prey item weight:

$$Ro = \frac{\Sigma (p_{ij} + p_{ik}) \log (p_{ij} + p_{ik}) - \Sigma p_{ij} \log p_{ij} - \Sigma p_{ik} \log p_{ik}}{2 \log 2} \quad (4)$$

where p_{ij} and p_{ik} represent the proportion of prey item i used by species j and k, respectively.

For further comparisons, prey items were classified into 12 trophic groups (Appendix C). The group 'crab' was considered benthic because all taxa were either benthic crabs or megalopae. The order Amphipoda was considered midwater because all but one individual were in the suborder Hyperiidea. Shrimp (other) and fish (other) include taxa that could not be placed in either benthic or midwater group.

Multidimensional scaling (MDS) analysis in the statistical program Primer was used to evaluate similarity of diet among rockfish species using trophic groups. This nonparametric method does not assume linearity among variables and transforms a similarity matrix into rank order relationships (Pimentel 1979). A Bray-Curtis similarity matrix was used and ten iterations of the algorithm were run. The resulting stress value is representative of the goodness-of-fit of the ordination (Clarke and Warwick 2001). For this analysis, individual fish stomachs were used as sample units, and proportion in weight of each prey trophic group per individual fish stomach was used. The resulting graphical ordination was used to evaluate similarities in diet among species.

Using prey item trophic groups, graphical comparisons of prey frequency of occurrence within each species among the different environmental factors of geographic area, season and year, and size were analyzed. Frequency of occurrence was adjusted so the total per group equaled 100%. A graphical representation of prey weight and frequency of occurrence per trophic group is also shown (as in Darnell 1961, Calliet et al. 1979).

Morphology analysis

Morphology samples were collected during 2003 and 2004 (Appendix A). Individuals were collected as time permitted from all trawls that contained rockfish species of interest. The heads were removed, tagged with individual fork length and an identifying code, and frozen for later analysis. The seven morphological features measured were chosen because of their use in previous studies (Adams 1980, Pequeño 1984, Hallacher and Roberts 1985) and their relevance to feeding capabilities (Fig. 2a & b). These were: fork length, head length, length of maxillary plus premaxillary bones, orbit width, number of gill rakers on the first gill arch, length of the angular gill raker on the first gill arch, and length of the bottom half of the first gill arch. Gill raker measurements were taken on the first gill arch on the left side of the fish.

The morphology data were analyzed using a multivariate discriminant analysis (MDA) to evaluate distinctness and potential overlap in feeding habits among species using samples in which all measurements were taken. This analysis was chosen because it minimizes variation within groups and maximizes differences among groups. Variation within species among geographic area may exist (tested using MDA among geographic area within species, not reported), and length is a covariate with other size measurements within rockfish species (Roberts 1979). Within-group influence of factors, such as geographic, seasonal, and size variation was thus minimized with this analysis. The resulting axes of the analysis represent multivariate dimensions that maximize differences among groups. Variation in multiple morphological traits is represented by discriminant scores along these axes. One-way ANOVA and Tukey's multiple range tests were used to evaluate differences in discrimination among species. Discriminant loadings represent correlation of a variable with the discriminant function and were used to calculate vectors, or the strength of each variable in discriminant space. In this case, the contribution of each morphological characteristic was relative to the strength of the resulting vector.

RESULTS

Habitat

Three *Delta* dives were made at each of six stations in 2002, with an average of 107 habitat patches per dive (Table 1, Fig. 1). The dominant habitat types at each station were similar to those in Stein et al. (1992) with the exception of station 4. In 1988-1990, station 4 was characterized mostly by boulder/cobble and ridge habitats (Stein et al. 1992), while in 2002 it was predominately mud and cobble/boulder. Correlations between habitat type and depth were similar to Stein et al. (1992) as well (Fig. 3). Sand and ridge habitats occurred at the shallowest depths, and muddy habitats at the deepest.

There were a total of 13,640 individuals of the six demersal rockfish species at all six stations combined (Table 4), and pygmy/Puget Sound were the most abundant with a total of 9,178 individuals. Demersal rockfish were most abundant at stations 4 and 6, which had dominant habitats of mud, cobble, boulder, and flat rock. Greenstriped was the only rockfish species seen at station 5, which was primarily mud habitat.

All six species of demersal rockfish overlapped to some degree among the dominant habitat types along a gradient of decreasing relief and particle size (Fig. 4). Although each rockfish species had a unique distribution pattern over habitat types, some species were relatively similar to others. Pygmy/Puget Sound, canary, and yelloweye rockfish were found primarily in ridge and boulder habitats, but some individuals occurred in cobble and mud habitats as well. Rosethorn rockfish were distributed ubiquitously over all dominant habitat types, and sharpchin and greenstriped rockfish were concentrated in the deeper boulder, cobble, and mud habitats.

The canonical correlation analysis of habitat and invertebrates with fish abundance described associations of demersal fishes, habitat, and invertebrates (Table 5). The first two axes both had high canonical correlation coefficients (0.966 and 0.906, respectively), representing high overall association of canonical variates between the two data sets. The third and fourth axes also had relatively high canonical correlation coefficients (0.710 and 0.657, respectively), and the cumulative proportion of variation explained by the first through fourth CCA axes was 92%. The redundancy coefficients were relatively low for axes two - four (0.12 – 0.02), representing a strong correlation among several fish species (data set 1) and habitat types and invertebrates (data set 2). The first axis had slightly higher redundancy coefficients (0.12 and

0.20), and was more representative of general associations among all variables in the two data sets.

The first four axes of the CCA described different ecological communities of habitat, invertebrates, and fishes. The first axis described a mud dominated habitat with fragile sea urchins (*Allocentrotus fragilis*) and *Pycnopodia* / *Rathbunaster* sunflower stars (Fig. 5). Canonical variate loadings indicate that eelpouts, hagfish, Pacific hake, shortspine thornyhead, poachers (*Agonidae*), Dover sole, slender sole, and rex sole, and sharpchin and greenstriped rockfish were associated with mud communities (Table 5).

The second CCA axis contrasted two different communities: those that were structurally complex and dominated by boulders, cobbles, and pebbles with vase and foliose sponges and brittlestars (*Ophiacanthidae*) (high positive canonical variate loadings), and those with little relief dominated by sand and mud habitats with *Parastichopus* sea cucumbers and sunflower stars (high negative canonical variate loadings) (Fig. 5). Canonical variate loadings indicated that yelloweye, rosethorn, pygmy/Puget Sound, sharpchin, and greenstriped rockfish were associated with boulder, cobble, and pebble communities and hagfish, eelpouts, and sturgeon poacher are associated with sand and mud habitats communities.

The third CCA axis contrasted rocky habitats. It described pebble-dominated habitats with fragile sea urchins (high positive canonical variate loadings) and ridge/boulder habitats with sunflower stars, brittlestars and *Henricia* spp. blood stars (high negative canonical variate loadings). Dover sole and sharpchin and greenstriped rockfish were associated with pebble communities and rosethorn, pygmy/Puget Sound, and yelloweye rockfish and kelp greenling were associated with ridge/boulder communities.

The fourth CCA axis contrasted communities of structural relief (Fig. 5) and was also representative of the correlations between habitat and depth (Fig. 3). The two contrasting communities described a gradient from shallow communities with high structural relief to deeper communities with low structural relief and sponges, which provide biotic relief. High positive canonical variate loadings indicate that pygmy/Puget Sound, rosethorn, yelloweye, and yellowtail rockfish, mottled sculpin (*Cottidae*), and kelp greenling were associated with high relief communities and sea cucumbers, crinoids, and blood stars (Table 5). High negative canonical variate loadings of vase and foliose sponges and sand and mud habitat contrasted the high relief communities on CCA axis 4. Negative canonical variate loadings indicated that greenstriped and sharpchin rockfish, threadfin sculpin, and Dover, slender, and rex sole were associated with low abiotic/high biotic relief communities.

The fourth CCA axis was used to assess demersal rockfish habitat utilization patterns because it was the most representative of a multivariate habitat gradient decreasing in relief and particle size. Rockfish abundance per habitat patch was plotted per frequency class of canonical variate scores along this gradient (Fig. 6). Habitat patches were grouped by canonical variate loadings into frequency classes along the fourth axis, and single observations in any frequency class were removed.

Most abundance patterns of demersal rockfish species over this gradient were similar to those described for dominant habitat types. Canary, pygmy/Puget Sound, and yelloweye rockfish were most abundant in communities with high structural relief, and rosethorn rockfish were distributed fairly evenly over the gradient. However, the patterns of greenstriped and sharpchin rockfish were slightly different. Both species were abundant on both ends of CCA axis 4, in communities with high abiotic relief and also in low abiotic/high biotic relief communities. A Kruskal–Wallis test indicated that distribution patterns among rockfish species along CCA axis 4 were significantly different ($p = 0.001$, $\alpha = 0.05$, $H = 725$). Tukey's multiple range tests indicated that three pairs of rockfish species were not significantly different ($\alpha = 0.05$) in distribution along CCA axis 4: rosethorn and pygmy/Puget Sound, greenstriped and sharpchin, and canary and yelloweye rockfish.

Stomach contents

Prey items were found in 234 non-empty and non-regurgitated stomachs out of a total of 347 examined. The majority of all sample populations used in stomach content analysis were comprised of mature fish: approximately 83% canary, 57% yelloweye, 93% rosethorn, 100% sharpchin, and 88% greenstriped rockfish (Table 3). All prey items, with the exception of unidentified material, were classified at some taxonomic level. Many items, including crustaceans and fishes, were whole or only partially digested and could be identified to species. Fish, euphausiids, and decapods were dominant prey, in weight and frequency of occurrence (FO).

Canary rockfish consumed entirely midwater prey, mostly euphausiids in measures of weight and FO (Appendix C, Fig. 7). Of those identified, *Euphausia pacifica* was the dominant species eaten. Digested bony fish and Gadiformes also contributed to the diet, as well as crustacean remains and *Cancer* spp. megalopa.

Euphausiids were also the dominant prey item in the diet of pygmy rockfish (Appendix C, Fig. 7). *Euphausia pacifica* was the dominant species in weight and FO, and *Thysanoessa spinifera* occurred approximately half as often as *E. pacifica*. Some calanoid copepod and amphipod FO values were comparable to euphausiid taxa, and copepods were the third most important trophic group by weight. Pygmy were the only species that consumed *Euchaeta* spp. copepods and snail-like gastropods.

Decapods, mostly midwater shrimp, were the dominant prey taxa consumed by greenstriped rockfish (Fig. 7). By weight, the dominant decapods were *Sergestes similis* and other unidentified members of the family Sergestidae (Appendix C). The galatheid crab *Munida quadrispina* and euphausiids, mostly *E. pacifica*, contributed both in weight and FO. Digested bony fish also occurred frequently. Greenstriped rockfish were unique in the consumption of an insect (pair of eyes found in stomach) and an unidentified mysid.

Rosethorn rockfish also predominantly preyed upon decapods, however these taxa were primarily benthic (Fig. 7). *Munida quadrispina* comprised approximately half of the total weight of prey items (39.5%) and occurred in exactly half of the examined stomachs (Appendix C). The benthic shrimp *Pandalus platyceros*, was found in two stomachs and comprised 22% of the total weight. Many other midwater taxa contributed little to the diet but were present. Bony fish remains and the myctophid *Tarletonbeania crenularis* were the dominant fishes. Rosethorn rockfish were the only species that consumed *Atylus* spp. copepods and one *Abraliopsis felis* squid.

The dominant prey trophic group of sharpchin rockfish was midwater fishes, including the myctophids *T. crenularis* and *Diaphus theta* (Appendix C, Fig. 7). Euphausiids occurred in sharpchin rockfish stomachs more frequently than myctophids, but were less important by weight. Copepods were also present, and *Neocalanus cristatus* occurred as frequently as other dominant prey items. Sharpchin and rosethorn rockfish were the two species observed to consume salps.

Yelloweye rockfish also primarily preyed upon fishes and decapods (Appendix C, Fig. 7). The epipelagic fish Pacific herring (*Clupea harengus pallasii*) comprised over 50% of the total weight of all prey items, but was less important in FO. Slender sole (*Lyopsetta exilis*), *Sebastes* spp., and unidentified Clupeidae were each present once. Decapods and cephalopods were also prey items of yelloweye rockfish, but were found less frequently and contributed less to the overall weight.

The cumulative prey species curves used to determine adequate sample size for stomach contents suggest that an adequate number of stomachs were sampled for greenstriped, canary, and pygmy rockfish (Fig. 8). The curves of these species reached an asymptote and leveled off at sample sizes less than the total number of stomachs sampled in this study. The curve of sharpchin rockfish may have also reached an asymptote, but this conclusion is less definitive than in other species. Rosethorn and yelloweye rockfish were not adequately sampled, as an asymptote was never reached.

In general, rockfish that had low prey diversity (pygmy, canary, and yelloweye) utilized prey more evenly than those that had wide diet breadth or high prey diversity (Table 6). For example, pygmy rockfish preyed upon a small number of taxa (n = 8), had a narrow breadth (B = 2.65), and had a moderately high evenness value (B_a = 0.24), a pattern typical of stenophagous predators. In contrast, europhagous diets, or use of many prey items but specialization on a few, were represented by rosethorn and greenstriped rockfish. Greenstriped rockfish utilized the greatest number (n = 21) of prey taxa, had the second highest diet breadth value (B = 4.65), but a low evenness value (B_a = 0.18). Sharpchin rockfish were the exception to these trends and had the widest diet breadth (B = 8.29) and the most even distribution among prey taxa (B_a = 0.52).

The majority of rockfish species pairs had either moderate or high diet overlap values in measures of both weight and frequency of occurrence for all prey taxa that weighed > 0.01% of the diet and could be identified to order (Table 7). For this evaluation, I used overlap values from 0.00 – 0.29 as low, 0.30 – 0.60 as medium, and those > 0.60 as high (Langton 1982). Using prey taxa weight, only the pair of pygmy and canary rockfish had a high diet overlap value (*Ro* = 0.877), which is because of the high proportion of euphausiids in the diet of both species. Most species paired with sharpchin and greenstriped rockfish had medium overlap values (*Ro* = 0.336 – 0.527) from calculations using prey weight. This is reflective of the substantial proportion in weight of euphausiids, decapods, and fishes in the diets of both species. All possible combinations involving yelloweye rockfish had low overlap values (*Ro* < 0.001 – 0.067) using prey taxa weight, which was representative of the unique fish species in the diet.

The presence of medium or high diet overlap among rockfish species pairs was more common when prey frequency of occurrence was used in the calculations (Table 7). Canary and pygmy rockfish had a high diet overlap value (*C* = 0.852), as did most pairs involving sharpchin rockfish (*C* = 0.625 – 0.905). All possible pairs involving greenstriped rockfish had medium or high overlap values (*C* = 0.423 – 0.905), and yelloweye rockfish had medium overlap values when paired with rosethorn (*C* = 0.474), sharpchin (*C* = 0.316), and greenstriped (*C* = 0.423). This difference in yelloweye diet overlap values among the two calculations was most likely because of the low frequency of occurrence but high weight values of the fish species found in the diet.

The ordination from the multidimensional scaling analysis using prey taxa trophic groups showed overlap in diet among most rockfish species (Fig. 9). The stress value for the two-dimensional plot was 0.1, which is representative of a good ordination (Clarke and Warwick

2001). There was separation among some species, but distinct groups were not formed. The ordination values of yelloweye rockfish were separate from pygmy and canary rockfish, but all other combinations overlapped to some degree.

Variation in prey frequency of occurrence among geographic areas, sizes of fish, and season and year existed for all demersal rockfish species (Fig. 10 – 12). Variation in diet seemed to be the most minimal with fish size (Fig. 10). There was evidence of significant differences in diet in all three factors within species (as determined from MDA, ANOVA, and Tukey's multiple range tests). However, sample size was not adequate in many of the categories within factors, so an adequate evaluation of differences within species was not possible.

Morphology

Morphological characteristics were measured on a total of 302 individual fish. Generally, demersal rockfish species were more dissimilar in morphology than in prey use. Those rockfish that had similar diets had similar feeding morphologies, but separation of species was more distinct. In body (fork length) and head (head length, orbit width, length of maxillary plus premaxillary) morphology characteristics, yelloweye and canary rockfish were the largest in all measurements except orbit width (Appendix D). Rosethorn and sharpchin rockfish had similar size ranges for body and head characteristics, and greenstriped and pygmy rockfish generally had the smallest. These trends also held for the length of bottom half of the first gill raker, but not for the gill raker count or the length of the angular gill raker. There was little overlap in gill raker count among species. Yelloweye had the least number of gill rakers and pygmy and canary had the most. Canary rockfish also had the longest angular gill raker measurements followed by sharpchin rockfish.

Multivariate discriminate analysis (MDA) described group differences in feeding morphology among the six rockfish species. MDA axes 1 and 2 had high canonical correlation (0.971 and 0.878, respectively), which represents strong goodness-of-fit of the discriminant function to the groups. The cumulative proportion of variation explained by the first two axes was 95%, and group centroids were significantly different (Wilks' Lambda p-value < 0.001, $\alpha = 0.05$) along the first axis.

Some rockfish species overlapped and some were distinct in ordination along the first two MDA dimensions (Fig. 13). In the graphical representation of the MDA, canary and yelloweye rockfish were distinct from all other species. Rosethorn and greenstriped rockfish overlapped as did pygmy and sharpchin rockfish. These two species pairs also had the smallest squared Mahalanobis distances (Table 8). Sharpchin and greenstriped rockfish were also close in multidimensional space. The strength of each morphological characteristic in group separation was represented by the size of the vector (Fig. 13b). Distribution of species along the first dimension was influenced by angular gill raker length and gill raker count (pooled within canonical structure variable loadings), which are indicative of the size of prey that are prevented from escaping the oral cavity. Maxillary plus premaxillary length and orbit width were influential in group separation along the second dimension, and these characteristics indicate the size of prey that can be seen and taken in by the mouth.

Along dimension one, three groups were visually apparent. Sharpchin, pygmy, and canary were similar in size of gill rakers, as were greenstriped and rosethorn. Yelloweye were the most distinct from all other species along this axis. Along the second dimension, yelloweye and canary were similar in jaw and orbit size, and pygmy, rosethorn, greenstriped, and sharpchin rockfish were also similar. Gill raker count separated canary rockfish from rosethorn and greenstriped and also influenced separation between pygmy and sharpchin rockfish.

Kruskal –Wallis and Tukey's multiple range tests indicate that there was minimal overlap among rockfish species in location along the first and second MDA dimensions. There were significant differences among all rockfish species along both dimensions (Kruskal -Wallis test, $p < 0.001$, $\alpha = 0.05$). Canary and pygmy rockfish were the only species that were not significantly different from each other (Tukey's multiple range test, $\alpha = 0.05$) in gill raker length and count (MDA dimension one). The low percentage of mature canary rockfish (10%) used in the morphological analysis may have affected this finding, as all other populations of rockfish samples were comprised of $\geq$ 50% mature fish (Table 3). Four pairs of rockfish species were similar in size of maxillary plus premaxillary and orbit width (MDA dimension two). Significant differences (Tukey's multiple range test, $\alpha = 0.05$) in species space along the second MDA dimension did not exist among the following pairs: canary and yelloweye, rosethorn and greenstriped, sharpchin and greenstriped, and rosethorn and sharpchin rockfish.

DISCUSSION

Resource partitioning in co-occurring species

In Northeast Pacific deep-water, demersal rockfish assemblages, competition theory would predict that partitioning of food or time of activity should have occurred when patterns of distribution were similar and resources were limited (Schoener 1974). Indeed, for those species with similar distribution patterns on the Northeast Pacific continental shelf, food resources were partitioned to some degree, which also reflects behavioral patterns. This complementary use of space and food indicates that resource partitioning occurs within this assemblage. The overall arrangement of these demersal rockfish species is depicted in Fig. 14, based on spatial distribution and feeding habits behavior.

Each of the six rockfish species displayed a distribution pattern that was similar to only one of the other species, creating three distinct pairs: canary and yelloweye, pygmy/Puget Sound and rosethorn, and greenstriped and sharpchin rockfish. Within each pair, there was one species that is known to exhibit schooling behavior (canary, pygmy/Puget Sound, and sharpchin) and one that displays more benthic, solitary behavior (yelloweye, rosethorn, and greenstriped) (Hixon et al. 1991, Stein et al. 1992, Love et al. 2002, Hart 2004). In addition, activity patterns with respect to time of day were similar within and different among these pairs (Hart, 2004). These previously documented behavioral patterns were reflected in diet, as those rockfish found higher in the water column were entirely midwater feeders while the more benthic species consumed a variety of prey items, both midwater and benthic.

The two deep-water demersal rockfish that are currently considered overfished, canary and yelloweye, overlapped in distribution on Heceta Bank but were very different in diet. The distribution patterns were statistically similar and consistent with those described in previous studies on Heceta Bank (Stein et al. 1992, Tissot et al. *in review 1*), on multiple rocky banks off Oregon (Hixon et al. 1991), in Alaska (O'Connell and Carlisle 1993), in Soquel Canyon, California (Yoklavich et al. 2000), and off British Columbia (Murie et al. 1994), supporting use of the patterns described here as representative of the Northeast Pacific continental shelf. Although both species were concentrated in shallow areas (60-90m) with high seafloor relief, yelloweye were also found in greater relative abundance in mid-depth communities (90-110m) with boulder and cobble habitats. This difference may exist because some canary rockfish exhibit schooling behavior, aggregating with conspecifics and individuals of other species around high relief areas, such as pinnacles and drop-offs (Love 1991), whereas yelloweye are usually solitary and are associated with benthic refuge space (O'Connell and Carlisle 1993, Love et al. 2002).

The previously documented behavioral patterns of canary and yelloweye rockfish were reflected in their respective feeding habits. Yelloweye and canary rockfish both consumed midwater prey, but prey taxa were entirely different. Euphausiids, which are abundant in the water column, were the main food item of canary rockfish. Midwater fishes (Gadiformes) were also present in canary rockfish stomachs, and other small fishes including juvenile rockfish and *S. jordani* have been found as prey items (Brodeur and Pearcy 1984, Lee 2003). In contrast, the majority of yelloweye rockfish prey weight consisted of a Pacific herring (*Clupea harengus pallasii*) found in the stomach of one fish. Pacific herring was found as a prey item only in the summer, when this species is abundant in midwater trawl catches off Oregon and Washington (Brodeur et al. 2004). A substantial proportion of yelloweye prey items also consisted of benthic fishes and shrimp, which is consistent with other studies (Rosenthal et al. 1988, Love et al. 2002, PFMC 2003). Yelloweye was the only species where individual fish were distinct from conspecifics in the non-metric multidimensional scaling analysis (Fig. 10), and this is most likely attributable to the unique presence of benthic fish in their diet.

Niche complementarity also occurred between rosethorn and pygmy/Puget Sound rockfish. These species were similar in distribution patterns, but pygmy rockfish consumed almost exclusively euphausiids while rosethorn rockfish specialized on benthic galatheid crabs and midwater shrimp. The similarity in distribution patterns between these two species differs from that of previous studies and may be due to the broader, multivariate nature of the CCA used in describe distribution. Studies of rosethorn rockfish generally agree that this species is a ‘habitat generalist’ because it does not seem to concentrate in any one type of rocky habitat (Hixon et al. 1991, Stein et al. 1992, Yoklavich et al. 2000, Tissot et al. *in review 1*).

In contrast, describing habitat utilization of pygmy/Puget Sound rockfish is difficult. Stein et al. (1992), Hixon et al. (1991), and Love et al. (2002) suggest pygmy rockfish are abundant in multiple habitat types, usually found schooling or individually above ridges, boulders, and cobbles. However, when pygmy and Puget Sound rockfish were pooled, for this analysis and in Tissot et al. (*in review 1*), there were interdecadal differences in distribution patterns. Tissot et al. (*in review 1*) suggests that in 1988 – 1990 these species were found inhabiting rocky ridges. Here pygmy/Puget Sound rockfish were found primarily in areas with high relief but were more widely distributed and similar to rosethorn rockfish. This pattern may indicate that the distribution patterns of pygmy/Puget Sound rockfish were different from those found in 1988 – 1990. The habitat distribution of pygmy/Puget Sound rockfish was significantly different among the three years of 1988 – 1990 (Tissot et al. *in review 1*), and interdecadal differences are entirely possible.

The third pair of demersal rockfish that overlap in distribution on Heceta Bank, greenstriped and sharpchin, differed in resource partitioning patterns by overlapping in habitat and prey use. Greenstriped rockfish have been described as the most habitat-specific of these six species (Tissot et al. *in review 1*), and were found primarily on mud/cobble habitats off of California (Yoklavich et al. 2000), Alaska (Richards 1986), and Oregon (Hixon et al. 1991, Stein et al. 1992, Tissot et al. *in review 1*), and on sand/mud habitats off British Columbia (Murie et al. 1994). The analyses here suggest that greenstriped rockfish were associated with some relief, either abiotic (boulders or cobbles) or biotic (sponges) in flat habitats but were concentrated in communities with deep (120-160m) mud, flat rock, and boulder.

The presence of sharpchin rockfish in habitats with limited abiotic structure, similar to greenstriped, differs from the findings of previous studies. Stein et al. (1992) and Tissot et al. (*in review 1*) suggest that sharpchin rockfish were sometimes found in mud habitat but always with boulders or cobbles. This difference may indicate that sharpchin rockfish had a broader habitat distribution pattern in 2002 than in 1988 – 1990. Love et al. (2002) describes sharpchin rockfish as utilizing boulder, cobble, and mud habitat and being associated with sponges and crinoids off Oregon. There is evidence that juvenile rockfish use crinoids as habitat (Carlson and Straty 1981, Stein et al. 1992, Puniwai 2002, Tissot et al. *in review 1*) and invertebrates such as sponges and sea pens can provide habitat for large, individual rockfish as well (Malatesta and Auster 1999, Brodeur 2001, Tissot et al. *in review 2*). Sharpchin and greenstriped rockfish may use vase and foliose sponges in a similar manner when abiotic relief is not available to them.

In contrast to the other two species pairs, greenstriped and sharpchin rockfish were similar in some dietary measures. Rosethorn and greenstriped overlapped in use of trophic groups and had high overlap values in regards to prey frequency of occurrence. In fact, sharpchin rockfish had high overlap values in prey frequency of occurrence with all other rockfish species except yelloweye. Both greenstriped and sharpchin rockfish were predators of benthic shrimp and crabs, but the majority of the diet consisted of midwater prey, including fishes (primarily Myctophiformes), shrimp (primarily *Sergestes similis*), and euphausiids.

Despite their use of similar prey, greenstriped and sharpchin rockfish differed in prey specialization when stomachs were pooled and when grouped into geographic area. When all stomachs were pooled, sharpchin rockfish had by far the most even utilization of prey items by weight, while greenstriped specialized on Sergestidae, a family of midwater shrimp. When stomachs were grouped by geographic area, sharpchin rockfish consumed the most euphausiids in Northern Washington and all midwater fish were consumed in the Columbia River region. Conversely, greenstriped rockfish consumed the most euphausiids in the Columbia River region. This may indicate that, overall, greenstriped and sharpchin rockfish were similar in prey use but partitioned dietary items regionally.

The morphological analyses also support differential use of prey by those species that overlap in distribution on Heceta Bank. All species that overlapped were similar in jaw size but different in gill raker characteristics. Past competitive actions may have forced these species with similar habitat use patterns and similar jaw size to specialize on different prey, which is reflected by gill raker differences (Pequeno 1983). An alternative hypothesis is that morphological traits developed independently as a result of prey use and environmental conditions, which allowed multiple species to invade similar habitats (Connell 1980). Resource partitioning as a result of interspecific competition has been demonstrated in shallow-water rockfish (Larson 1980), but experimental evidence is necessary to make such conclusions.

Prey behavior and temporal feeding habits

The presence of midwater items in the diet of these six rockfish species indicates that prey behavior is important in predicting food utilization patterns of demersal rockfish. Vertical migratory behavior of some zooplankters and midwater fishes allows benthic predators to feed on otherwise unavailable midwater prey. Many species of euphausiids, including *Euphausia pacifica*, the dominant euphausiid in all demersal rockfish diets, migrate vertically from the surface at night to below 250 meters during the day (Brinton 1967). A few species of midwater decapods, including *S. similis* (Krygier and Pearcy 1981), and myctophids, including *Diaphus theta* (Pearcy and Laurs 1966) also migrate in a pattern similar to euphausiids. Thus, all demersal rockfish should have access to vertically migrating prey, and those feeding on midwater items can be benthic-dwelling.

Daytime activity of rockfish feeding on vertically migrating zooplankton and nekton, including canary, pygmy, rosethorn, sharpchin, and greenstriped rockfish, is expected. In a study of diel activity on Heceta Bank using a remotely operated vehicle (ROV), pygmy/Puget Sound and rosethorn rockfish were more abundant during the day, and canary and yelloweye were considered to be crepuscular piscivores, displaying activity during the day and night (Hart 2004). Conversely, sharpchin and greenstriped rockfish showed activity during the day but were considered dominant nighttime fishes on Heceta Bank. The wide variety of prey items consumed by greenstriped and sharpchin may reflect activity at multiple time periods. Other rockfish, including canary and yellowtail, have exhibited diel feeding patterns, with a greater percentage of fish present during the night and morning (Brodeur and Pearcy 1984). Because all stomach samples were collected during the day during this study, prey eaten at night may have been partially or fully digested, biasing results of feeding habits. Submersible transects were also conducted during daylight hours only, which may bias habitat utilization patterns, especially for those more active at night or during crepuscular periods.

Conclusions

The patterns of resource partitioning in this assemblage of deep-water demersal rockfish were similar to those found in the shallow-water kelp forest assemblage (Hallacher and Roberts 1985) in that species with high overlap in habitat and temporal activity patterns partitioned food resources in some manner. Most species that had a high degree of overlap in distribution on the Northeast Pacific continental shelf preyed on completely different food resources. The others preyed on similar items but in different proportions and were morphologically capable of focusing on different prey depending on environmental conditions. Differential use of prey items in all species was reflected in behavior and use of vertical space, as species that school or are commonly found higher up in the water column had different diets than those that are more benthic.

Although niche complementarity and resource partitioning were found to occur within this demersal fish assemblage, the role of competition and other ecological interactions in development of these patterns is unknown. There are multiple alternative hypotheses that may explain these resource utilization patterns, such as changes in prey availability, prey density, competition with other organisms, or predation (Schmitt and Coyer 1983). In order to investigate competitive interactions when experimental work is not feasible, studies of resource use between areas of sympatry and allopatry or over periods of low prey availability would be useful. Dunham et al. (1979) were able to attribute morphological characteristics of sympatric and allopatric populations of suckers (Catostomidae) to multiple factors, including interspecific competition. A more extensive investigation of geographic and seasonal changes in diet and habitat use would also lead to better descriptions of essential fish habitats for these species. Incorporation of physical data, such as bathymetry and ocean current patterns may also help explain prey availability.

This study also highlights the importance of vertical space as a resource dimension utilized in ecological communities, which has been previously noted in groups of aquatic and terrestrial organisms. Here, differential use of vertical space seems to be related to prey choice. This is likely because food is the most commonly partitioned resource in marine fish communities (Ross 1986). Other mechanisms causing vertical partitioning of space include displacement as a result of invasion (Crowder 1984) and environmental factors such as light availability (Schoener 1970). Because spatial arrangement of prey and habitat are often multidimensional, it is important to assess vertical space of co-occurring species in studies of resource partitioning, as it can indicate factors important to community organization.

The information provided here provides a more holistic description of essential fish habitat for these rockfish, including distribution among microhabitats (both horizontally and vertically) and use of prey resources. If these kinds of characteristics are known for more groundfish species, ecosystem management is more likely to be successful. Identifying resource use patterns of, and potential competition between, groundfish is especially important in managing overfished species. The two overfished species in this deep-water rockfish assemblage, yelloweye and canary, showed some degree of overlap in diet and habitat use with at least one other rockfish species, and all six species in the assemblage showed some spatial overlap. Changes in oceanographic conditions or fishing pressure may alter abundance or distribution patterns of one species or prey item, and this could have potential impacts on all other rockfish species within the assemblage. For instance, the impacts of yearly variation in zooplankton abundance have been demonstrated to have a significant effect on all trophic levels in other oceanic systems (Brodeur and Pearcy 1992). Therefore, identifying important habitat guilds and understanding resource utilization patterns within them is especially important in light of the many changing pressures on continental shelf communities.

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Table 1. Summary of *Delta* submersible dives. Dominant habitat types are the two or three most common in a dive in order of abundance. R = ridge, B = boulder, C = cobble, P = pebble, F = flat rock, S = sand, M = mud.

Station	**Dive**	**Number of habitat patches**	**Average depth (m)**	**Dominant habitat types**
1	5693	182	80.1	RR, SC, CB
1	5694	158	79.3	RR, SC, CB
1	5695	174	81.0	RR, SC, CB
2	5699	84	142.5	MM, MB
2	5700	100	140.0	MM, MB, CB
2	5701	108	146.4	MM, MB, CB
3	5696	170	93.9	CB, PS, RR
3	5697	138	81.5	RR, CB
3	5698	170	94.6	RR, SC, MM
4	5702	106	127.1	MM, CB
4	5703	100	128.0	MM, CB, MB
4	5707	172	126.3	MM, CB, MB
5	5704	12	265.0	MM
5	5705	10	287.6	MM
5	5706	8	287.8	MM
6	5708	30	212.3	MM
6	5709	175	181.3	MM, CB, MB
6	5710	30	176.3	CB, MM, MB
	Total	1927		
	Average	107.1	151.7	

Table 2. Sampling locations in geographic areas sampled in 2003 and 2004. Latitudinal boundaries are based on Brodeur and Pearcy (1984), with the addition of Central California. The number of sampling locations within each area includes trawling locations at which stomach and/or morphological samples were taken.

Geographic area	**Latitude South**	**Latitude North**	**Number of sampling locations**
Central California	37º00'	41º00'	2
Northern California / Southern Oregon	41º00'	43º50'	6
Heceta Bank / Central Oregon	43º50'	45º00'	17
Columbia Region	45º00'	47º00'	19
Northern Washington / Vancouver BC	47º00'	50º00'	16

Table 3. Percent of sample populations that were considered mature (size at 50% maturity) for morphology and stomach samples collected in 2003 and 2004. Reference information is unknown for pygmy rockfish (*S. wilsoni*) and given for Oregon and Washington for sharpchin rockfish. All lengths were converted to standard length using conversions for blue rockfish (MacGregor 1983). Number of unknown length includes both sexes.

	Total length at 50% maturity (cm)			Percent at size of 50% maturity Stomach samples (Morphology samples)				
Rockfish species	Male	Female	Reference	Male	Female	Unknown sex	**Total**	Number of unknown length
Pygmy	Unknown	Unknown						
Canary	40	44	(Calliet et al. 2000)	88% (7%)	75% (0%)	0% (21%)	**83% (10%)**	1 (0)
Yelloweye	40	40	(Calliet et al. 2000)	100% (100%)	40% (50%)	0% (75%)	**57% (72%)**	1 (14)
Rosethorn	22	23	(Calliet et al. 2000)	86% (88%)	97% (100%)	0% (86%)	**93% (91%)**	0 (0)
Sharpchin	21 (Oregon and Washington)	22	(Love et al. 2002)	100% (93%)	100% (90%)	0% (100%)	**100% (94%)**	1 (1)
Greenstriped	23	23	(Calliet et al. 2000)	88% (59%)	88% (57%)	0% (67%)	**88% (58%)**	0 (1)

Table 4. Summary of demersal rockfish characteristics from *Delta* submersible dives. Density is the total number of fish per station, and total length (in mm) was estimated visually by each observer during submersible transects.

Rockfish species		Station 1	2	3	4	5	6	Total	Mean
Pygmy (*S. wilsoni*) / Puget Sound (*S. emphaeus*)	Density	1905	1276	630	3290	0	2077	**9178**	**1530**
	Mean total length (mm)	104.2	116.5	120.0	112.5	0	158.1		**101.8**
Canary (*S. pinniger*)	Density	9	31	3	21	0	6	**70**	**14**
	Mean total length (mm)	362.5	453.6	466.7	507.1	0	480.0		**454.0**
Yelloweye (*S. ruberrimus*)	Density	8	8	12	16	0	7	**51**	**10**
	Mean total length (mm)	425.0	462.5	504.2	534.4	0	414.3		**468.1**
Rosethorn (*S. helvomaculatus*)	Density	214	100	218	256	0	252	**1040**	**208**
	Mean total length (mm)	184.6	172.8	190.4	195.5	0	202.7		**189.2**
Sharpchin (*S. zacentrus*)	Density		172	2	13	0	2576	**2763**	**691**
	Mean total length (mm)		158.9	200.0	154.2	0	187.7		**175.2**
Greenstriped (*S. elongatus*)	Density	3	306	39	117	4	69	**538**	**90**
	Mean total length (mm)	200.0	171.3	141.3	140.1	250.0	200.0		**183.8**

Table 5. Results of canonical correlation analysis. Variables with high positive loadings in boldface, high negative loadings underlined. Positive loadings on first axis, CC1, indicate fish found in mud communities, negative ridge and sand communities. Positive loadings on second axis, CC2, indicate fish in boulder, cobble, and pebble communities, negative loadings mud and sand communities. Positive loadings on third axis, CC3, indicate fish found in pebble communities, negative loadings ridge and boulder communities. Positive loadings on fourth axis, CC4, indicate fish found in ridge and boulder communities, negative loadings flat rock and mud communities. Demersal rockfish species in boldface.

	CC1	**CC2**	**CC3**	**CC4**
Adjusted Canonical Correlation	0.965	0.901	0.690	0.657
F-value	17.24	10.96	7.23	6.01
Degrees of freedom	459	416	375	336
Canonical variate loadings				
Fish				
Rex sole (*Glyptocephalus zachirus*)	**0.694**	0.057	0.147	-0.125
Slender sole (*Lyopsetta exilis*)	**0.728**	-0.004	0.232	-0.118
Dover sole (*Microstomus pacificus*)	**0.738**	0.003	**0.393**	-0.125
Threadfin sculpin (*Icelinus filamentosus*)	0.126	**0.330**	0.152	-0.233
Greenstriped rockfish (*Sebastes elongatus*)	0.170	**0.201**	**0.328**	-0.298
Sharpchin rockfish (*Sebastes zacentrus*)	0.152	**0.896**	-0.022	-0.131
Unidentified ronquil (Bathymasteridae)	0.067	**0.283**	0.135	-0.043
Lingcod (*Ophiodon elongatus*)	0.039	**0.223**	-0.025	0.210
Spotted ratfish (*Hydrolagus colliei*)	0.319	**0.238**	**0.571**	0.148
Hagfish (*Eptatretus* spp.)	**0.802**	-0.657	0.193	0.156
Pacific hake (*Merluccius productus*)	**0.754**	-0.050	0.032	0.074
Unidentified flatfish (*Pleuronectiformes*)	**0.719**	-0.086	0.157	0.008
Shortspine thornyhead (*Sebastolobus alascanus*)	**0.737**	-0.095	**0.489**	0.149
Unidentified eelpout (Zoarcidae)	**0.939**	-0.158	0.114	0.075
Sturgeon poacher (*Agonus acipenserinus*)	**0.554**	-0.137	-0.152	0.001
Unidentified poacher (Agonidae)	**0.732**	-0.088	**0.387**	0.073
Sablefish (*Anoplopoma fimbria*)	0.399	0.049	**0.533**	0.180
Unidentified sculpin (Cottidae)	0.081	0.196	0.257	0.082
Canary rockfish (*Sebastes pinniger*)	0.017	0.180	-0.054	0.121
Unidentified juvenile rockfish (*Sebastes* spp.)	-0.033	-0.024	-0.081	0.212
Unidentified mottled sculpin (Cottidae)	-0.025	-0.044	0.117	**0.326**
Kelp greenling (*Hexagrammos decagrammus*)	-0.046	-0.017	-0.124	**0.447**
Pygmy rockfish (*Sebastes wilsoni*) / Puget Sound rockfish (*S. emphaeus*)	0.059	**0.610**	-0.145	**0.236**
Rosethorn rockfish (*Sebastes helvomaculatus*)	0.033	**0.589**	-0.137	**0.561**
Yelloweye rockfish (*Sebastes ruberrimus*)	0.009	**0.316**	-0.166	**0.203**
Yellowtail rockfish (*Sebastes flavidus*)	-0.016	0.076	-0.116	**0.375**
Variance extracted	0.219	0.079	0.062	0.048
Redundancy	0.204	0.064	0.031	0.021
Habitat and invertebrates				
Mud	**0.961**	-0.192	-0.136	-0.044
Flat rock	0.010	0.034	0.052	-0.059
Sand	-0.061	-0.105	-0.042	0.000
Pebble	0.244	**0.259**	**0.739**	0.164
Cobble	0.095	**0.770**	-0.136	0.115
Boulder	0.036	**0.552**	-0.188	**0.244**
Ridge	-0.083	-0.058	-0.191	**0.650**
Vase sponge	0.094	**0.620**	-0.014	-0.241
Foliose sponge	0.152	**0.878**	-0.039	-0.229
Brittlestar (Ophiacanthidae)	-0.006	**0.504**	-0.194	0.323
Shelf sponge	-0.008	-0.012	0.007	0.049
Sand star (*Luidia foliolata*)	0.255	-0.030	-0.046	0.379
Fragile sea urchin (*Allocentrotus fragilis*)	**0.581**	-0.086	**0.385**	0.105
Sunflower star (*Pycnopodia helianthoides / Rathbunaster californicus)*	**0.771**	-0.200	-0.264	-0.007
Sea cucumber (*Parastichopus californicus*)	0.156	-0.138	-0.142	**0.622**
Crinoid (*Florometra serratissima*)	-0.118	-0.085	-0.071	**0.598**
Blood star (*Henricia* spp.)	-0.117	-0.054	-0.180	**0.594**
Variance extracted	0.123	0.147	0.058	0.117
Redundancy	0.115	0.121	0.029	0.051

Table 6. Diet breadth values for all six demersal rockfish species using samples collected in 2003 and 2004. All prey taxa that comprised > 0.1% of the diet and could be identified to order were used in the analysis (n), and the top three taxa by percent weight. *B* = diet breadth calculated by Levins's measure (Levins 1968). B_a = standardized Levins values; a measure of breadth if all diet items were in equal proportion, or a measure of the evenness of prey utilization (Hurlbert 1978).

Rockfish species	Sample size	Principal prey types (top three taxa by percent weight)	*n*	*B*	B_a
Pygmy (*S. wilsoni*)	49	*Euphausia pacifica*, Euphausiacea, *Thysanoessa spinifera*	8	2.65	0.24
Canary (*S. pinniger*)	29	*Euphausia pacifica*, Euphausiacea, *Thysanoessa spinifera*	6	2.00	0.20
Yelloweye (*S. ruberrimus*)	9	*Clupea harengus pallasii*, Clupeidae, *Lyopsetta exilis*	11	3.04	0.20
Rosethorn (*S. helvomaculatus*)	60	*Munida quadrispina, Pandalus platyceros*, Pandalidae / Crangonidae	19	3.66	0.15
Sharpchin (*S. zacentrus*)	36	Myctophiformes, *Euphausia pacifica, Diaphus theta*	15	8.29	0.52
Greenstriped (*S. elongatus*)	51	Sergestidae, *Sergestes similis, Euphausia pacifica*	21	4.65	0.18

Table 7. Diet overlap values for all possible pairs of rockfish species collected in 2003 and 2004. All prey taxa that weighed > 0.1% of the diet and could be identified to order were used in the analysis. Overlap was calculated by Horn's index (Horn 1966) using weight of prey taxa (upper values) and by Morisita's index (Morisita 1959) using frequency of occurrence. Overlap values considered high are in boldface character (> 0.60) and those considered medium (0.29 – 0.60) are underlined.

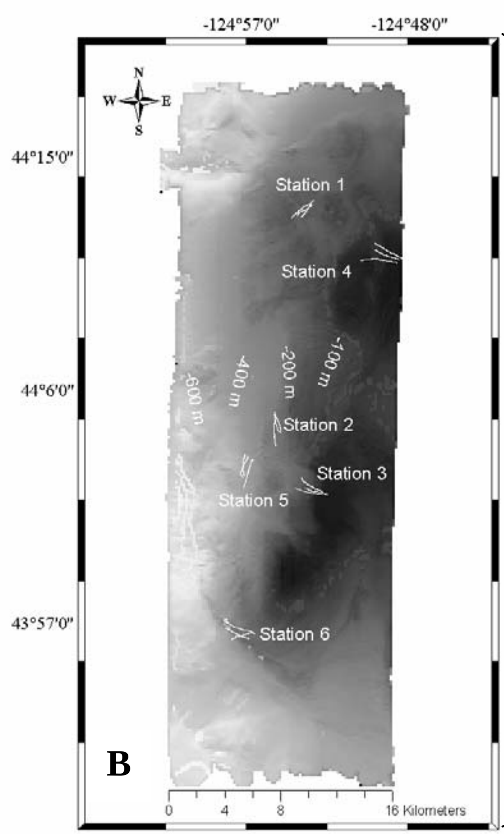
Rockfish species	Pygmy	Canary	Yelloweye	Rosethorn	Sharpchin	Greenstriped
Pygmy		**0.877**	0.018	0.054	<u>0.527</u>	<u>0.384</u>
Canary	**0.852**		<0.01	0.014	<u>0.467</u>	<u>0.381</u>
Yelloweye	0.073	0.111		0.067	0.031	0.052
Rosethorn	0.264	0.134	<u>0.474</u>		<u>0.448</u>	<u>0.336</u>
Sharpchin	**0.787**	**0.625**	<u>0.316</u>	**0.730**		<u>0.512</u>
Greenstriped	<u>0.591</u>	<u>0.550</u>	<u>0.423</u>	<u>0.560</u>	**0.905**	

WEIGHT

FREQUENCY OF OCCURRENCE

Table 8. Squared Mahalanobis distance values from multivariate discriminate analysis (MDA) of feeding morphology characteristics for all pairs of rockfish species. All distances were significant ($p < 0.001$, $\alpha = 0.05$). Pairs that overlap visually on the plot of the first and second MDA dimensions are in boldface.

Rockfish species	Canary	Greenstriped	Pygmy	Rosethorn	Sharpchin	Yelloweye
Canary						
Greenstriped	60					
Pygmy	19	41				
Rosethorn	77	**4**	51			
Sharpchin	27	16	**12**	25		
Yelloweye	219	96	222	77	173	



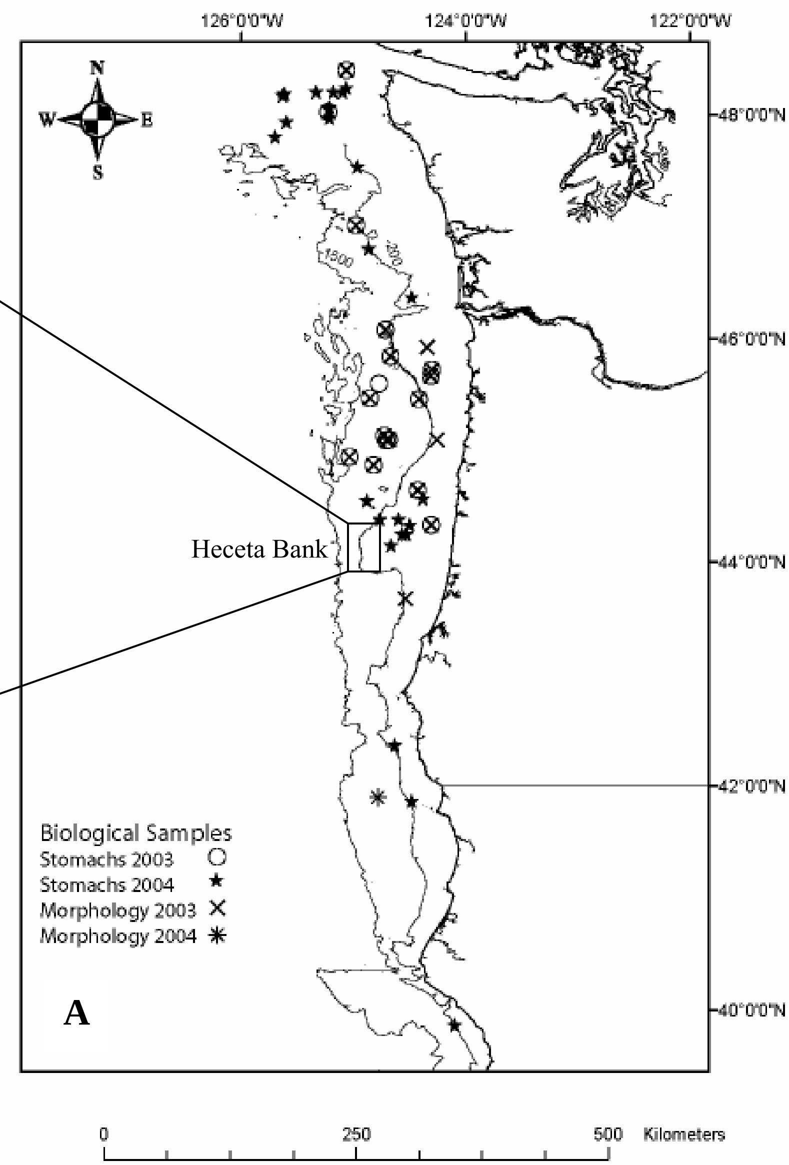


Figure 1. **A.** Location of morphology and stomach samples collected in 2003 and 2004 from the NWFSC annual bottom trawl survey and location of Heceta Bank, OR, in relation to the U.S. northwest coast. Multiple samples were collected from each location. Depth in meters. **B.** Location of *Delta* submersible dives on Heceta Bank during September 2002. Each dive consisted of two transects.

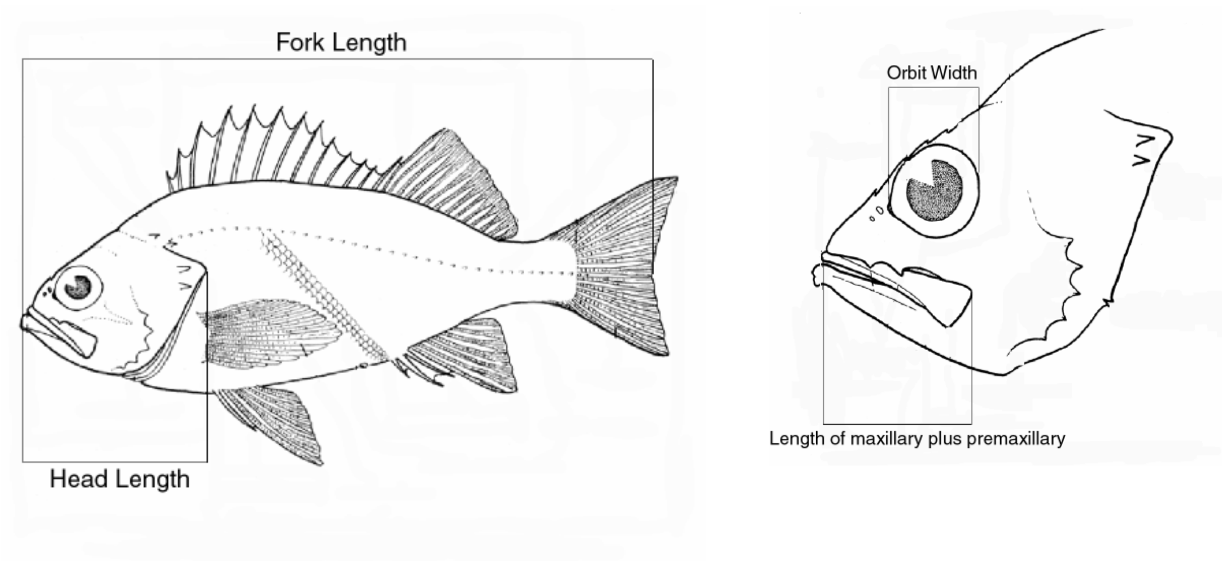


Figure 2a. Body and head measurements on demersal rockfish used in the morphological analysis. Modified from Phillips (1957).

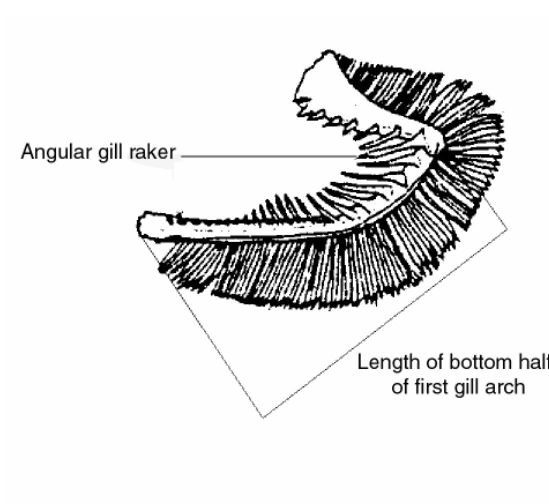


Figure 2b. Gill raker measurements on demersal rockfish used in morphological analysis. All measurements were done on the first gill arch on the left side of the fish. The length of the angular gill raker on the first gill arch, the number of gill rakers, and the length of the bottom half of the first gill arch were measured. Modified from Pequeño (1983).

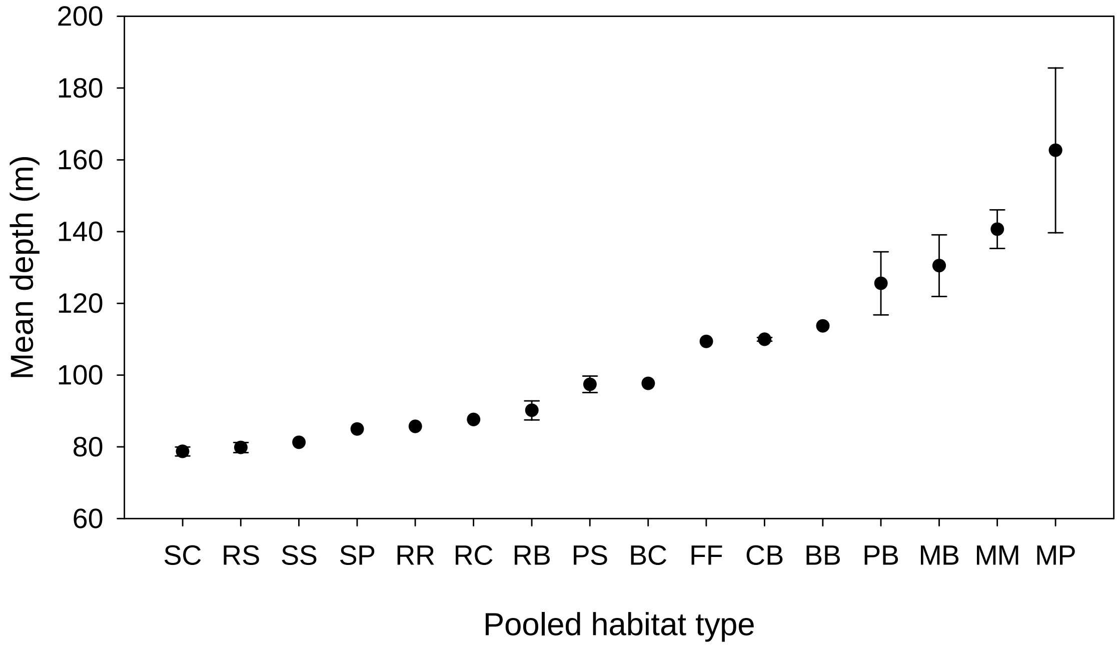


Figure 3. Mean depth ($\pm$1 standard error) of the 16 most dominant pooled habitat types on Heceta Bank, Oregon in 2002, pooled across all submersible dives. In order of decreasing relief, R = ridge, B = boulder, C = cobble, P = pebble, S = sand, F = flat rock, and M = mud.

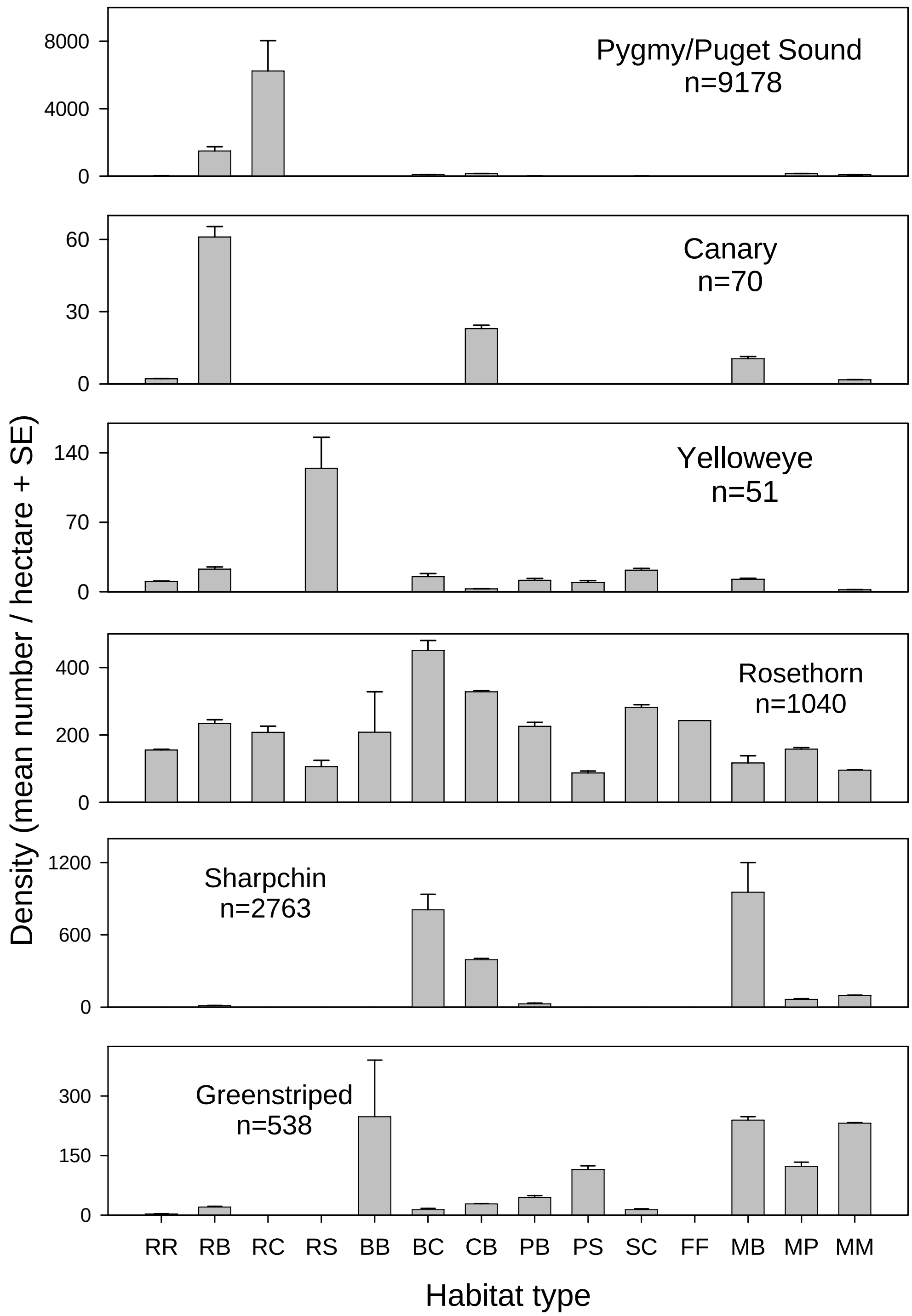


Figure 4. Density (mean number / hectare + SE) of demersal rockfish species among pooled dominant habitat types found on Heceta Bank in 2002. Habitat types are listed by decreasing relief and particle size. The first letter of each habitat type represents the primary substratum type, and the second letter the secondary substratum type: R = rock ridge, B = boulder, C = cobble, P = pebble, S = sand, F = flat rock, M = mud. n = number of individuals observed per species.

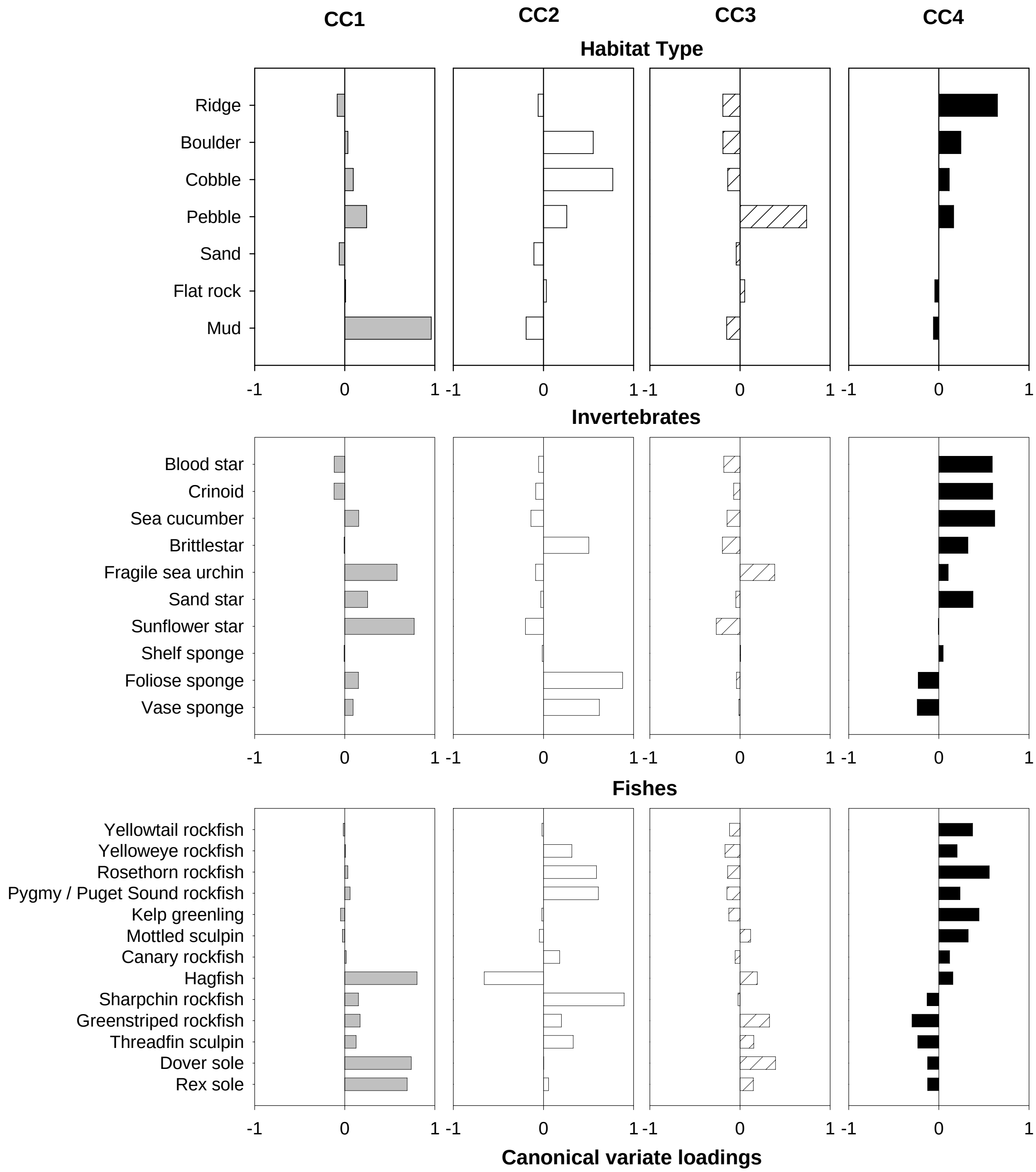


Figure 5. Canonical variate loadings for habitat types, invertebrates, and selected fishes for CCA axes 1-4. All habitat types and invertebrates used in the CCA are displayed, along with selected fishes that had high positive or negative variate loadings on CCA axis 4.

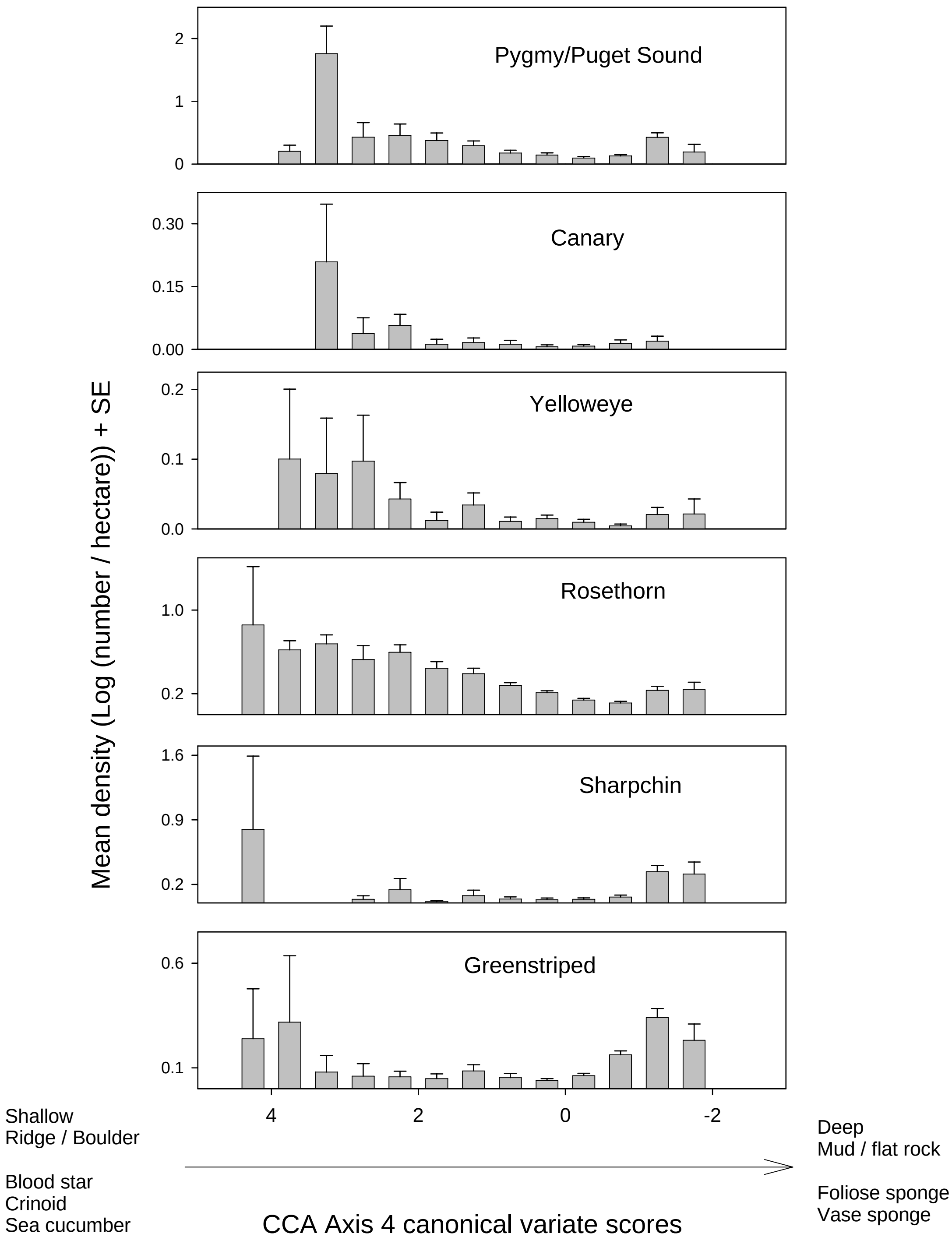


Figure 6. Mean density (log abundance / hectare + 1 SE) of demersal rockfish over canonical variate scores for CCA axis 4. CCA axis 4 contrasts ridge and boulder communities (positive canonical scores) with mud and flat rock communities (negative canonical scores). This axis is representative of decreasing relief and increasing depth from positive to negative variate scores. The distribution of demersal rockfish over this axis is similar to that of the distribution over dominant habitat types.

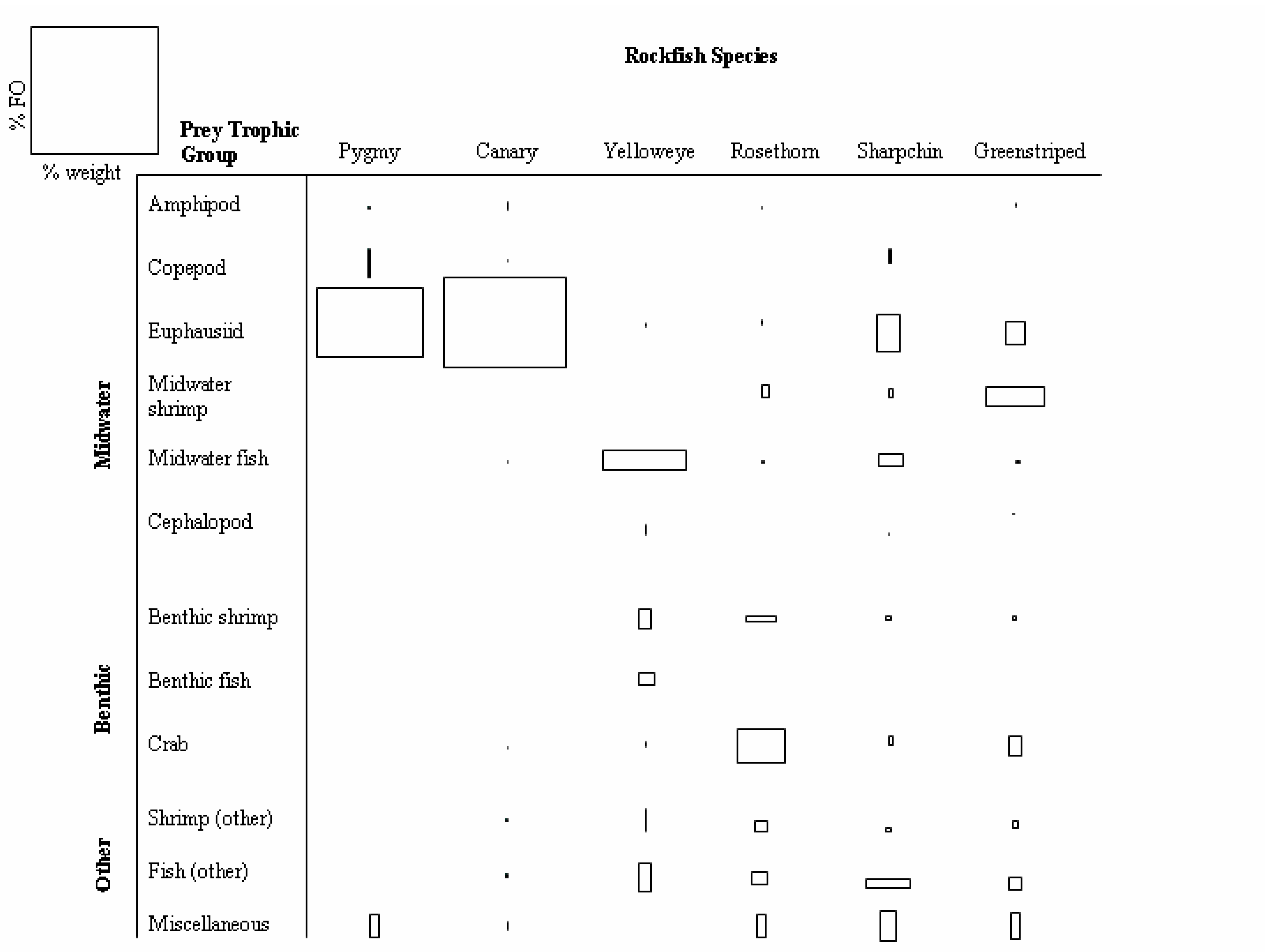


Figure 7. Importance of prey trophic groups for all rockfish stomach contents combined. Blocks represent percent weight on the x-axis and % frequency of occurrence (FO) on the y-axis. Size of blocks is scaled to represent the importance of each trophic group to each rockfish species. Scale of 100% x 100% in upper left corner. 'Shrimp' (other) and 'fish' (other) represent taxa that could not be placed in either trophic group.

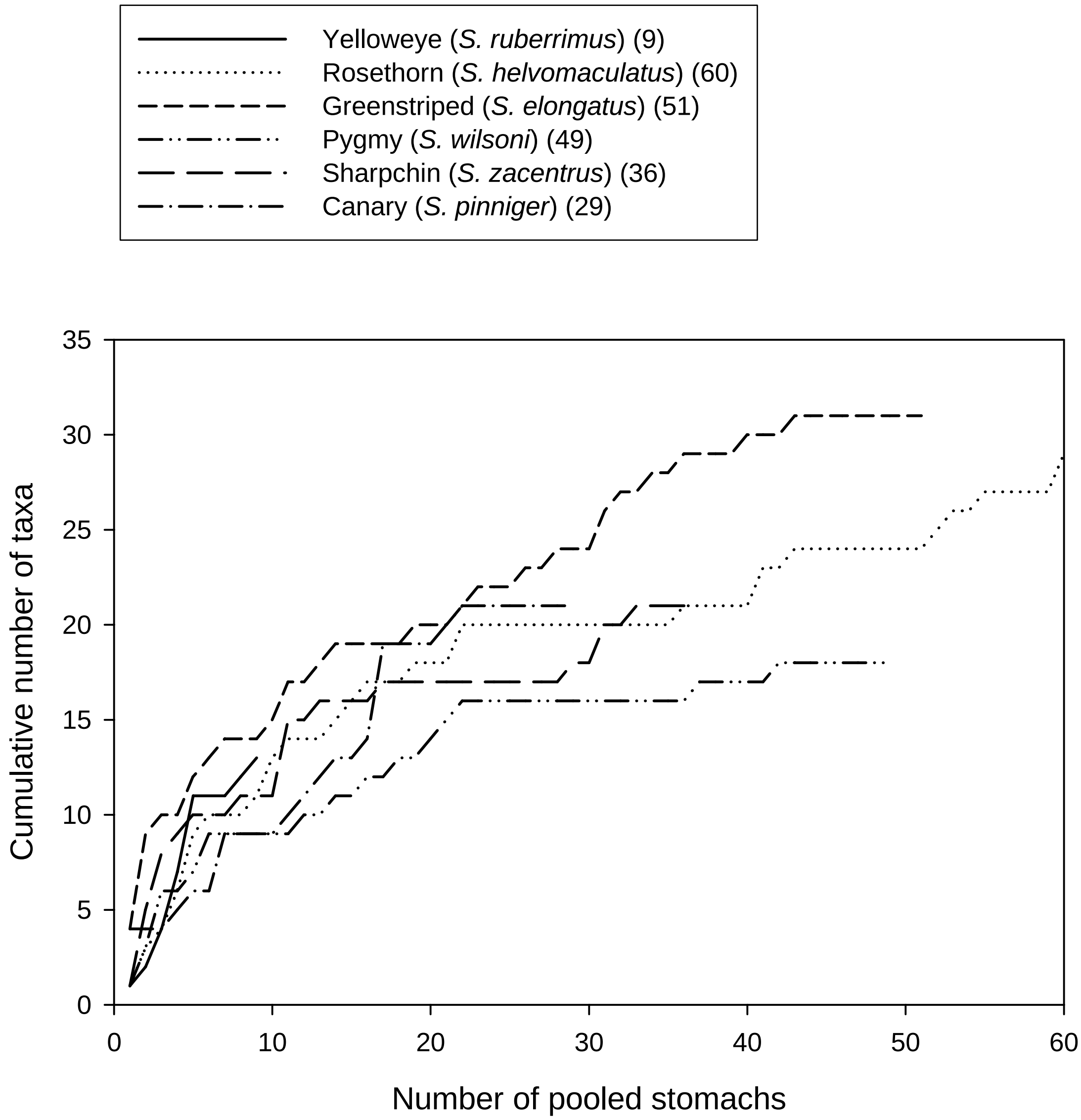


Figure 8. Cumulative prey species curves for all stomachs used in the diet analysis for each rockfish species. The point at which an asymptote is reached is considered an adequate sample size. Prey items were identified to the lowest taxa possible and stomachs were pooled randomly per species. Number of stomachs sampled are in parentheses.

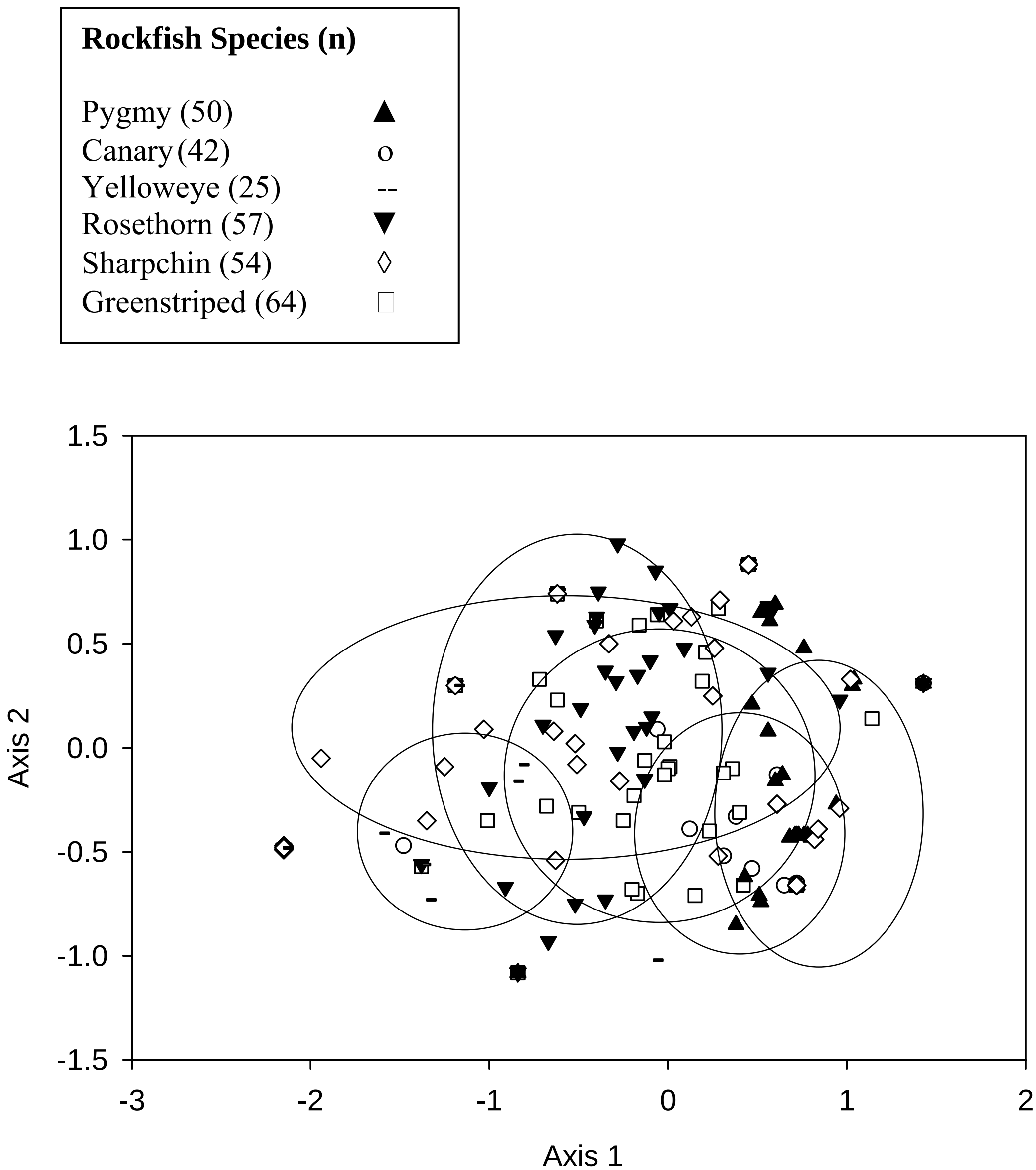


Figure 9. Nonmetric multidimensional scaling ordination of prey item trophic groups for rockfish species. Circles represent approximate clusters of individuals by rockfish species. Number of stomach samples (n) is in legend parentheses.

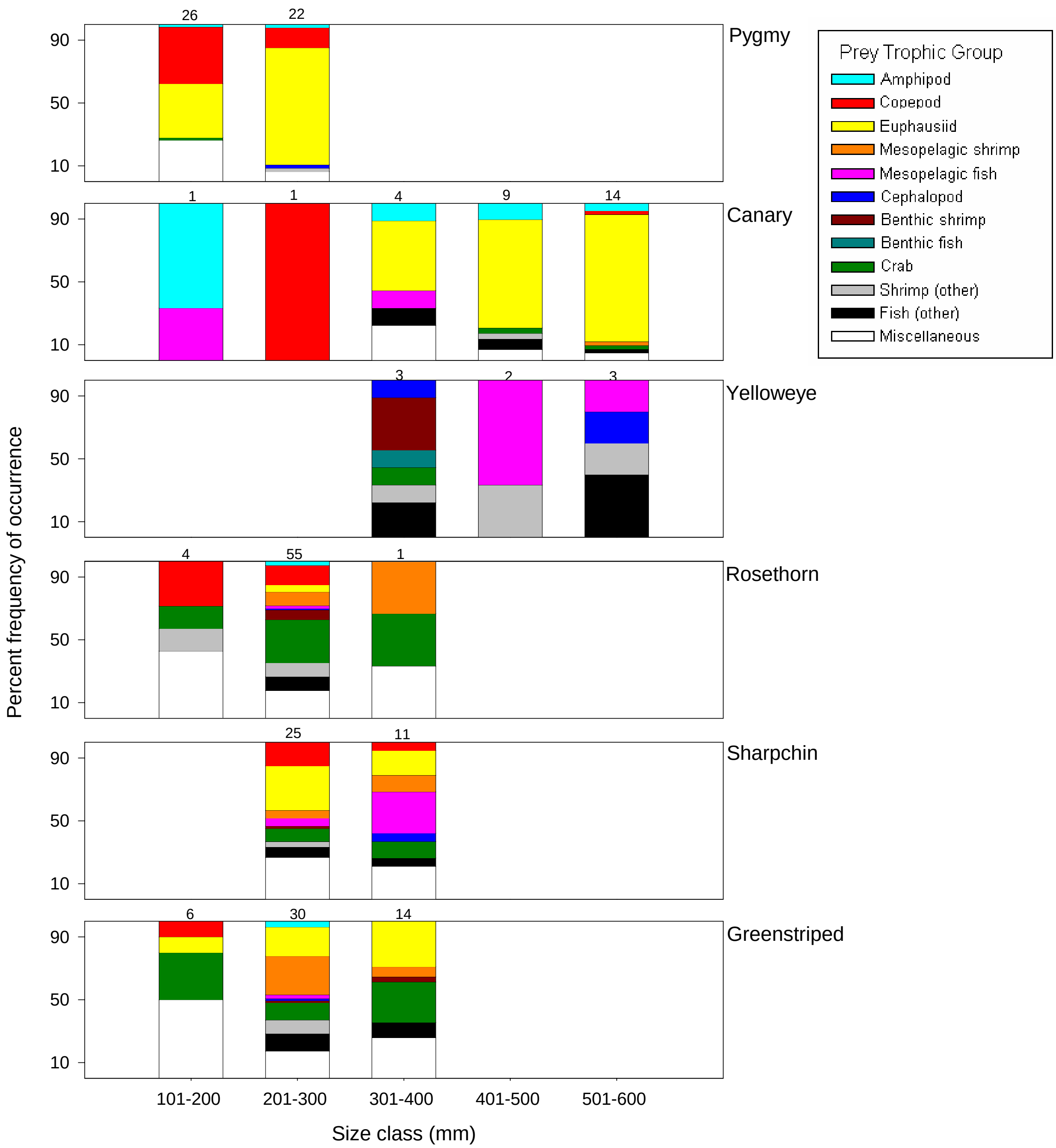


Figure 10. Percent frequency of occurrence of prey trophic groups in all sampled size classes for each demersal rockfish species. Size class in millimeters (mm). Number of stomachs is above respective size class.

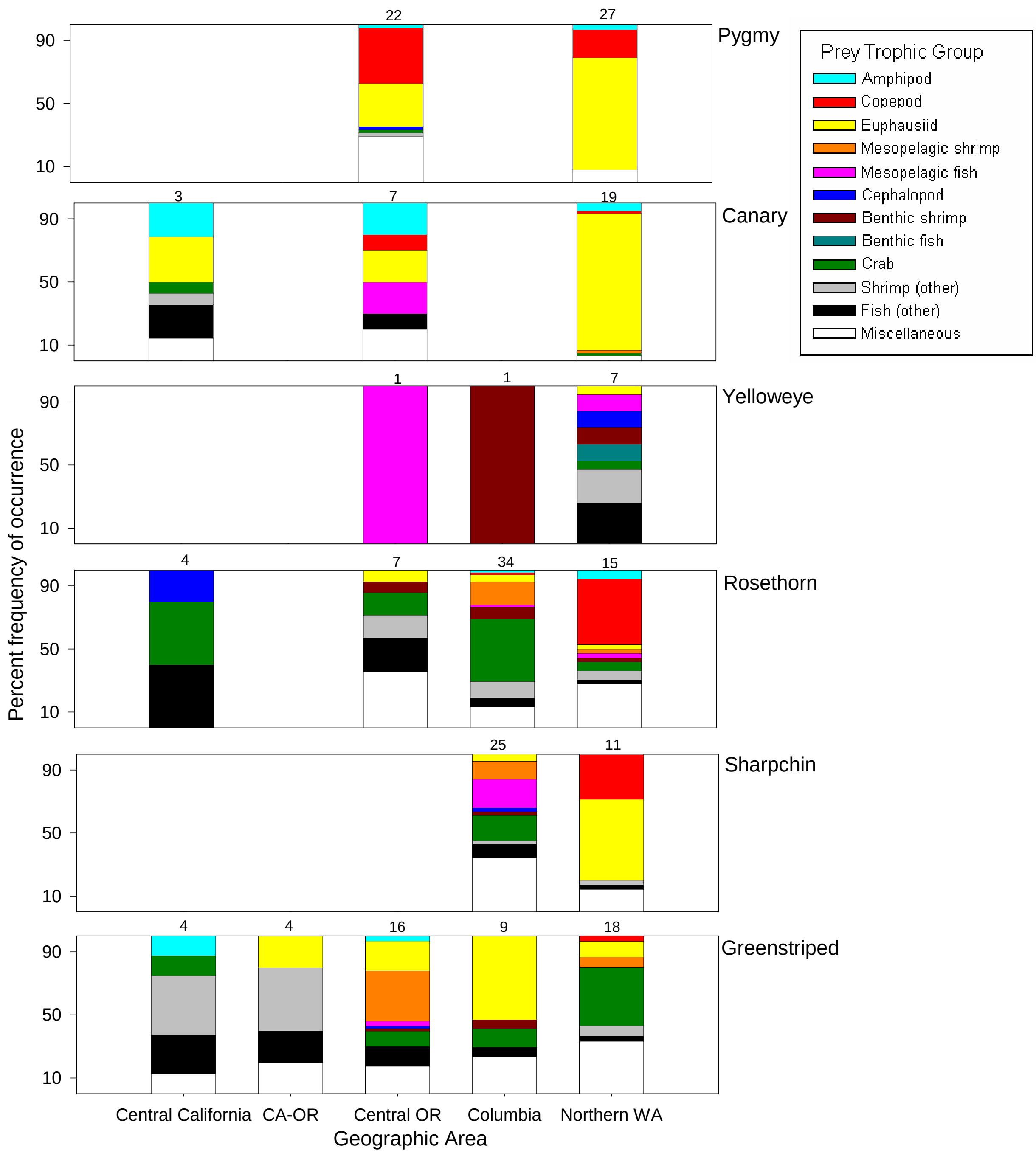


Figure 11. Percent frequency of occurrence of prey trophic groups in all sampled geographic areas for each demersal rockfish species. Latitude ranges of geographic areas in text. Number of stomachs is above respective geographic area. CA = California, OR = Oregon, WA = Washington.

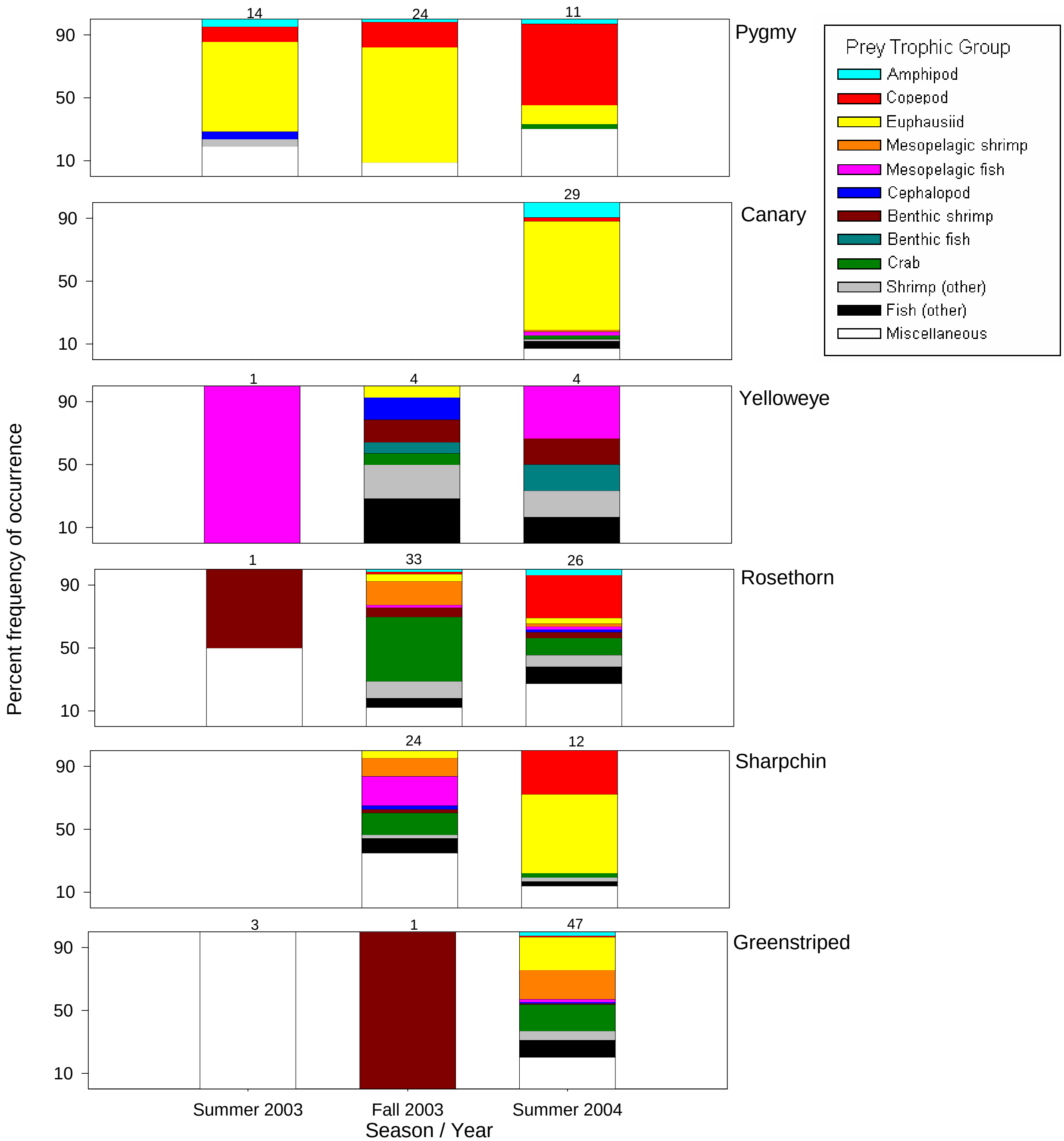


Figure 12. Percent frequency of occurrence of prey trophic groups in all sampled seasons and years for each demersal rockfish species. Seasons were based on shifts in hydrographic regime (Huyer 1977): Summer: June – August, Fall : September – October. Number of stomachs is above respective season/year.

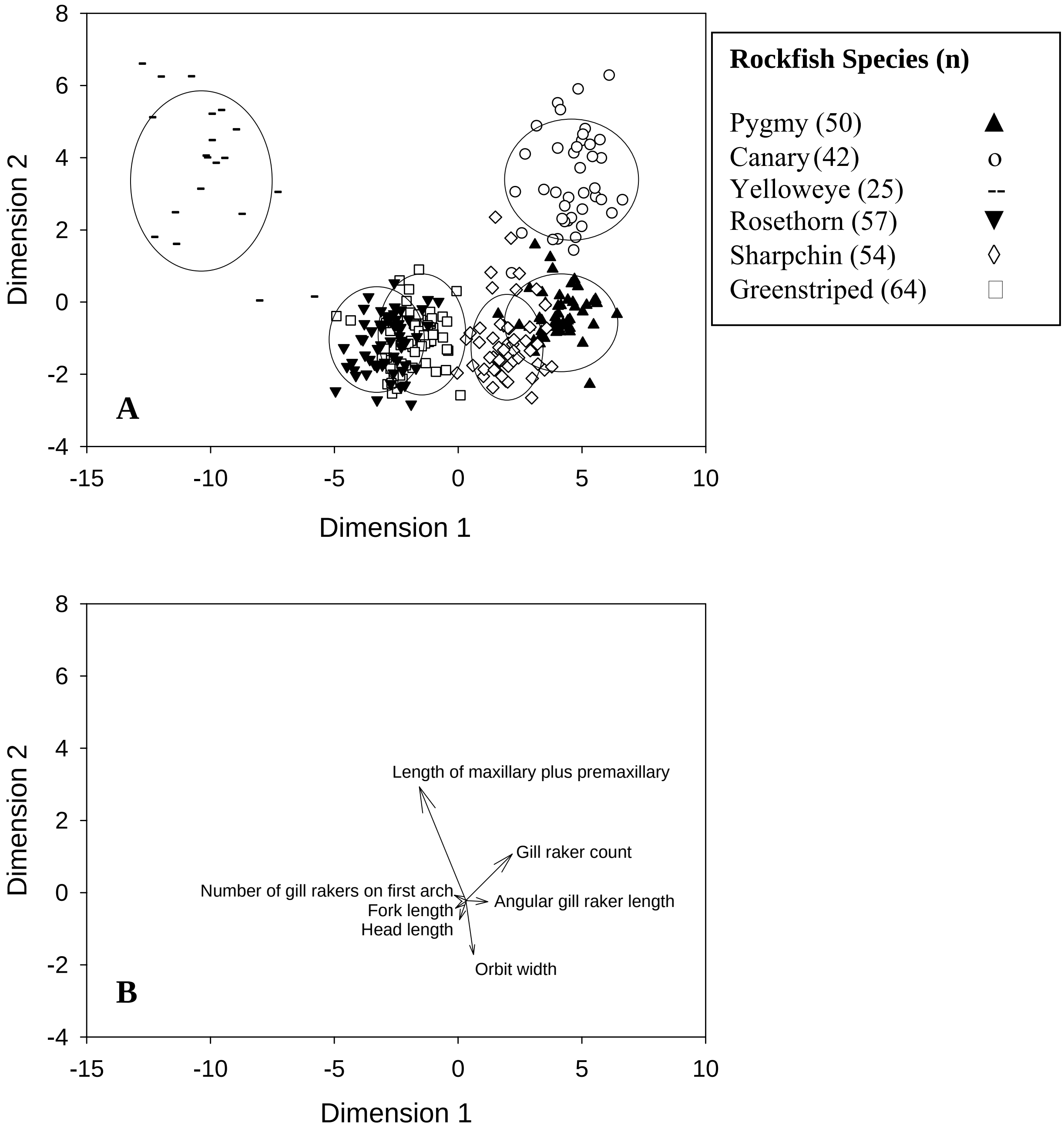


Figure 13. Multivariate discriminate analysis of morphological characteristics of demersal rockfish species. **A**. Ordination plot of discriminant analysis. Circles represent the approximate groups of species. Sample size (n) for both plots is indicated in legend. **B**. Magnitude and direction of each morphological characteristic measured.

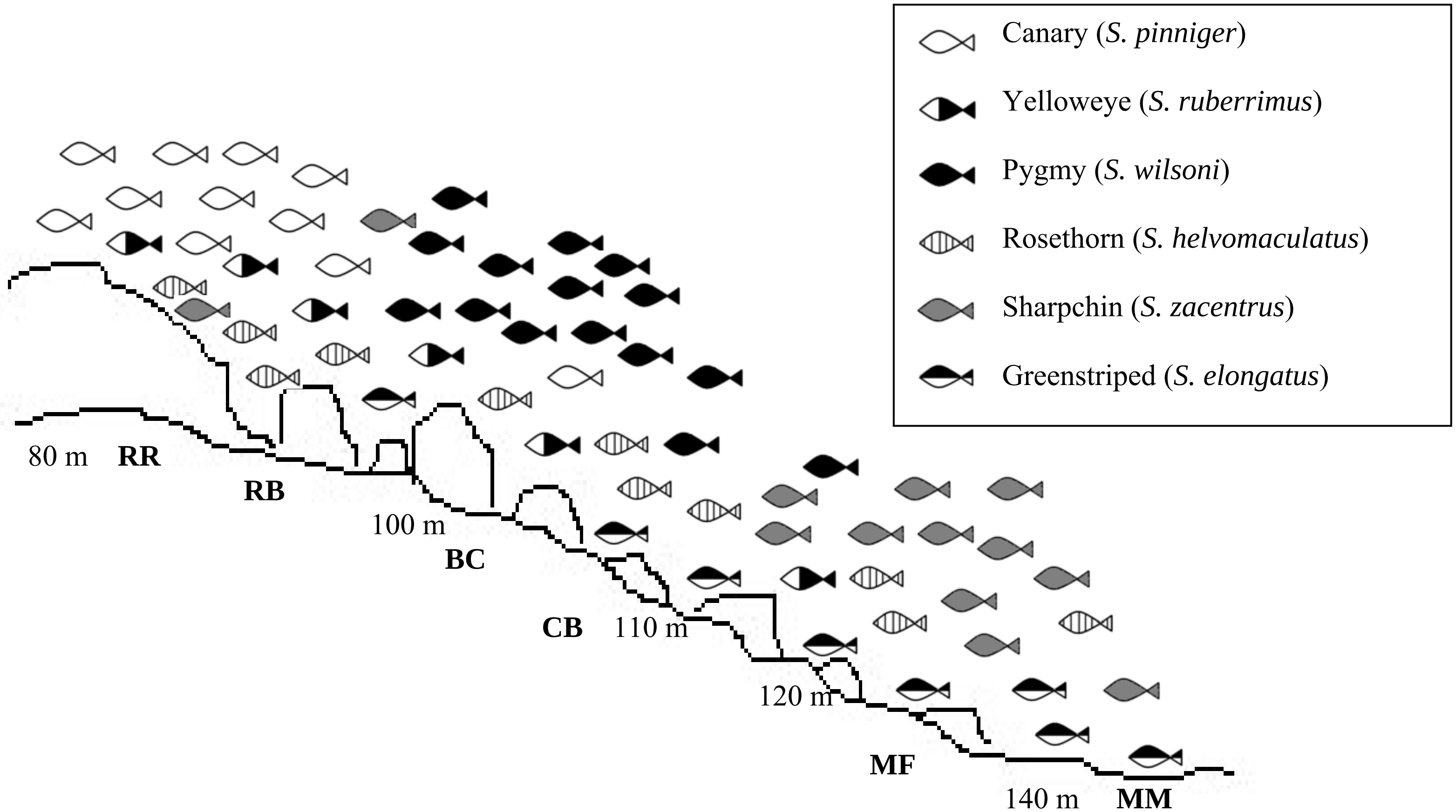


Figure 14. Stylized depiction of deep-water, demersal rockfish distribution on the Northeast Pacific continental shelf. Numbers of fish figures are not scaled to abundance. Size of fish figures, depth, substrate particle size, and distribution of fish figures and habitat not drawn to scale. Habitat types are, in order of decreasing particle size: R = ridge, B = boulder, C = cobble, P = pebble, S = sand, F = flat rock, M = mud.

Appendix A. Summary of stomach and morphology samples taken during the NOAA Fisheries NWFSC West Coast bottom trawl survey in 2003 and 2004. Number of non-regurgitated and non-empty stomach samples (S) and number of morphology samples collected (M) are given for each demersal rockfish species. Summer = June – August, Fall = September – October. Latitude and longitude range of geographic areas is described in Table 2. CA = California, OR = Oregon, WA = Washington. Haul number refers to individual vessel haul number for the respective year; X = haul number unknown.

Year	Season	Geographic Area	Vessel	Haul number	Canary		Greenstriped		Pygmy		Rosethorn		Sharpchin		Yelloweye	
					S	M	S	M	S	M	S	M	S	M	S	M
2003	Summer	CA – OR	*Ms. Julie*	64		1		6								
2003	Summer	Central OR	*Captain Jack*	57					14	19						
2003	Summer	Central OR	*Ms. Julie*	54								5				
2003	Summer	Central OR	*Ms. Julie*	56		26										
2003	Summer	Central OR	*Ms. Julie*	57				8				1			1	1
2003	Summer	Columbia	*Ms. Julie*	44		1		1								
2003	Summer	Columbia	*Ms. Julie*	45			3	13								
2003	Summer	Columbia	*Ms. Julie*	46				18						3		
2003	Summer	Columbia	*Ms. Julie*	48				1								
2003	Summer	Columbia	*Ms. Julie*	50							1	6		1		
2003	Fall	Central CA	*Excalibur*	102												1
2003	Fall	Central OR	*Blue Horizon*	56		8										
2003	Fall	Central OR	*Excalibur*	64											2	
2003	Fall	Columbia	*Blue Horizon*	41							1	7	5	24		
2003	Fall	Columbia	*Blue Horizon*	43			1	6								
2003	Fall	Columbia	*Blue Horizon*	44				2								
2003	Fall	Columbia	*Blue Horizon*	48				10								
2003	Fall	Columbia	*Blue Horizon*	49							1	8				
2003	Fall	Columbia	*Blue Horizon*	50							11	13	5	9		
2003	Fall	Columbia	*Blue Horizon*	51							20	21	14	16		
2003	Fall	Columbia	*Excalibur*	45											1	3
2003	Fall	Northern WA	*Blue Horizon*	5		4			22	23						5
2003	Fall	Northern WA	*Blue Horizon*	13												3
2003	Fall	Northern WA	*Excalibur*	8												1
2003	Fall	Northern WA	*Excalibur*	21		1				3					3	2
2003	Fall	Northern WA	*Excalibur*	25					2	5						
2004	Summer	Central CA	*Ms. Julie*	107	3		4				4					
2004	Summer	CA – OR	*Ms. Julie*	88			2									
2004	Summer	CA – OR	*Ms. Julie*	95												1
2004	Summer	CA – OR	*Ms. Julie*	96			2									

Appendix A. cont.

Year	Season	Geographic Area	Vessel	Haul number	Canary		Greenstriped		Pygmy		Rosethorn		Sharpchin		Yelloweye	
					S	M	S	M	S	M	S	M	S	M	S	M
2004	Summer	Central OR	*Ms. Julie*	59							3					
2004	Summer	Central OR	*Ms. Julie*	66	5				8		2					
2004	Summer	Central OR	*Ms. Julie*	68	2		2									
2004	Summer	Central OR	*Ms. Julie*	70							2					
2004	Summer	Central OR	*Ms. Julie*	71			2									
2004	Summer	Central OR	*Ms. Julie*	72			1									
2004	Summer	Central OR	*Ms. Julie*	76			11									
2004	Summer	Columbia	*Ms. Julie*	5									1			
2004	Summer	Columbia	*Ms. Julie*	35			5									
2004	Summer	Northern WA	*BJ Thomas*	10			2				4		1		1	
2004	Summer	Northern WA	*BJ Thomas*	21			3		2		3		2			
2004	Summer	Northern WA	*Ms. Julie*	7							1		2			
2004	Summer	Northern WA	*Ms. Julie*	9			1				7		4			
2004	Summer	Northern WA	*Ms. Julie*	11	1										2	4
2004	Summer	Northern WA	*Ms. Julie*	12			4									
2004	Summer	Northern WA	*Ms. Julie*	16					1							
2004	Summer	Northern WA	*Ms. Julie*	17	18											
2004	Summer	Northern WA	*Ms. Julie*	20			4									
2004	Summer	Northern WA	*Ms. Julie*	25			3									
2004	Summer	Northern WA	*Ms. Julie*	26			1						2		1	5
2004	Summer	Northern WA	*Ms. Julie*	X												2
2004	Summer	Northern WA	*Excalibur*	X												1

Appendix B. List of references used in stomach content identification.

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Pittard, R. 1977. Ocean Plankton, 2nd ed. Consolidated Printing and Stationary, Inc., Astoria, OR. 95 pp.

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Appendix C. Summary of rockfish stomach contents from all sampling locations in 2003 and 2004: a. Canary (*S. pinniger*), b. pygmy (*S. wilsoni*), c. greenstriped (*S. elongatus*), d. rosethorn (*S. helvomaculatus*), e. sharpchin (*S. zacentrus*), and f. yelloweye (*S. ruberrimus*). Prey organisms were placed in trophic groups based on life history characteristics. F.O. = frequency of occurrence.

a. Canary rockfish (*S. pinniger*)

Prey Organism	**Weight of prey (g)** Total	Percentage	**% F.O.**	**Trophic group**
Amphipoda				
Lycianacidae	<0.01	----	3.45	Amphipod
Hyperia spp.	<0.01	----	3.45	Amphipod
Hyperoche spp.	0.012	0.01	10.34	Amphipod
Amphipoda unidentified	0.005	----	3.45	Amphipod
Hyperiidea unidentified	<0.01	----	3.45	Amphipod
Gammeridea unidentified	<0.01	----	3.45	Amphipod
Copepoda				
Calanus marshallae	<0.01	----	3.45	Copepod
Calanoida unidentified	0.08	0.07	3.45	Copepod
Decapoda				
Fabia subquadrata zoea	<0.01	----	3.45	Crab
Cancer spp. megalopa	0.42	0.36	3.45	Crab
Pandalidae/Crangonidae	<0.01	----	3.45	Benthic shrimp
Sergestes similis	0.07	0.06	3.45	Midwater shrimp
Euphausiacea				
Thysanoessa spinifera	4.09	3.50	34.48	Euphausiid
Euphausia pacifica	36.81	31.48	51.72	Euphausiid
Euphausiid unidentified	9.28	7.94	41.38	Euphausiid
Euphausiid remains	61.98	53.00	72.41	Euphausiid
Osteichthyes				
Gadiformes	0.88	0.75	6.90	Midwater fish
Osteichthyes remains	2.41	2.06	13.79	Fish
Isopoda unidentified	0.03	0.03	3.45	Miscellaneous
Unidentified digested material	0.67	0.57	6.90	Miscellaneous
Crustacean remains	0.174	0.15	10.34	Miscellaneous
Number of stomachs sampled		**29**		
Mean fork length of rockfish		**474.76 $\pm$ 84.28 (SD)**		
Number of unique prey taxa		**21**		
Number of unique sample locations		**5**		

b. Pygmy rockfish (*S. wilsoni*)

Prey Organism	Weight of prey (g) Total	Percentage	%F.O.	Trophic group
Amphipoda				
Paraphronima phrocipes	0.02	0.08	2.04	Amphipod
Hyperiidea unidentified	0.03	0.14	4.08	Amphipod
Copepoda				
Neocalanus cristatus	0.20	0.84	4.08	Copepod
Calanus spp.	0.24	1.01	16.33	Copepod
Candacia columbiae	0.008	0.03	4.08	Copepod
Euchaeta spp.	0.06	0.27	8.16	Copepod
Calanoida unidentified	0.72	3.02	24.49	Copepod
Decapoda				
Brachyuran megalopa	0.02	0.08	2.04	Crab
Natantia unidentified	0.41	1.72	2.04	Shrimp
Euphausiacea				
Thysanoessa spinifera	2.33	9.77	20.41	Euphausiid
Euphausia pacifica	11.44	47.97	48.98	Euphausiid
Euphausiid unidentified	4.00	16.77	26.53	Euphausiid
Euphausiid remains	2.12	8.91	20.41	Euphausiid
Cephalopoda unidentified	0.02	0.08	2.04	Cephalopod
Isopoda unidentified	0.01	0.04	2.04	Miscellaneous
Gastropoda unidentified	0.01	0.05	6.12	Miscellaneous
Unidentified digested material	1.31	5.51	22.45	Miscellaneous
Crustacean remains	0.88	3.69	8.16	Miscellaneous
Number of stomachs sampled		**49**		
Mean fork length of rockfish		**176.60 ± 49.26**		
Number of unique prey taxa		**18**		
Number of unique sample locations		**6**		

C. Greenstriped rockfish (*S. elongatus*)

Prey Organism	Weight of prey (g) Total	Percentage	%F.O.	Trophic group
Amphipoda				
Hyperiidea unidentified	0.04	0.03	5.88	Amphipod
Copepoda				
Calanoida unidentified	0.80	0.58	1.96	Copepod
Decapoda				
Munida quadrispina	4.04	2.94	7.84	Crab
Cancer spp. megalopa	0.96	0.70	13.73	Crab
Hemigrapsis megalopa	0.01	0.01	1.96	Crab
Brachyuran megalopa	0.084	0.06	5.88	Crab
Galatheidae remains	2.34	1.70	9.80	Crab
Pandalidae	3.41	2.48	1.96	Benthic shrimp
Crangon spp.	0.15	0.11	1.96	Benthic shrimp
Pandalidae/Crangonidae	0.19	0.14	1.96	Benthic shrimp
Sergestidae	40.09	29.16	21.57	Midwater shrimp
Sergestes similis	29.47	21.44	19.61	Midwater shrimp
Pasiphaea pacifica	0.22	0.16	1.96	Midwater shrimp
Caridea megalopa	2.59	1.88	5.88	Shrimp
Natantia megalopa	0.27	0.20	1.96	Shrimp
Natantia unidentified	0.84	0.61	3.92	Shrimp
Euphausiacea				
Thysanoessa spinifera	0.31	0.23	5.88	Euphausiid
Euphausia pacifica	13.55	9.86	15.69	Euphausiid
Euphausiid unidentified	0.42	0.31	1.96	Euphausiid
Euphausiid remains	8.92	6.49	25.49	Euphausiid
Osteichthyes				
Tarletonbeania crenularis	0.76	0.08	1	Midwater fish
Myctophiformes	2.00	1.45	1.96	Midwater fish
Osteichthyes remains	14.79	10.76	25.49	Fish
Cephalopoda unidentified	1.84	1.34	1.96	Cephalopod
Mysida unidentified	0.47	0.34	3.92	Miscellaneous
Isopoda unidentified	0.42	0.31	3.92	Miscellaneous
Insecta unidentified	<0.01	----	1.96	Miscellaneous
Rocks	0.04	0.03	1.96	Miscellaneous
Unidentified digested material	7.32	5.33	27.45	Miscellaneous
Crustacean remains	1.11	0.81	13.73	Miscellaneous
Number of stomachs sampled		**51**		
Mean fork length of rockfish		**273.99 ± 54.31**		
Number of unique prey taxa		**30**		
Number of unique sample locations		**17**		

d. Rosethorn rockfish (*S. helvomaculatus*)

	Weight of prey (g)			
Prey Organism	**Total**	**Percentage**	**%F.O.**	**Trophic group**
Amphipoda				
Hyperoche spp.	0.01	0.01	1.67	Amphipod
Lycianacidae	<0.01	----	1.67	Amphipod
Hyperiidea unidentified	0.01	0.01	1.67	Amphipod
Copepoda				
Neocalanus cristatus	0.748	0.83	11.67	Copepod
Atylus spp.	0.03	0.03	1.67	Copepod
Neocalanus pulmchrus	<0.01	----	1.67	Copepod
Calanoida unidentified	0.36	0.40	11.67	Copepod
Decapoda				
Munida quadrispina	35.79	39.48	50.00	Crab
Cancer productus	1.25	1.38	1.67	Crab
Majidae	0.86	0.95	3.33	Crab
Pandalidae	2.18	2.41	6.67	Benthic shrimp
Pandalus platyceros	20.15	22.23	3.33	Benthic shrimp
Spirontocaris holmesi	0.60	0.83	1.67	Benthic shrimp
Pandalidae/Crangonidae	6.93	7.33	8.33	Benthic shrimp
Sergestidae	2.19	2.79	6.67	Midwater shrimp
Sergestes similis	3.81	3.14	11.67	Midwater shrimp
Natantia unidentified	1.71	4.09	10.00	Shrimp
Euphausiacea				
Euphausia pacifica	0.28	0.35	6.67	Euphausiid
Euphausiid unidentified	0.03	0.04	1.67	Euphausiid
Osteichthyes				
Tarletonbeania crenularis	1.89	1.67	1.67	Midwater fish
Myctophiformes	0.28	0.40	1.67	Midwater fish
Sebastes spp.	0.24	0.26	1.67	Fish
Osteichthyes remains	4.47	4.93	15.00	Fish
Cephalopoda				
Abraliopsis felis	0.10	0.11	1.67	Cephalopod
Isopoda unidentified	0.25	0.28	1.67	Miscellaneous
Salpa	0.92	1.01	5.00	Miscellaneous
Rocks	0.09	0.10	1.67	Miscellaneous
Unidentified digested material	2.14	2.36	18.33	Miscellaneous
Crustacean remains	3.31	3.66	13.33	Miscellaneous
Number of stomachs sampled		**60**		
Mean fork length of fish		**261.14 ± 25.72**		
Number of unique prey taxa		**29**		
Number of unique sample locations		**13**		

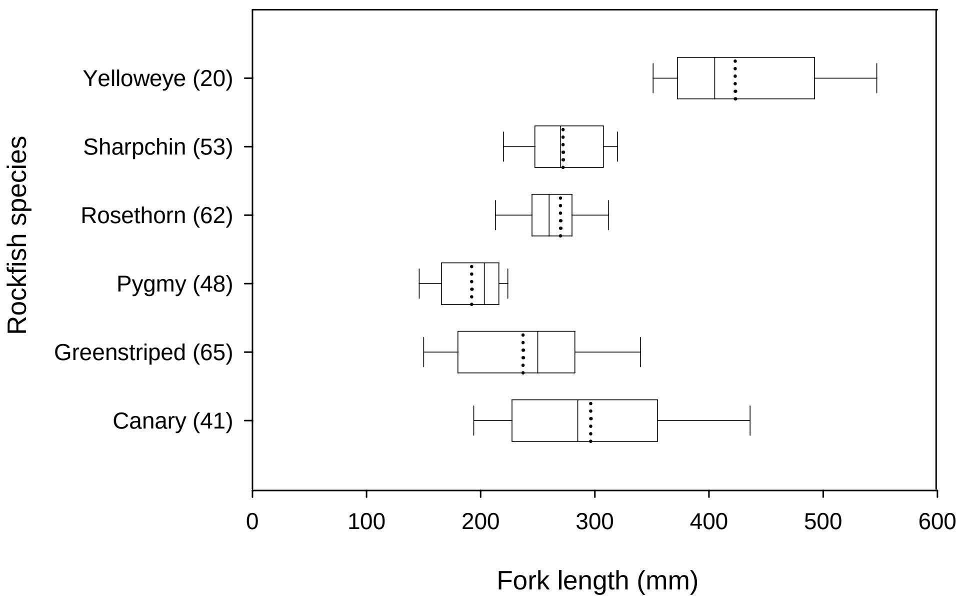
e. Sharpchin rockfish (*S. zacentrus*)

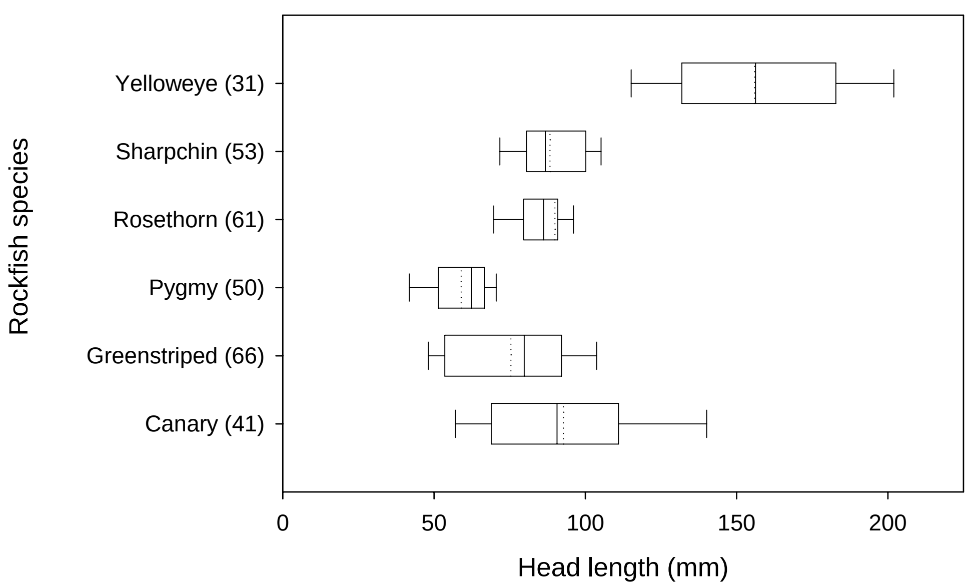
Prey Organism	Weight of prey (g) Total	Percentage	%F.O.	Trophic group
Copepoda				
Neocalanus cristatus	0.55	1.57	13.89	Copepod
Calanus spp.	<0.01	0.01	2.78	Copepod
Calanoida unidentified	0.13	0.38	11.11	Copepod
Decapoda				
Munida quadrispina	2.05	5.85	16.67	Crab
Galatheidae remains	0.01	0.03	2.78	Crab
Pandalus platyceros	1.17	3.34	2.78	Benthic shrimp
Sergestidae	0.85	2.43	2.78	Midwater shrimp
Sergestes similis	0.76	2.17	11.11	Midwater shrimp
Natantia unidentified	1.52	4.34	5.56	Shrimp
Euphausiacea				
Thysanoessa spinifera	0.83	2.37	5.56	Euphausiid
Euphausia pacifica	3.48	9.93	19.44	Euphausiid
Euphausiid unidentified	1.02	2.91	13.89	Euphausiid
Euphausiid remains	1.94	5.54	16.67	Euphausiid
Osteichthyes				
Tarletonbeania crenularis	2.02	5.76	2.78	Midwater fish
Diaphus theta	2.44	6.96	5.56	Midwater fish
Myctophiformes	6.17	17.61	13.89	Midwater fish
Osteichthyes remains	3.28	9.36	13.89	Fish
Cephalopoda				
Rossia pacifica	0.41	1.17	2.78	Cephalopod
Salpa	0.32	0.91	5.56	Miscellaneous
Unidentified digested material	1.87	5.35	33.33	Miscellaneous
Crustacean remains	4.21	12.02	16.67	Miscellaneous
Number of stomachs sampled	**36**			
Mean fork length of fish	**271.58 ± 36.48**			
Number of unique prey taxa	**21**			
Number of unique sample locations	**9**			

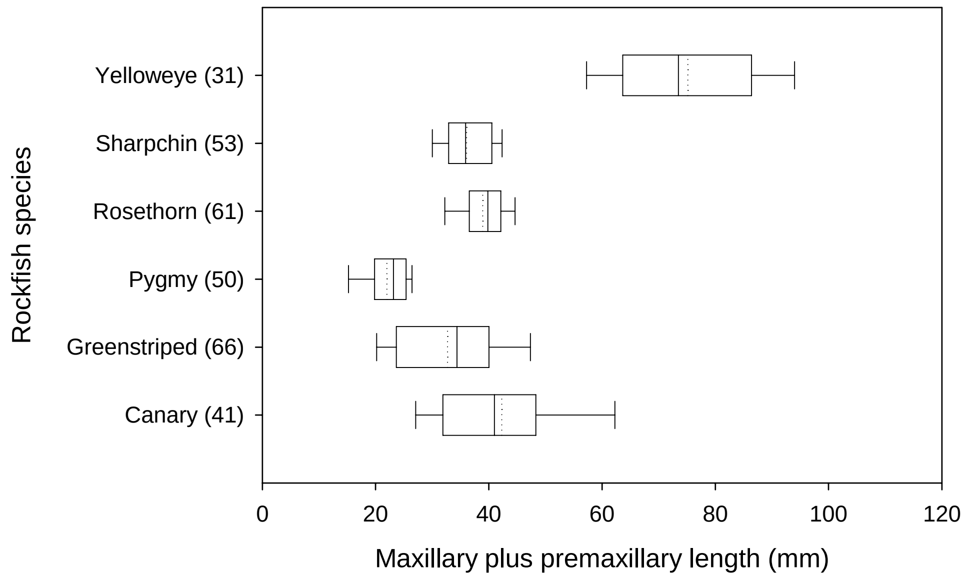
f. Yelloweye rockfish (*S. ruberrimus*)

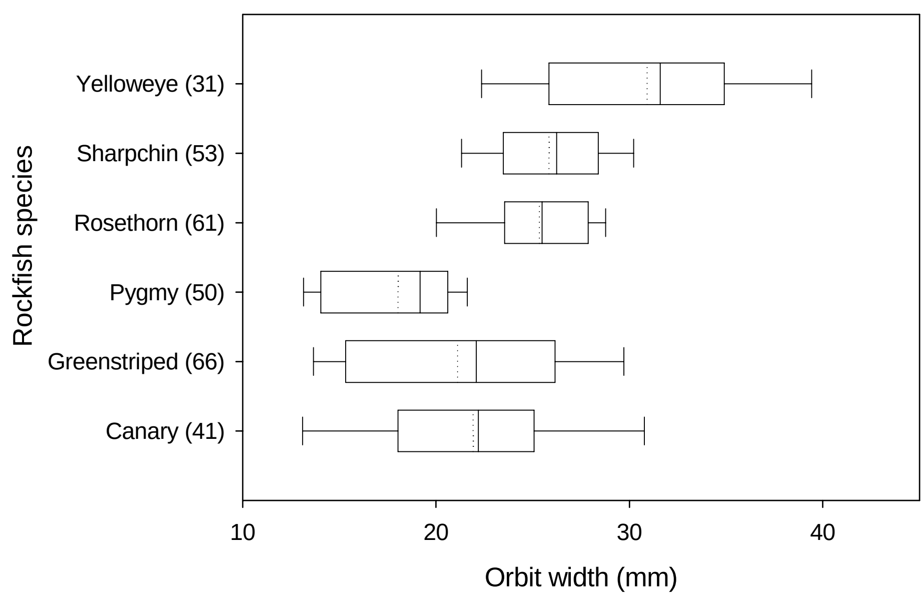
Prey Organism	Weight of prey (g) Total	Percentage	F.O.	Trophic group
Decapoda				
Munida quadrispina	0.13	0.03	11.11	Crab
Pandalus jordani	5.85	1.51	11.11	Benthic shrimp
Pandalidae	19.62	5.08	11.11	Benthic shrimp
Pandalopsis dispar	13.14	3.40	11.11	Benthic shrimp
Natantia unidentified	6.40	1.66	44.44	Shrimp
Euphausiacea				
Thysanoessa spinifera	0.04	0.01	11.11	Euphausiid
Osteichthyes				
Lyopsetta exilis	41.00	10.62	11.11	Benthic fish
Clupeidae	42.59	11.04	11.11	Midwater fish
Clupea harengus pallasii	205.02	53.12	22.22	Midwater fish
Sebastes spp.	39.41	10.21	11.11	Fish
Pleuronectiformes unidentified	8.00	2.07	11.11	Benthic fish
Osteichthyes remains	4.61	1.19	44.44	Fish
Cephalopoda	0.14	0.03	22.22	Cephalopod
Number of stomachs sampled		**9**		
Mean fork length of fish		**352.06 ± 191.94**		
Number of unique prey taxa		**13**		
Number of unique sample locations		**6**		

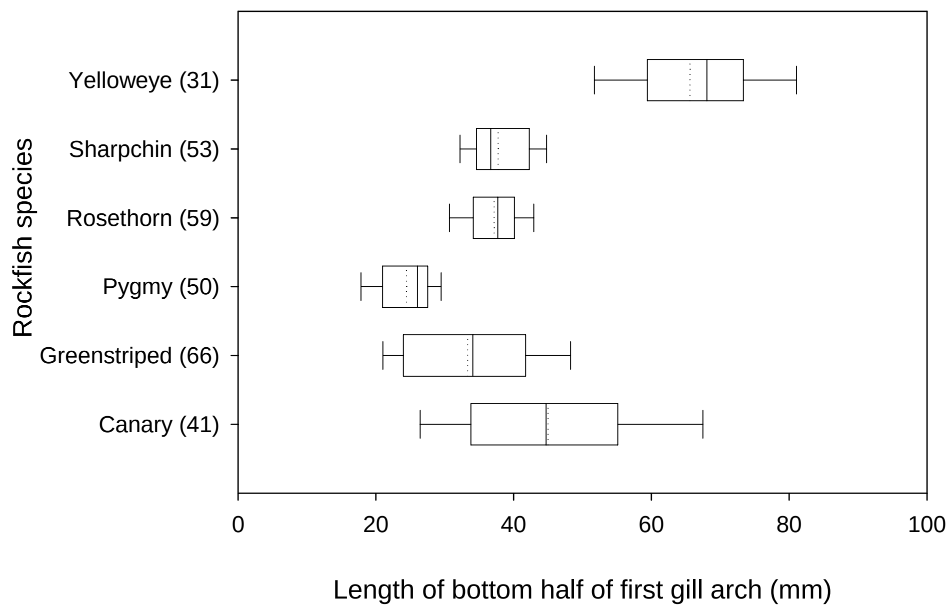
Appendix D. Boxplots displaying median (solid line), mean (dotted line), 25th and 75th percentile (box boundaries), and 5th and 95th percentile (whiskers) of morphological measurements for all demersal rockfish species collected in 2003 and 2004. Number of samples in parentheses. Characteristics measured were: fork length, head length, maxillary plus premaxillary length, orbit width, length of bottom half of first gill arch, gill raker number, and angular gill raker length.

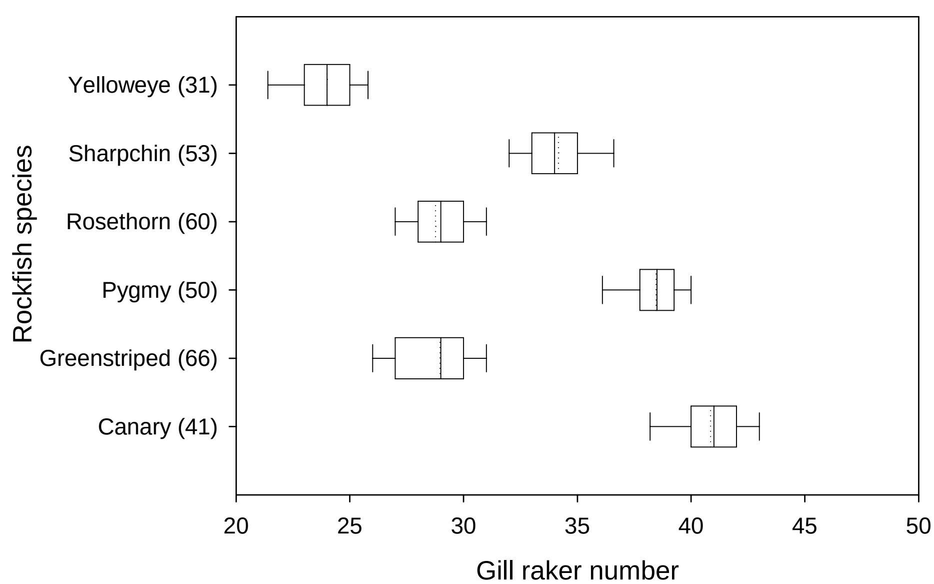


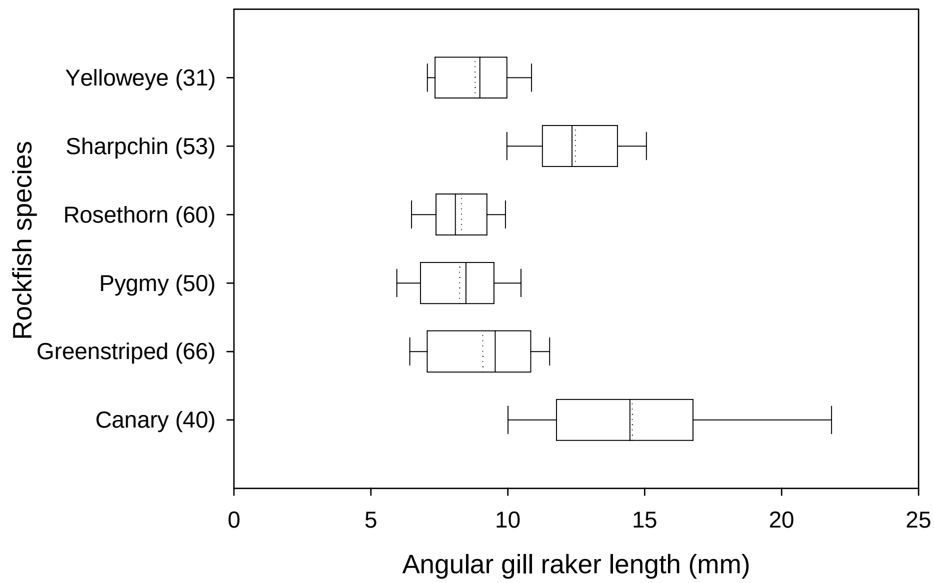



Rockfish species
Yelloweye (31)
Sharpchin (53)
Rosethorn (61)
Pygmy (50)
Greenstriped (66)
Canary (41)
0
20
40
60
80
100
120
Maxillary plus premaxillary length (mm)


Rockfish species
Yelloweye (31)
Sharpchin (53)
Rosethorn (61)
Pygmy (50)
Greenstriped (66)
Canary (41)
10
20
30
40
Orbit width (mm)


Yelloweye (31)
Sharpchin (53)
Rosethorn (59)
Pygmy (50)
Greenstriped (66)
Canary (41)
Rockfish species
0
20
40
60
80
100
Length of bottom half of first gill arch (mm)


Yelloweye (31)
Sharpchin (53)
Rosethorn (60)
Pygmy (50)
Greenstriped (66)
Canary (41)
Rockfish species
20
25
30
35
40
45
50
Gill raker number



Yelloweye (31)
Sharpchin (53)
Rosethorn (60)
Pygmy (50)
Greenstriped (66)
Canary (40)
Rockfish species
0
5
10
15
20
25
Angular gill raker length (mm)