An ecological analysis of rockfish (*Sebastes* spp.) assemblages in the North Pacific Ocean along broad-scale environmental gradients

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Abstract—Environmental variability affects the distributions of most marine fish species. In this analysis, assemblages of rockfish (*Sebastes* spp.) species were defined on the basis of similarities in their distributions along environmental gradients. Data from 14 bottom trawl surveys of the Gulf of Alaska and Aleutian Islands (n=6767) were used. Five distinct assemblages of rockfish were defined by geographical position, depth, and temperature. The 180-m and 275-m depth contours were major divisions between assemblages inhabiting the shelf, shelf break, and lower continental slope. Another noticeable division was between species centered in southeastern Alaska and those found in the northern Gulf of Alaska and Aleutian Islands. The use of environmental variables to define the species composition of assemblages is different from the use of traditional methods based on clustering and nonparametric statistics and as such, environmentally based analyses should result in predictable assemblages of species that are useful for ecosystem-based management.

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Ecosystem-based management of marine fish species requires all ecosystem components to be accounted for in the management framework (Livingston et al., 2005). This necessitates knowing the major environmental gradients along which important species are organized within marine systems. Rockfish (*Sebastes* spp.) comprise an important component of marine ecosystems; they are abundant, diverse, and a widely dispersed group found across a wide range of habitats on the Pacific coast of North America. Rockfish management is problematic because of the different habitat requirements of these species at different life history stages (Love et al., 1991; Rooper et al., 2007), their episodic recruitment (Ralston and Howard, 1995; Field and Ralston, 2005), and their susceptibility to overfishing (Parker et al., 2000). Knowledge of the environmental gradients upon which rockfish organize themselves should be useful in predicting where different species and age groups co-occur and, thus, the best strategies for managing rockfish as an important component of the marine ecosystem.

Analyses used to define fish assemblages typically are based on methods that cluster characteristics of the catch, such as the Bray-Curtis dissimilarity index (Weinberg, 1994; Williams and Ralston, 2002) and other measures of co-occurrence (Weinberg, 1994; Mueter and Norcross, 2002), or that classify stations into categories of similar catch (Methratta and Link, 2006; Zimmermann, 2006). These analyses do not explicitly take into account the distribution of species across environmental gradients, even though fish species are known to respond to characteristics such as water depth, temperature, salinity, and sediment type (Friedlander and Parrish, 1998; Rooper et al., 2005). According to ecological theory, species will inhabit a preferred niche of environmental conditions (Hutchinson, 1957). Application of this principle can be useful in predicting the biological basis for co-occurrence of rockfish species (Murawski and Finn, 1988), as well as for defining groups of species with similar habitat requirements. Additionally, the species comprising assemblages defined by ecological relationships may be expected to respond to environmental changes in a predictable fashion.

The objective of this study was to analyze the distribution of rockfish species across two large ecosystems: the Gulf of Alaska and the Aleutian Islands. Relationships based on niche theory were developed for rockfish life history stages, sexes, and species subgroups with depth, temperature, and geographical position in order to test for important overlaps and to infer common distributions among species. The co-occurrence of species in bottom trawl catches was compared to their environmental overlap to determine whether species with similar distributions were likely to be captured together. Finally, the major gradients along which rockfish species organize themselves were examined in relation to the varying life history stages of the species. These methods should allow for a more robust analysis of the assemblage of similar species, as well

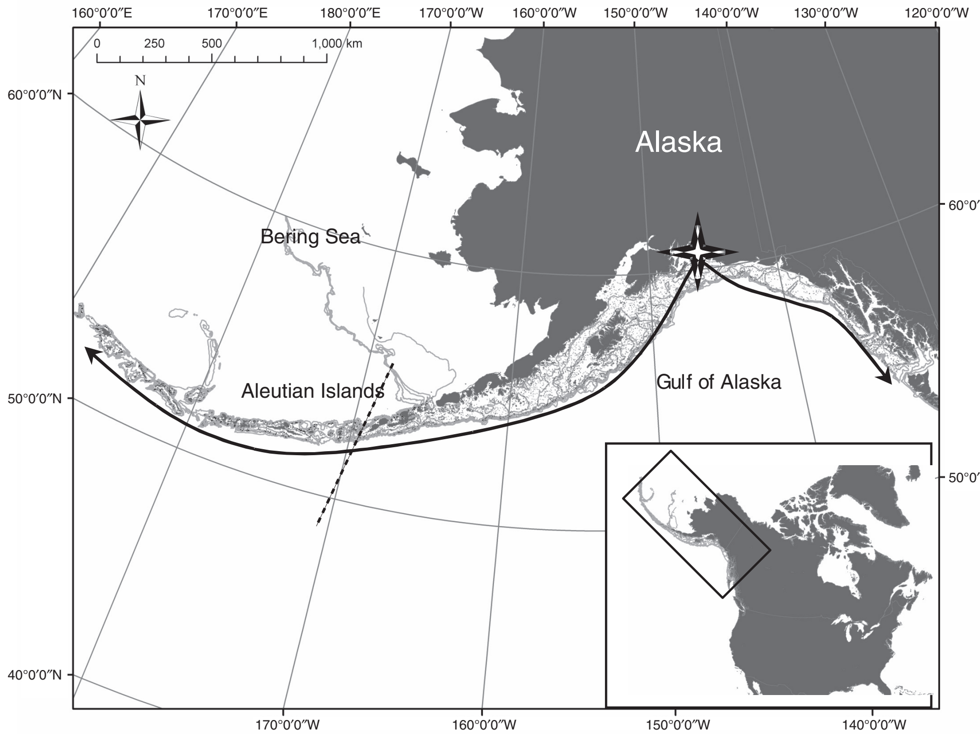

Figure 1

Map of Alaska showing the Gulf of Alaska and Aleutian Islands ecosystems (separated by a dashed line). The geographical position of each bottom trawl haul was calculated as the distance from Hinchinbrook Island (star). The distance of trawl hauls from Hinchinbrook Island along the southeastward arrow was coded as negative, and the distance along the westward arrow was coded as positive.

as documentation of the important differences among life-stage and species subgroups along environmental gradients.

Materials and methods

Study area

The data used for these analyses were collected during bottom trawl surveys of the Gulf of Alaska and Aleutian Islands ecosystems (Britt and Martin, 2001; Zenger, 2004). The Aleutian Islands are a chain of volcanic islands stretching from the Alaska Peninsula in southwest Alaska across the North Pacific Ocean and dividing the western Gulf of Alaska from the Bering Sea. The upper continental slope in the Aleutian Islands is narrow and steep. In the Gulf of Alaska, the continental shelf ranges in width from 20 km to greater than 200 km and the continental slope is steep and features periodic gullies and submarine canyons extending into the continental shelf. These two ecosystems encompass a large area of the Alaska continental shelf, from Dixon Entrance (133°W) in the southeastern Gulf of Alaska to Stalemate Bank (170°E) at the far western end of the Aleutian Islands (Fig. 1). The Gulf of Alaska bottom trawl survey is conducted from the Islands of Four Mountains (170°W) to Dixon Entrance. The Aleutian Islands bottom trawl survey is conducted along the island chain from 165°W to Stalemate Bank on the Bering Sea side and from the Islands of Four Mountains (170°W) to Stalemate Bank on the Gulf of Alaska side.

The Aleutian Islands and Gulf of Alaska ecosystems are connected by oceanic currents over the shelf. The Alaska Coastal Stream and Alaska Coastal Current flow westward (counter-clockwise) around the Gulf of Alaska from Dixon Entrance to the end of the Aleutian Island chain, whereas on the Bering Sea side of the Aleutian Islands the current flows eastward and provides extensive transport through passes in the chain from the Gulf of Alaska to the Bering Sea (Stabeno et al., 1999, 2002). The Islands of Four Mountains area is thought to be an area of change in both oceanographic properties (a higher influence of marine waters to the west) and biological properties (Ladd et al., 2005; Logerwell et al., 2005).

Trawl survey data

The National Marine Fisheries Service (NMFS) Alaska Fisheries Science Center (AFSC) has conducted standard bottom trawl surveys in the Gulf of Alaska and the

Aleutian Islands region since 1980 (Britt and Martin, 2001; Zenger, 2004). Surveys were conducted triennially between 1990 and 2000 and biennially thereafter (Table 1). For this analysis, the AFSC bottom trawl data from 1990 through 2005 were combined across years and survey areas in order to maximize the number of useful data points for each species. A Poly Nor'Eastern high-opening bottom trawl (with 24.2-m roller gear equipped with 36-cm rubber bobbins that are separated by 10-cm rubber disks) was used in these AFSC bottom trawl surveys. Trawl hauls were conducted at a speed of 5.6 km/h (3 knots) for 15 or 30 minutes. Bottom contact and net dimensions were recorded throughout each trawl haul by using net mensuration equipment. In a few cases, net width was not recorded (n=35); therefore the overall average net width (15.84 m, standard error [SE]=0.01) was used. For these analyses, records were used only if trawl performance was satisfactory and if the distance fished, geographical position, average depth, and bottom water temperature were recorded (n=6767). Trawl hauls were deemed satisfactory if the net opening was within a predetermined normal range, the roller gear maintained contact with the seafloor, and the net suffered little or no damage during the tow (Zenger, 2004).

All fish captured during a survey tow were sorted by species, counted, measured for total or fork length, and the total weight of each species in the catch was determined. For large catches, the total catch was weighed and subsampled for length data. Catch per unit of effort (CPUE, no of fish/ha) for each rockfish species was calculated by using the area swept computed from the net width for each tow multiplied by the distance towed recorded with geographical positioning systems. The rockfish catch data were transformed by using natural log (CPUE+1) before analyses, hereafter shortened to CPUE.

Table 1

Summary of the number of Alaska Fishery Science Center bottom trawl survey hauls used in the analysis of rockfish (*Sebastes* spp.) assemblages in the North Pacific Ocean. Data from trawl hauls with no temperature, depth, latitude, longitude, and inadequate gear performance were not used in the analyses. The Gulf of Alaska and Aleutian Islands bottom trawl surveys were the data source for each ecosystem, although in some years (i.e., 1998) a full survey of the ecosystem was not conducted.

Year	Ecosystem	Number of trawl hauls
1990	Gulf of Alaska	286
1991	Aleutian Islands	63
1993	Gulf of Alaska	727
1994	Aleutian Islands	389
1996	Gulf of Alaska	716
1997	Aleutian Islands	399
1998	Gulf of Alaska	5
1999	Gulf of Alaska	765
2000	Aleutian Islands	415
2001	Gulf of Alaska	550
2002	Aleutian Islands	417
2003	Gulf of Alaska	795
2004	Aleutian Islands	415
2005	Gulf of Alaska	825
Total		6767

Environmental variables

Three environmental variables were included in the analyses: depth, temperature, and geographic position along the Alaska coastline. Temperature measurements were collected throughout each trawl haul with a calibrated Branker bathythermograph, either a SeaBird-19 or SeaBird-39 microbathythermograph (Sea-Bird Electronics, Inc., Bellevue, WA) attached to the net. Depth was also recorded during each trawl haul either off the vessel echosounder or from the microbathythermograph attached to the net. The average bottom temperature and average depth from each trawl haul were used in the analyses. The final environmental variable included in the analyses was the relative position of each trawl haul along the Alaska coastline. Because the major axes of the Alaska coastline are from south to north in the southeastern Gulf of Alaska and from east to west in the remainder of the Gulf of Alaska and Aleutian Islands (Fig. 1), a reference point was chosen to standardize the spatial patterns in trawl hauls. The reference point was chosen in the central Gulf of Alaska at the eastern side of Hinchinbrook Island, (146.08°W, 60.37°N). The distance from this point to each trawl haul provided the change in spatial distribution (both by latitude and longitude) of rockfish species and the variable is hereafter referred to as the position of each trawl. Thus, a negative position indicates a trawl haul occurring in southeastern Alaska, and a positive position indicates a trawl haul occurring west of Hinchinbrook Island. Although geographical position is not actually an environmental variable, it was used as a proxy for longitudinal and latitudinal gradients that affect fish distribution and ranges.

Data analyses

In every bottom trawl haul, the CPUE of each rockfish species was divided into adult and juvenile stages by fish length (Table 2). The juvenile stage was broadly defined to include all subadult fish with lengths less than the size at 50% maturity from literature sources (Paraketsov, 1963; McDermott, 1994; NPFMC, 1998, 2005; Love et al., 2002; Pearson and Gunderson, 2003). The adult rockfish of each species were further divided into male and female CPUE components. Trawl hauls from which no length or sex data were collected were eliminated from the analyses for that species. Species for which catches occurred in fewer than 100 trawl hauls were also excluded from the analyses. For each trawl haul, these divisions resulted in three estimates of CPUE for each species: juveniles, adult females, and adult males.

Table 2

Species of rockfish captured in the Gulf of Alaska and Aleutian Islands trawl surveys across all years (1990–2005). The number captured in all years combined, the number of trawl hauls with catch, and the length distributions (FL, in mm) of juvenile and adult rockfish captured in the bottom trawl surveys are also provided. Dashed lines indicate either no catch in that category or insufficient length data were collected to distinguish juveniles and adults.

Species	Common name	No. captured	No. of trawl hauls with catch	Juvenile length distribution	Adult length distribution
Sebastes alutus	Pacific ocean perch	1,651,753	3059	40–250	250–620
Sebastes aleutianus	Rougheye rockfish	36,250	1894	50–439	439–820
Sebastes polyspinis	Northern rockfish	459,372	1547	50–361	361–500
Sebastolobus alascanus	Shortspine thornyhead	171,405	1515	40–215	215–770
Sebastes borealis	Shortraker rockfish	14,549	676	50–449	449–1030
Sebastes variabilis	Dusky rockfish	22,622	633	130–428	428–560
Sebastes babcocki	Redbanded rockfish	2985	509	110–420	420–630
Sebastes variegatus	Harlequin rockfish	28,834	462	60–230	230–420
Sebastes zacentrus	Sharpchin rockfish	63,343	442	Females 70–265, Males 70–240	Females 265–660, Males 240–660
Sebastes brevispinis	Silvergray rockfish	11,279	340	Females 150–415, Males 150–395	Females 415–720, Males 395–720
Sebastes helvomaculatus	Rosethorn rockfish	2447	158	100–215	215–360
Sebastes proriger	Redstripe rockfish	17,868	151	Females 100–290, Males 100–280	Females 290–480, Males 280–480
Sebastes ruberrimus	Yelloweye rockfish	287	125	Females 90–450, Males 90–540	Females 450–740, Males 540–740
Sebastes elongatus	Greenstriped rockfish	750	77	Females 100–220, Males 100–240	Females 220–380, Males 240–380
Sebastes ciliatus	Dark rockfish	1607	65	210–428	428–500
Sebastolobus altivelis	Longspine thornyhead	4463	46	60–190	190–340
Sebastes wilsoni	Pygmy rockfish	514	44	—	—
Sebastes crameri	Darkblotched rockfish	122	43	Females 120–390, Males 120–370	Females 390–500, Males 370–500
Sebastes melanops	Black rockfish	542	34	230–400	400–590
Sebastes maliger	Quillback rockfish	98	30	230–290	290–480
Sebastes reedi	Yellowmouth rockfish	690	20	Females 240–380, Males 240–370	Females 380–550, Males 370–550
Sebastes pinniger	Canary rockfish	182	20	Females 390–510, Males 390–430	Females 510–630, Males 430–630
Sebastes diploproa	Splitnose rockfish	55	20	90–270	270–270
Sebastes flavidus	Yellowtail rockfish	423	17	Females 330–405, Males 330–380	Females 405–580, Males 380–580
Sebastes entomelas	Widow rockfish	86	14	Females 350–365	Females 365–570, Males 345–570
Sebastes paucispinis	Bocaccio	9	8	—	690–720
Adelosebastes latens	Aleutian scorpionfish	6	3	—	—
Sebastes emphaeus	Puget Sound rockfish	11	2	—	170–180
Sebastes saxicola	Stripetail rockfish	9	2	—	100–270
Sebastolobus macrochir	Broadfin thornyhead	4	2	—	—
Sebastes miniatus	Vermilion rockfish	2	1	—	—
Sebastes nigrocinctus	Tiger rockfish	1	1	—	—

In order to determine the species composition of rockfish assemblages, the CPUE-weighted distribution of each of the species subgroups was computed for each environmental variable with the formulation given in May (1973) and Murawski and Finn (1988) (Fig. 2). A weighted mean value for each environmental variable

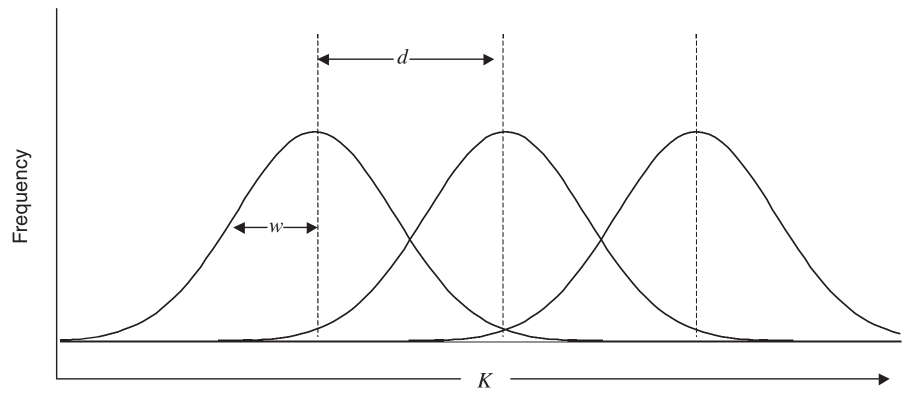

Figure 2

Theoretical distribution of three species along an environmental gradient (K). In this study, K was depth, temperature, or distance. The value w is the standard deviation of the resource utilization curve for a single species and d is distance between the weighted means for two species along a resource continuum. Reproduced from May (1973).

(depth, temperature, and position) was computed as

$$Mean = \frac{\sum (f_i x_i)}{\sum f_i},$$

where f_i = the CPUE of each rockfish species group in tow i; and
x_i = the value of the environmental variable at tow i.

The weighted standard deviation (SD) was then computed as

$$SD = \sqrt{\frac{\left(\sum \left(f_i x_i^2\right) \right) - \left(\left(\sum f_i\right) * mean^2\right)}{\left(\sum f_i\right) - 1}}.$$

These calculations yielded the niche dimensions for each species group defined along each of the three environmental gradients.

The overlap of each species group across each environmental gradient (A) can then be calculated as

$$A_{ij} = C_{ij} \exp\left[\frac{-d^2}{2\left(w_i^2 + w_j^2\right)}\right],$$

where the normalization constant (C_{ij}) is calculated by

$$C_{ij} = \sqrt{\frac{2 w_i w_j}{\left(w_i^2 + w_j^2\right)}};$$

where d = the distance between means for a pair of species i and j;
w_i = the standard deviation (SD) for species i; and
w_j = the SD for species j (Murawski and Finn, 1988).

Overlap indices for each variable were calculated for each species and within each species, by the groupings of males, females, and juveniles. The overlaps between males and females were first examined and if the overlap index was greater than 0.9 across all three environmental gradients, these males and females were combined and the means and SDs for each environmental gradient were recalculated. The resulting groupings (adults and juveniles) were then compared and, again, where the indices exceeded 0.9, the catches for the entire species (all size and sex classes) were combined and the means and SDs for each environmental gradient were recalculated.

Finally, the overlap indices were compared to determine the amount of separation among both species and the remaining groupings by size and sex. The multinomial intersection in the overlap indices across the three environmental gradients was calculated by multiplying the individual overlap coefficients together. This was used as a measure of the relative similarity in environmental preferences computed for each pair of species subgroups and resulted in a matrix of overlap coefficients for all species-group pairs. The matrix was then clustered into assemblages with similar distributions across environmental gradients by using Primer Analysis software (PRIMER-E Ltd., Plymouth, UK). The combined overlap index was used as a measure of similarity and the average cluster linkage method was used to determine the species composition of rockfish

Table 3

The estimated mean weighted values and niche width (w) across each of the three resource gradients (position, depth, and temperature) for the species-subgroups examined in this analysis. Although the species were initially split into male, female, and juvenile components, they were recombined if overlaps within a species (i.e., between sexes or between juveniles and adults) were greater than 0.9 across all three environmental variables.

			Position (km)		Depth (m)		Temperature (°C)	
Species	Common name	Group	mean	w	mean	w	mean	w
Sebastes variabilis	Dusky rockfish	All	757	780	141.3	57.0	5.4	0.9
Sebastes variegatus	Harlequin rockfish	All	200	1124	159.8	50.3	5.6	0.7
Sebastes polyspinis	Northern rockfish	Adults	1265	818	134.1	54.4	5.0	0.9
		Juveniles	1819	1180	137.6	56.0	4.7	1.0
Sebastes alutus	Pacific ocean perch	Adults	1205	1176	211.8	75.9	4.7	0.9
		Juveniles	857	1231	164.2	47.9	5.1	0.9
Sebastes babcocki	Redbanded rockfish	All	–443	1532	232.5	78.5	5.4	0.6
Sebastes proriger	Redstriped rockfish	All	–676	1720	193.8	42.3	5.6	0.6
Sebastes helvomaculatus	Rosethorn rockfish	All	–779	1760	215.1	54.7	5.6	0.6
Sebastes aleutianus	Rougheye rockfish	Adults	1112	1043	315.7	164.6	4.4	1.0
		Juveniles	685	987	244.3	112.9	5.0	0.9
Sebastes zacentrus	Sharpchin rockfish	All	–430	1482	195.9	45.9	5.6	0.6
Sebastes borealis	Shortraker rockfish	All	1325	1124	354.4	194.5	4.2	1.1
Sebastolobus alascanus	Shortspine thornyhead	All	468	1160	318.4	192.9	4.7	0.9
Sebastes brevispinis	Silvergray rockfish	Adults	–713	1737	202.4	49.1	5.7	0.7
		Juveniles	–186	1319	153.0	54.2	6.0	1.0
Sebastes ruberrimus	Yelloweye rockfish	All	66	1101	143.8	45.8	5.7	0.7

assemblages that had similar distributions along the environmental gradients. The combined overlap indices for each species pair were also compared to the frequency of co-occurrence for the species pair in trawl hauls by using linear regression to determine if the distribution of species across environmental variables was directly linked to their co-occurrence in trawl hauls.

Results

There was little difference in the distributions of the examined rockfish species among sexes. For all species, the overlap indices exceeded 0.9 across all three environmental gradients between males and females and, thus, the CPUE data were combined across sexes. Some differences between adults and juveniles were observed in their distributions across all three environmental variables (Table 3). Juvenile Pacific ocean perch (POP) (*Sebastes alutus*) and silvergray rockfish (*S. brevispinis*) were distributed at shallower depths than were adults of the same species. There was also a distinct separation between juvenile and adult rougheye rockfish (*S. aleutianus*) along the temperature gradient; juveniles were found at slightly higher temperatures than were adults. Juvenile northern rockfish (*S. polyspinis*) were found farther west (approximately 600 km) along the Alaska Peninsula than were adults. In total, these preliminary analyses indicated that there were four species where juveniles and adults were found to be separate and nine species that did not have different distributions between either sexes or life stages for any of the three environmental gradients. As a result, 17 species subgroups were analyzed (Table 3).

The cluster analysis resulted in five assemblages of rockfish species subgroups (Fig. 3). There was a relatively shallow-water assemblage (Aleutian Islands-shelf) containing northern rockfish, juvenile POP, and dusky rockfish (*S. variabilis*). These species had mean weighted depths from 134 to 164 m and were widely distributed around the northern Gulf of Alaska and Aleutian Islands (mean weighted distances from 757 to 1819 km). A similar assemblage (central Gulf of Alaska-shelf) had mean weighted depths from 144 to 160 m and was distributed from 200 to –186 km. This assemblage contained three species subgroups: yelloweye rockfish (*S. ruberrimus*), harlequin rockfish (*S. variegatus*), and juvenile silvergray rockfish. The third assemblage (southeastern Alaska-break) consisted of a group of species found predominantly in southeastern Alaska (mean weighted distance –430 to –779) at depths centered around 208 m. These species included adult silvergray rockfish, redbanded rockfish (*S. babcocki*), rosethorn rockfish (*S. helvomaculatus*), sharpchin rockfish (*S. zacentrus*), and redstripe rockfish (*S. proriger*). The

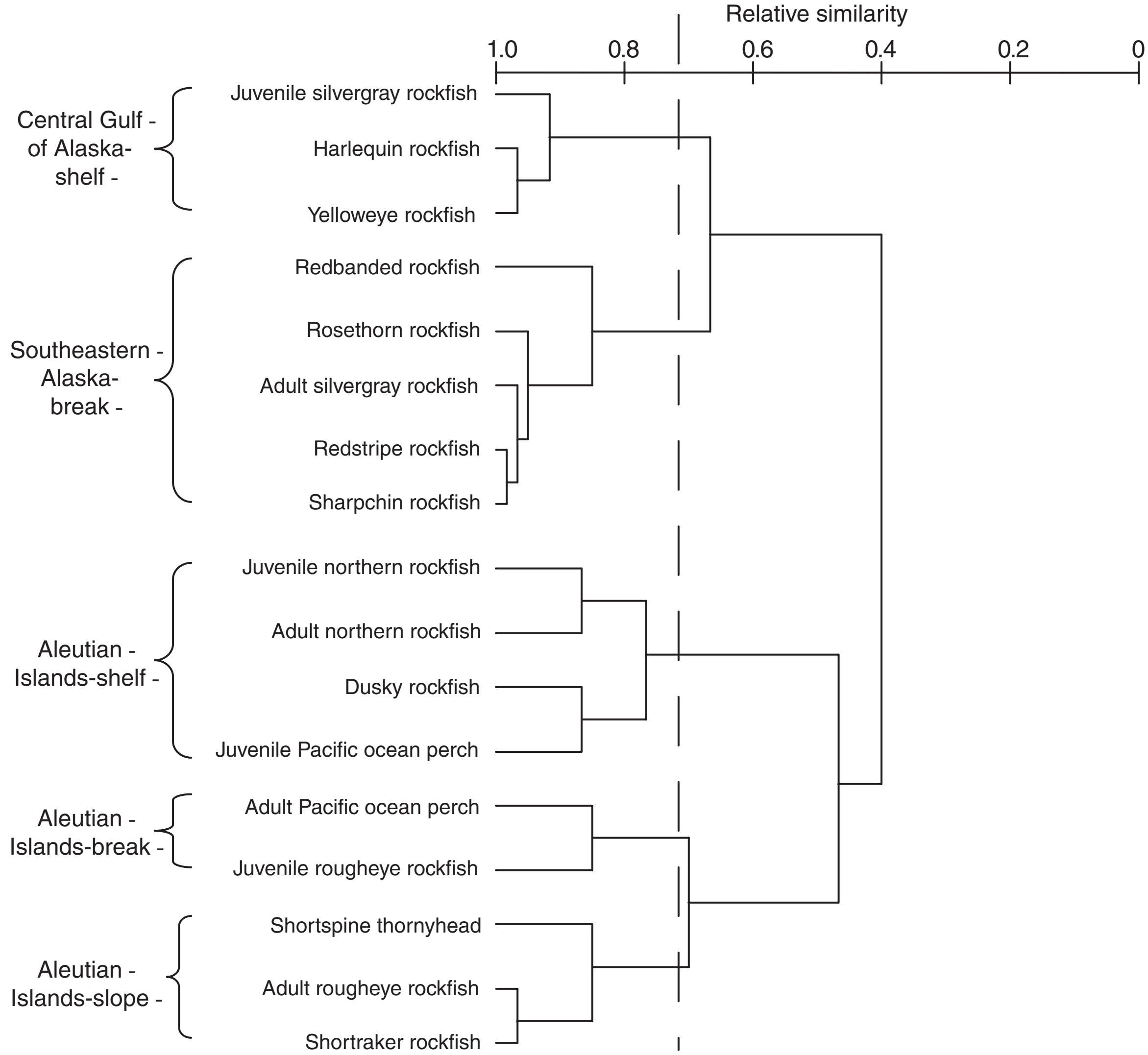

Figure 3

The results of cluster analysis of rockfish showing relative similarity amongst species-subgroups. The *x*-axis shows the relative similarity amongst species derived from the multinomial overlap indices among species-group pairs along the three environmental gradients (depth, position, and temperature). The dashed line (0.73) is where rockfish species assemblages were defined based on a similarity of 0.9 across the three environmental gradients.

fourth assemblage (Aleutian Islands-break) included juvenile rougheye rockfish and adult POP. These species were distributed at the shelf break at depths of 244 and 212 m, in the north Gulf of Alaska and Aleutian Islands (mean weighted distances 1205 and 685 km). A final assemblage (Aleutian Islands-slope) was composed of adult rougheye rockfish, shortraker rockfish (*S. borealis*), and shortspine thornyhead (*Sebastolobus alascanus*). These species were generally distributed in the north Gulf of Alaska and Aleutian Islands, at depths from 318 to 355 m. Bivariate plots of the three environmental variables indicate that the assemblages had very different distributions across the depth and position variables, and less distinct separation around the temperature variable (Fig. 4). There were clear lines of division along the depth variable between shelf and shelf break assemblages at 180 m, and between shelf break and slope assemblages at 275 m. There were also divisions along the position variable between southeastern Alaska species, central Gulf of Alaska species, and the Aleutian Island species at approximately Icy Strait (–350 km) and Seward, Alaska (250 km).

According to the trawl survey CPUE, the most abundant 10 species subgroups captured were adult POP, shortspine thornyhead, juvenile POP, juvenile northern rockfish, juvenile rougheye rockfish, adult northern

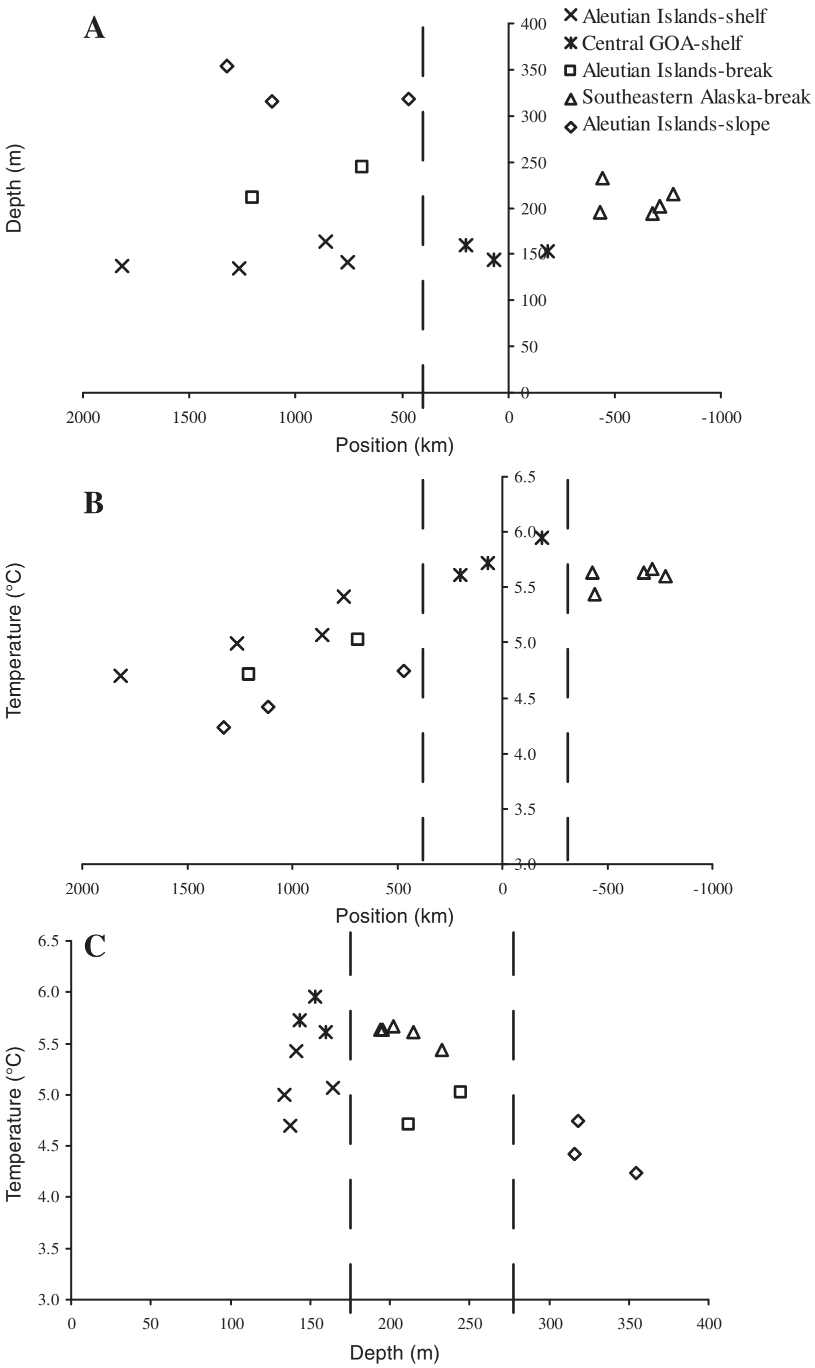

Figure 4

Plots of mean weighted (by catch per unit of effort) distributions of each rockfish species-group (n=17) along three environmental variables. Mean weighted distributions of rockfish species-groups are shown for (**A**) depth versus position, (**B**) temperature versus position, and (**C**) temperature versus depth. Position is the distance from Hinchinbrook Island, Alaska; positive values are west of this central point in the trawl surveys and negative values are southeastward. Dashed lines indicate break points in the mean-weighted environmental variables. Symbols indicate the assemblage membership (from Fig. 3) of each species-group as belonging to the Aleutian Islands-shelf, central Gulf of Alaska (GOA shelf), Aleutian Islands-break, southeastern Alaska-break, or Aleutian Islands-slope assemblage.

rockfish, adult rougheye rockfish, shortraker rockfish, sharpchin rockfish, and dusky rockfish. For these species the co-occurrence in trawl survey catches had a strong linear relationship to the amount of overlap in their distributions across environmental variables, and over 50% of the variance in co-occurrence was explained by species group overlap (Fig. 5). When all species subgroups were considered, the relationship was significant, but the overlap index explained only 32% of the variance in co-occurrence among pairs of species subgroups. This demonstrates that the co-occurrence of rockfish in the trawl survey data is positively correlated to their overlap in environmental preferences.

Discussion

The method used in this study provided resolution of the species composition of rockfish assemblages across large-scale environmental gradients that influence fish distribution (depth and geographical position). The results of these analyses were similar to findings on fish assemblages in other areas. Rockfish (and other species) on the west coast of North America distribute themselves by depth and latitude into distinct assemblages (Weinberg, 1994; Williams and Ralston, 2002; Tolimieri and Levin, 2006). In the Gulf of Alaska, an analysis conducted on 72 groundfish species (including rockfish species) with data from five NMFS trawl surveys revealed that the major gradients for variation in species diversity were depth and alongshore distance, whereas temperature and temporal gradients had only minor effects on species composition (Mueter and Norcross, 2002). As in the current study, Mueter and Norcross (2002) and Williams and Ralston (2002) found a peak in groundfish species richness near the shelf break (200 m), in the region of overlap between shallower species and those occurring at deeper depths.

The method of defining rockfish assemblages described here is very different from more commonly used methods where trawl survey catches or stations with similar components are clustered together. More commonly used approaches define assemblages by comparing patterns of catch by species in trawl hauls (i.e., Weinberg, 1994; Williams and Ralston, 2002; Zimmermann, 2006). Although these methods are highly effective for determining patterns in catches, they typically are based on complex analyses such as nonmetric multidimensional scaling, principle components, and cluster analyses that can make interpretation difficult. Determining the scaling method to apply to catch data for abundant versus rare species, the patchy distribution of some species, and inherent differences in catchability (such as between small and large fish of the same species) are all problems that must be addressed with these methods. By first defining the relationship of a species to environmental variables, and then comparing the parameters of that relationship to parameters for other species or life history stages, this analysis method may avoid some of those potential pitfalls. For example, the absolute abundance or catchability should not matter in the identification of the correct assemblage membership for a species. If the proper distribution of a species along a depth gradient is known from the trawl data; the species will be placed within a group of species with similar depth distributions regardless of its total abundance.

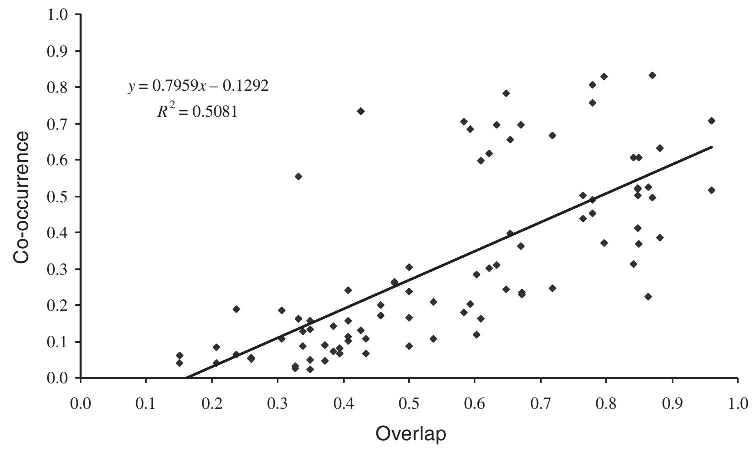

Figure 5

Frequency of co-occurrence of species in trawl hauls versus combined multinomial overlap index. Data are shown for the top 10 species-subgroups in terms of total catch per unit of effort for the Gulf of Alaska and Aleutian Island trawl surveys, and each dot represents a comparison of species-groups (n=90).

The issue of whether trawl survey data can be used to determine the underlying relationship of rockfish species to large-scale environmental gradients may have some limitations. Less sampling effort was directed at shallow inshore depths (0–50 m) than at greater depths; therefore shallow-water species were likely under-represented in the catches. Although this analysis included three environmental gradients, there are obviously more variables needed to fully describe the niche dimensions for any of the rockfish species. One important feature that was omitted from this analysis was the effect of small-scale habitat features on rockfish distribution. Variability in rockfish species assemblages on a small scale is often related to the local habitat, where higher habitat heterogeneity is correlated with higher diversity and abundance (Matthews, 1990; Stein et al., 1992; Yoklavich et al., 2000). The data used in this analysis was collected only on trawlable ground, and large tracts of untrawlable area were unsampled. Species composition and abundance can be starkly different between trawlable and untrawlable locations (Matthews and Richards, 1991). Even within trawlable areas, habitat characteristics such as presence of epibenthic invertebrates can be correlated with increased catches of some life history stages of rockfish, such as juveniles that seek out complex habitat features (Rooper and Boldt, 2005; Rooper et al., 2007). Larger-scale phenomena, such as patterns in prey productivity and the effects of local currents on rockfish distribution, were also absent from this analysis and can certainly affect the distribution of those species that prey on planktonic organisms. Geographical position was used as a proxy for these large-scale phenomena and other unknown variables influencing rockfish distributions. By pooling the data, I did not take into account interannual changes in geographical position due to climate events, such as El Nino or the Pacific decadal oscillation shifts. The effects of El Nino events are typically exhibited through changes in water temperature and there was only a weak response of the species to temperature gradients, and major climate shifts were not detected in Alaska during the years examined. Knowledge of the effects of climate shifts and local habitat features would further improve future assemblage analyses.

Because these analyses were based on rockfish relationships with environmental variables, they should result in predictable species assemblages useful for ecosystem-based management. For example, species that co-occur in trawl catches due to overlapping distributions with environmental variables would be likely to experience similar fishing mortalities. Additionally, based on these assemblage analyses, marine protected areas could be designed for specific depth and geographical areas that would protect portions of rockfish populations. A series of marine protected areas has been suggested for shortraker and rougheye rockfishes in the Gulf of Alaska as a first step towards spatial management (Soh et al., 2000). The spatial and depth separation of juveniles and adults in many of the species examined here could also provide information to implement spatially based management systems for some species, where bycatch of smaller, immature members of a population would be protected from harvest.

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