

Seasonal and interannual variability in the community structure of small demersal fishes off the central Oregon coast

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ABSTRACT: Small demersal fishes were collected along the central Oregon coast using a shrimp trawl with small-mesh liner. The trawl was deployed bimonthly in 1989 along 3 transects and along a single transect in March 1989 to 1994. Forty species, 19 of which are not commercially important and rarely reported in other studies, occurred in >5% of the samples. Species assemblages were structured primarily by depth, with mid-shelf stations dominated by flatfishes; on the outer shelf and slope, gadids, scorpaenids, osmerids, and zoarcids were also important. Additionally, 4 out of 5 identified station groups were more closely associated with a single season. Seasonal assemblage structure included a broad range of species whose distributions shifted inshore in summer. This phenomenon, previously described for only a few species off Oregon, further accentuated the correlation of assemblages with depth. Seasonal shifts in distributions appeared to be a function of juvenile settlement and ontogenetic changes in nursery habitat and of seasonal inshore-offshore movements of individuals of many sizes, which indicated that sediment type was not the only feature important in habitat selection. March assemblages were weakly structured by interannual differences, in spite of environmental conditions ranging from the cold La Niña of 1989 to the warm El Niño of 1992. The largest annual differences were among short-lived species and likely reflected differences in recruitment. This study targeted smaller fish than are collected in most bottom trawl surveys and illustrates the importance of seasonal changes in habitat for smaller fish and the value of understanding all life stages in a demersal fish community.

KEY WORDS: Fish communities · Demersal habitat · Size · Density · Diversity · Depth · Oregon Coast

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INTRODUCTION

A key principle of ecosystem-based fisheries management is to take a broad view of the patterns of distribution and associations of all potentially interacting species and life stages within a system rather than focus on single-species abundance trends (Pikitch et al. 2004, Francis et al. 2007). It is also critical to examine the physical features which influence these patterns, and how these features may vary spatially and temporally. An initial step in this process is the identi-

fication of fish assemblages and evaluation of their stability and sensitivity to environmental variations.

The soft-bottom habitat of the continental shelf and slope is characterized by a diverse fish fauna with many commercially important species. In the northern portion of the Oregonian zoogeographical province (Briggs 1974), most studies to date have examined species distribution and community structure of these fishes based on collections with large-mesh commercial bottom trawls (e.g. Day & Pearcy 1968, Alton 1972, Rogers & Pikitch 1992, Jay 1996, Lee & Sampson 2000,

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Tolimieri & Levin 2006, Juan-Jordá et al. 2009). These studies describe demersal fish communities that are broadly structured by depth and relatively stable, characteristics also common in other regions (e.g. Mahon & Smith 1989, Labropoulou & Papaconstantinou 2000).

Because of sampling restrictions due to mesh size, the recently-settled juvenile stages and adults of taxa that do not grow to a large size are seldom collected on soft-bottom environments, and generally in a non-quantitative fashion. Knowledge of recently-settled juveniles is important because the pelagic-to-benthic transition has been identified as a critical life history stage for some species (e.g. Blaxter 1988) and abundance and dynamics of recently-settled juveniles can be a better indicator of adult recruitment than earlier larval stages (Bradford 1992, Myers & Cadigan 1993, Houde 2008). The few surveys that have targeted juvenile and small adult fishes in the northern California Current (e.g. Demory 1971, Pearcy 1978, Krygier & Pearcy 1986, Toole et al. 1997, Donohoe 2000) have focused primarily on a single species or taxonomically related groups of species (flatfishes) and have not examined overall species assemblages.

The west coast of North America is a typical eastern boundary system that is highly variable seasonally and interannually due to the dynamics of wind-driven upwelling on the shelf and larger-scale physical forcing from the subarctic Pacific and, during El Niño conditions, from the tropics (Huyer et al. 2007). During the summer (April through October) upwelling period, equatorward wind stress displaces the surface layer offshore by means of Ekman transport, and these waters are replaced with cooler, nutrient-laden deep water, leading to generally high production compared to non-upwelling zones at similar latitudes. During the remainder of the year, the predominant source of winds is from the southwest, leading to coastal downwelling and onshore transport. Marine fishes in this region have developed reproductive adaptations for retention of eggs and larvae within the productive coastal zone, primarily through spawning during the winter months (Parrish et al. 1981, Shanks & Eckert 2005, Brodeur et al. 2008). Settlement of juvenile fishes to demersal habitats occurs primarily from late spring through early fall (e.g. Pearcy et al. 1977).

Benthic habitat along Oregon's narrow continental shelf is composed primarily of soft substrate, grading from coarse sand and shell at shallow depths to finer sand on the inner and middle continental shelf (extending to ~100 m depth) and fine silt and mud on the outer shelf (~100 to 200 m) and slope (>200 m) (Runge 1966, Romsos et al. 2008). Rocky reefs and rock outcrops also punctuate the inner shelf area. Bottom temperature and dissolved oxygen generally decrease with depth and distance from shore, while bottom salinity generally increases with depth (Carey 1972).

The purpose of this study is to examine community structure of small demersal fishes along the central Oregon coast based on the dominant species. We examined (1) within-year changes based on bimonthly collections along 3 transects during 1989 and (2) among-year changes based on March sampling from 1989 to 1994 along a single transect. These surveys were designed to capture late-larval and juvenile post-settlement flatfishes (Toole et al. 1997, Donohoe 2000), but the entire trawl contents were identified. We use these additional data to describe spatial and temporal variability in community composition and structure and to identify species that may be indicative of the various communities.

MATERIALS AND METHODS

Survey design. Demersal fishes were collected from sampling stations along 3 transects orientated perpendicular to the isobaths off Netarts Bay, Cape Foulweather, and Heceta Head (Fig. 1). Each transect was 18.5 km wide and divided into 6 depth strata delineated by the 50–79, 80–99, 100–119, 120–159, 160–219, 220–400 m isobaths. The first 2 strata (50 to 99 m) correspond to Allen & Smith's (1988) 'middle shelf' zone, the 3 strata between 100 to 219 m are primarily within the 'outer shelf' zone, which ends at 200 m, and the 220 to 400 m stratum is within the 'mesobenthal slope' zone. Tows were made from the same vessel at random locations within each depth stratum with the exception that rocky areas were avoided. A commercial shrimp trawl (27.4 m headrope, 28.5 m footrope) lined with a 6.4 mm mesh cod end was towed during daylight hours for an average of 9 min along the isobaths (~0.3 km at ~2 km h⁻¹). Although the vessel captain standardized tows based on past experience determining time for the gear to settle and effectively fish on the bottom, net sounder data available from a subset of surveys indicated that actual time on the bottom was variable and not predictable based on depth or recorded time and distance. The efficiency of the net for catching and retaining most species was also unknown. Because net efficiency and the area swept could not be quantified, the number of each species caught during each standardized tow (catch-per-tow) was used as an estimate of abundance. Some analyses were also performed using presence/absence data to determine if the results were robust in light of uncertainty regarding abundance estimates.

During 1989, sampling was conducted in January, March, May, July, September and November on all 3 transects. At least 3 tows were attempted in each depth stratum of each transect during a cruise, but the number of successful tows was sometimes less. During

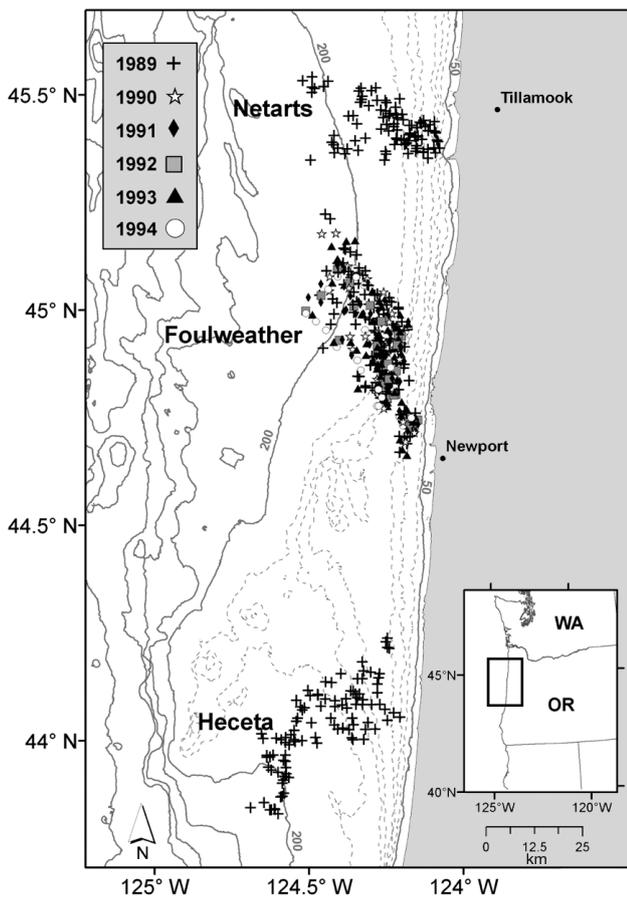


Fig. 1. Location and depth (m) of sampling stations for bottom trawl tows along 3 transects off central Oregon, 1989 to 1994

1990–1994, sampling was conducted primarily in March on the Cape Foulweather transect, so with the addition of the March 1989 sampling, a total of 6 years were sampled to examine interannual variability along one transect in one season.

All fish were identified to the lowest possible taxon and counted. Many of the smaller fish were frozen or preserved in formalin at sea for subsequent identification and measurement in the laboratory. Most fish were measured to the nearest millimeter or centimeter, although large catches were subsampled. Location, depth, and surface temperature ($^{\circ}\text{C}$) from a hull-mounted thermometer were recorded for all samples. Bottom temperature ($^{\circ}\text{C}$) was recorded for 1991–1994 samples from a Seabird profiler mounted on the net. Monthly means of broader-scale environmental variables were obtained from the National Oceanic and Atmospheric Administration (NOAA) Pacific Fishery Environmental Group website (www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/NA/data_download.html) for monthly upwelling indices ($\text{m}^3 \text{s}^{-1} 100 \text{ m coast}^{-1}$) at $44^{\circ}\text{N } 125^{\circ}\text{W}$ and from the NOAA Earth Research Laboratory ([\[ple/klaus.wolter/MEI/\]\(http://ple/klaus.wolter/MEI/\)\) for the multivariate El Niño-Southern Oscillation index \(MEI, expressed as the standardized departure from the first principal component on the covariance matrix\). An index of 1989 average monthly bottom temperatures \(\$^{\circ}\text{C}\$ \) at the mid-shelf \(100 m\) off Newport was estimated from the regression of Kruse & Huyer \(1983\) using monthly sea level heights from Neah Bay, Washington \(\[ilikai.soest.hawaii.edu/uhs/c/woce.html\]\(http://ilikai.soest.hawaii.edu/uhs/c/woce.html\)\).](http://www.cdc.noaa.gov/peo-</p>
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Data analysis. Prior to analysis, a fourth-root transformation was applied to the catch-per-tow abundance index to reduce the impact of very large catches. Because transformed catch data and diversity estimates were not distributed normally (Shapiro-Wilkes test, Madansky 1988; $p < 0.001$) and variances were unequal for most of the comparisons (Levene's test, Brown & Forsythe 1974; $p < 0.05$), we calculated median (instead of mean) catch per tow, diversity, and evenness and used the non-parametric Kruskal-Wallis (K-W) test (Kruskal & Wallis 1952) to evaluate differences in medians among depths, months, and years. Confidence intervals of the medians were calculated with Moods Median test (Brown & Mood 1951). Diversity was measured as Shannon's $H' = -\sum p_i \log p_i$, in which p_i is the probability that a randomly selected individual belongs to species i (Shannon & Weaver 1949). The index is summed over all species and has a maximum value of $\ln(\text{total no. of species})$, or ~ 3.6 in this study. Evenness was measured as Pielou's (1977) $V' = H'/\ln(\text{total no. of species})$, which ranges from 0 to 1.

To reduce the potential for spurious correlations from rare species, we restricted the analysis to species that occurred in at least 5% of the samples. We excluded vertically migrating species of the family Myctophidae that were caught occasionally in large numbers, possibly while the net was being set or retrieved. We also excluded one higher level taxonomic group (*Sebastes* spp.) that occurred in over 5% of samples so that all taxa would be at the species level.

We used 3 sets of multivariate analyses to explore relationships among species and the relationship between species and explanatory variables (McCune & Grace 2002):

(1) Multi-response permutation procedure (MRPP; Mielke et al. 1976), an iterative, nonparametric procedure, was used to test hypotheses that there were no differences related to depth stratum, month, transect, and year among groups of stations. The test's 'A-statistic' indicates the degree of within-group homogeneity, compared to random expectation. When all items are identical within groups, $A = 1$; when within-group homogeneity equals that expected by chance, $A = 0$; and when it is less than that expected by chance, $A < 1$.

The distance matrix for stations and species used the Bray-Curtis distance measure, which retains sensitivity in more heterogeneous datasets and gives less weight to outliers than Euclidean distances (McCune & Grace 2002). The Bray-Curtis distances were then rank-transformed to further correct for the loss of sensitivity of distance measures as community heterogeneity increases (McCune & Grace 2002). Sample weighting was equal to $n/\Sigma(n)$. Each grouping factor was treated separately in the MRPP analysis and interactions between depth and season were inferred from an examination of changes in the depth distribution of each species by season, including significant indicator species. A procedure that would have simultaneously tested for interactions among variables, such as PERMANOVA (Anderson 2001, McCune & Grace 2002) was not possible because they require a balanced sampling design, with equal numbers of stations in each depth stratum during each month.

(2) We used a 2-way agglomerative hierarchical cluster analysis based on Bray-Curtis distances and the flexible beta ($\beta = -0.25$) linkage function, which is equivalent to Ward's hierarchical linkage function (Sneath & Sokal 1973, McCune & Grace 2002), to arrange both stations and species into homogeneous groups. When each station or species is considered a cluster, 100% of information is retained and when all are lumped into one cluster, 0% of the information remains. We searched for a balance between a meaningful number of clusters and retention of as much information as possible.

(3) Indicator species analysis (ISA; Dufrene & Legendre 1997) was used to identify species that were abundant within a group of stations as well as restricted primarily to that group. Indicator values range from 0 (no indication) to 100 (dominant and found only in that group). All multivariate analyses were conducted using PC-ORD v.6 (McCune & Mefford 1999).

RESULTS

Species composition and distribution

A total of 153 taxa were collected from all stations and sampling dates (473 total samples) considered in this study. Most taxa were rare, with only 40 species occurring in >5% of total samples (35 species in the 1989 seasonal collections and 33 species in the March 1989–1994 interannual collections) (Table 1).

The most common group of species occurring in at least 5% of samples was the flatfish (11 species in 2 families). Four flatfish species (Pacific sanddab *Citharichthys sordidus*, rex sole *Glyptocephalus zachirus*, slender sole *Lyopsetta exilis*, and Dover sole *Microsto-*

mus pacificus) were collected in at least 60% of samples. Other families with 3 to 4 common species each were Zoarcidae (eelpouts), Scorpaenidae (rockfishes and thornyheads), and Agonidae (poachers).

Although some species were distributed within a relatively narrow depth range, many were collected over most of the continental shelf and slope. The species with the widest depth distributions are known, in some cases, to change depth with ontogenetic development (e.g. Dover sole: Toole et al. 1997 and Pacific sanddab: Donohoe 2000). We considered splitting these species into ontogenetic 'pseudo-species' with more restricted depth distributions. However, it was not possible to assign life history stages from field observations for most species. Additionally, after examining size versus depth plots for each common species, we determined that the patterns were too variable to objectively define 'pseudo-species' based on size or location. For example, English sole *Parophrys vetulus* initially settled in very shallow areas not sampled in our study and then moved into progressively deeper water as they matured (Fig. 2). In contrast, recently settled Pacific sanddab moved from the outer shelf and slope to inshore areas <175 m depth (Fig. 2), where they remained as they matured. Dover sole had a more complex pattern. They settled as small juveniles on the outer continental shelf and slope, moved inshore to nursery areas <150 m depth, and after growing to ~20 cm, moved into progressively deeper water (Fig. 2).

Seasonal community structure in 1989

The seasonal pattern of environmental conditions along the central Oregon coast in 1989 was characterized by downwelling during winter months (January to March and November to December), with particularly strong downwelling in March (Fig. 3). Upwelling dominated during summer months. An index of bottom temperature generally indicated warmer bottom temperatures at 100 m during the downwelling season than during the upwelling season, with the warmest bottom temperature in March 1989. Surface temperatures were cool and relatively constant over the continental shelf and slope during the winter downwelling season. During the summer upwelling season, near-shore surface temperatures were cool while offshore temperatures were warm.

Median catch-per-tow for all months combined varied with depth (K-W, $p < 0.01$) (Fig. 4a), and the highest catches occurred in the 120 to 159 m depth stratum. Median diversity (H') also varied with depth (K-W, $p < 0.01$; Fig. 4b), with highest diversity in the 100 to 119 m and 120 to 159 m depth strata. Median evenness (V') was very high (>0.95) in all depth strata.

Table 1. Percent occurrence and size range for the 40 most common species collected during this study. Abb. = Abbreviation, Comm. imp. = commercial importance, C = commercially important, NC = not commercially important, * = listed as threatened under the Endangered Species Act

Family Species	Common name	Abb.	Comm. imp.	Percent occurrence		Length (cm)	
				1989 all seasons	March 1989–1994	Mean	Range
Myxinidae							
<i>Eptatretus stoutii</i>	Pacific hagfish	Epta_sto	NC	11	16	30.0	10–52
Squalidae							
<i>Squalus acanthias</i>	Spiny dogfish	Squa_aca	C	19	6	57.7	23–95
Rajidae							
<i>Raja binoculata</i>	Big skate	Raja_bin	C	<5	6	49.8	29–86
Chimeridae							
<i>Hydrolagus colliei</i>	Spotted ratfish	Hydr_col	NC	19	20	46.0	14–63
Clupeidae							
<i>Clupea pallasii</i>	Pacific herring	Clup_pal	C	12	25	15.6	8–30
Engraulidae							
<i>Engraulis mordax</i>	Northern anchovy	Eng_mor	C	10	<5	11.8	8–16
Osmeridae							
<i>Thaleichthys pacificus</i>	Eulachon	Thal_pac	NC*	61	28	10.8	5–23
<i>Allosmerus elongatus</i>	Whitebait smelt	Allo_elo	NC	29	22	9.4	5–19
Gadidae							
<i>Microgadus proximus</i>	Pacific tomcod	Micr_pro	NC	36	45	15.2	1–50
Merlucciidae							
<i>Merluccius productus</i>	Pacific hake	Merl_pro	C	35	16	36.4	3–80
Zoarcidae							
<i>Lycodes cortezianus</i>	Bigfin eelpout	Lycor_cor	NC	48	47	13.8	6–41
<i>Lycodes brevipes</i>	Shortfin eelpout	Lycor_bre	NC	11	<5	4.8	4–8
<i>Lycodes pacificus</i>	Blackbelly eelpout	Lycor_pac	NC	10	<5	13.2	5–29
<i>Lycodes diapterus</i>	Black eelpout	Lycor_dia	NC	<5	6	19.9	4–32
Scorpaenidae							
<i>Sebastes cramerii</i>	Darkblotched rockfish	Seba_cra	C	37	19	16.0	3–37
<i>Sebastes diploproa</i>	Splitnose rockfish	Seba_dip	C	22	20	13.5	4–32
<i>Sebastes elongatus</i>	Greenstriped rockfish	Seba_elo	C	18	16	19.4	6–34
<i>Sebastes maliger</i>	Shortspine thornyhead	Seba_mal	C	13	13	13.9	3–38
Anoplopomatidae							
<i>Anoplopoma fimbria</i>	Sablefish	Lycor_fim	C	26	6	34.1	4–59
Hexagrammidae							
<i>Ophiodon elongatus</i>	Lingcod	Ophi_elo	C	<5	6	23.0	2–67
Cottidae							
<i>Radulinus asprellus</i>	Slim sculpin	Radu_asp	NC	40	32	8.5	1–12
<i>Chitonotus pugetensis</i>	Roughback sculpin	Chit_pug	NC	5	12	8.9	6–14
Agonidae							
<i>Agonopsis vulsa</i>	Northern spearnose poacher	Agon_vul	NC	8	<5	8.4	4–17
<i>Xeneretmus latifrons</i>	Blacktip poacher	Xene_lat	NC	33	21	14.2	3–26
<i>Xeneretmus triacanthus</i>	Bluespotted poacher	Xene_tri	NC	16	19	12.7	5–20
Embiotocidae							
<i>Cymatogaster aggregata</i>	Shiner surfperch	Cyma_agg	NC	32	60	9.9	6–21
Ammodytidae							
<i>Ammodytes hexapterus</i>	Pacific sandlance	Ammo_hex	NC	<5	9	10.5	9–11
Stichaeidae							
<i>Plectobranchus evides</i>	Bluebarred pricklyback	Plec_evi	NC	8	<5	7.4	4–10
<i>Poroclinus rothrocki</i>	Whitebarred pricklyback	Poro_rot	NC	20	<5	13.2	5–20
Bothidae							
<i>Citharichthys sordidus</i>	Pacific sanddab	Cith_sor	C	64	80	16.6	2–34
<i>Citharichthys stigmaeus</i>	Speckled sanddab	Cith_sti	NC	14	26	7.7	1–15
Pleuronectidae							
<i>Atheresthes stomius</i>	Arrowtooth flounder	Athe_sto	C	29	20	25.3	3–57
<i>Eopsetta jordani</i>	Petrale sole	Eops_jor	C	18	14	27.2	9–47
<i>Glyptocephalus zachirus</i>	Rex sole	Glyp_zac	C	79	81	18.7	1–60
<i>Hippoglossoides elassodon</i>	Flathead sole	Hipp_ela	C	06	<5	24.5	12–37
<i>Isopsetta isolepis</i>	Butter sole	Isop_iso	C	10	7	18.3	1–45
<i>Lyopsetta exilis</i>	Slender sole	Lyop_exi	NC	74	81	14.1	1–31
<i>Microstomus pacificus</i>	Dover sole	Micr_pac	C	68	77	13.2	3–55
<i>Parophrys vetulus</i>	English sole	Paro_vet	C	47	52	21.8	2–41
<i>Psetichthys melanostictus</i>	Sand sole	Pset_mel	C	<5	10	20.6	6–38

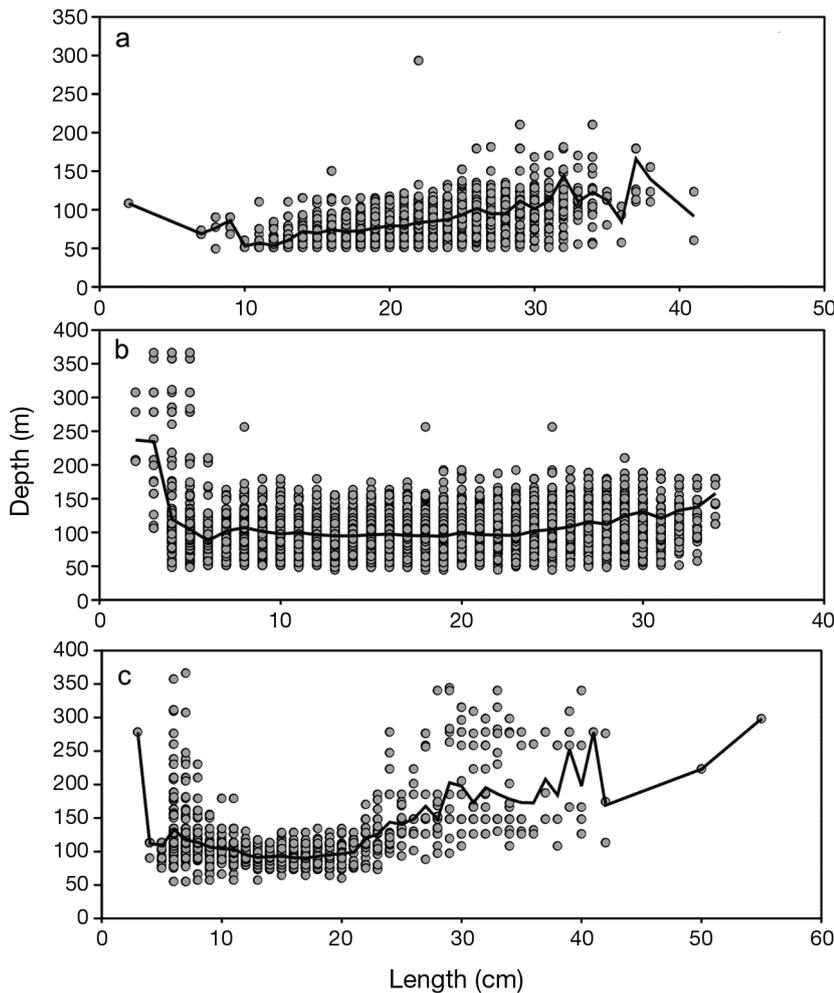


Fig. 2. Length vs. depth for (a) English sole *Parophrys vetulus* ($n = 4071$) (b) Pacific sanddab *Citharichthys sordidus* ($n = 39,172$), and (c) Dover sole *Microstomus pacificus* ($n = 2433$). Each circle represents an individual fish and lines reflect mean values. Depth range of samples was 50 to 400 m

When all depths were combined, median catch-per-tow was at least twice as high in the study area during the winter months of November, January, and March as in the summer months of May, July and September during 1989 (K-W, $p < 0.01$) (Fig. 4c). H' also was higher during winter than during summer months (K-W, $p < 0.01$) (Fig. 4d). V' was high (>0.95) in all months. In contrast to catch-per-tow, species composition across all depths appeared fairly consistent among seasons (Fig. 5). A few species, such as shiner surfperch *Cymatogaster aggregata* (Embiotocidae in Fig. 5), were clearly most common in only one season, but in general, differences among months were more subtle.

MRPP analysis revealed strong differences in community structure by depth, statistically significant but smaller differences in community structure by season, and very small, but statistically significant, differ-

ences among the 3 latitudinal transects (Table 2). These results were nearly identical when presence/absence data were used for the comparisons. Pairwise comparisons indicated that all depth strata were significantly different, with the least differences among adjacent strata and greatest differences for those strata with the greatest separation. Of the adjacent depth strata, those that were most similar (i.e. with lowest 'A-statistic' values) were the 80 to 99 m and 100 to 119 m strata. All pairwise comparisons of months showed significant differences; however, the strongest similarities were within winter (November, January, March) and within summer (May, July, September) months.

Hierarchical cluster analysis also indicated a fish community structured primarily by depth and season (Fig. 6). Clustering identified 2 groups of stations when 8% of the total information remained. These groups were comprised of 157 stations that were mainly on the outer shelf and slope and 123 primarily mid-shelf stations. With 18% of information remaining, the deeper group was further subdivided into 'Outer shelf and slope/summer' and 'Outer shelf and slope/mixed season' clusters of 54 and 103 stations, respectively. The stations at shallower depths were subdivided into 'Mid-shelf/summer' (57 stations), 'Mid-shelf/winter' (38 stations), and 'Outer shelf <160 m/winter' (62 stations). In this classification, summer and winter correspond to the months identified in the MRPP analysis. The most closely related station clusters were the Outer shelf <160 m/winter and Mid-shelf/winter groups. Splitting the station clusters further yielded small incremental increases in information, with 13 clusters required to exceed 30% of remaining information. Most of the subsequent splits identified small groups of more homogeneous stations, particularly among the deeper stations, and did not substantively add to our general interpretation of the station structure.

The relation of species to the station clusters is displayed in Table 3 and Fig. 6. When the hierarchical cluster analysis dendrogram was pruned with 33% of information remaining, 5 groups of species resulted. Additional subdivisions did not appear meaningful since the 6th group consisted of only one species and

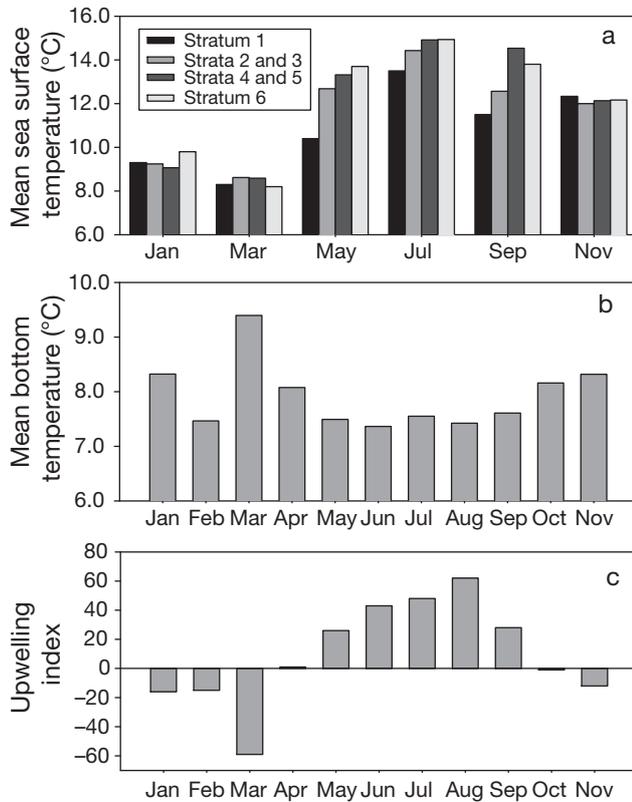


Fig. 3. Summary of 1989 environmental variables: (a) mean sea surface temperature at sampled stations along the Foul-weather transect; (b) index of monthly bottom temperature at 100 m, based on sea level height relationship in Kruse & Huyer (1983); (c) upwelling index at 45° N 125° W expressed as $\text{m}^3 \text{s}^{-1} 100 \text{ m coast}^{-1}$. Positive values represent upwelling, and negative values represent downwelling. Depth strata described in 'Material and methods'

the 7th group of only 2 species. The species groups generally represent a transition from those associated with the deeper station groups (Species Groups I and II) to shallower station groups (Species Groups IV and V) (Fig. 6). Species Group III was nearly equally distributed among all but the Outer shelf and slope/summer station cluster. All but 4 of the 35 species were significant indicators of a station group. The indicator species identify the single station cluster that best fits each species, but several species, particularly those in Species Groups II and IV, were common in more than one station cluster (Table 3).

Flatfishes, particularly Pacific sanddab, dominated the 2 mid-shelf and the Outer shelf <160m/winter station clusters, comprising 5 to 7 of the 10 most important species in each group (Table 3). Two species of smelt, shiner surfperch, and Pacific tomcod *Microgadus proximus* were also very common. Species that were less common, but had a high affinity for these station groups, included 2 species of sculpin, northern anchovy *Engraulis mordax*, and the northern spearnose

poacher *Agonopsis vulsa* (Fig. 6). The main seasonal difference for the mid-shelf clusters was the higher importance of whitebait smelt *Allosmerus elongatus* and shiner surfperch during the winter and higher importance of rex sole and slender sole during the summer (Table 3).

Flatfish were less important in the 2 outer shelf and slope station clusters, comprising only 3 or 4 of the 10 most important species in each group (Table 3). Eulachon *Thaleichthys pacificus*, Pacific hake *Merluccius productus*, 2 rockfish species, bigfin eelpout *Lycodes cortezianus*, and the blacktip poacher *Xeneretmus latifrons* were also very important. Other rockfishes and thornyheads, eelpouts, pricklebacks (Stichaeidae), and Pacific hagfish *Eptatretus stoutii* were less common but had a high affinity for these station clusters (Fig. 6). The main seasonal difference for outer shelf and slope clusters was the high summer importance of Pacific hake and eulachon compared to their importance during winter (Table 3).

Many species shifted distribution across seasons, occurring at greater depths during the winter months and shallower depths during the summer (Fig. 7). Indicator species analysis for the 6 depth strata identified 13 species (37%) that were significant indicators of a deeper stratum in the winter than in the summer (Fig. 7). When presence/absence data were applied, 2 additional species (bigfin eelpout and darkblotched rockfish *Sebastes crameri*) were indicators of seasonal changes, whereas Pacific sanddab was no longer an indicator of seasonal change.

Interannual variability in March community structure 1989–1994

March environmental conditions varied considerably among the 6 years of the study (Fig. 8), in that 1989 was a cold La Niña year with the lowest surface temperatures of the 6 years, whereas 1992 was an El Niño year with the warmest surface temperatures. Of the 4 years for which bottom temperatures were available, the highest bottom temperatures in the shallower strata also occurred in 1992, but the warmest temperatures in deeper strata occurred in 1993. Bottom temperatures were colder at most depths in 1991 than in 1992 to 1994. On average, March 1989 and March 1993 were characterized by strong downwelling. In the other years, there was little or no net average upwelling or downwelling.

Median catch-per-tow was highest in March 1990 and lowest in March 1994 and March 1991 (K-W, $p < 0.01$) (Fig. 9a). Annual differences in H' followed the same pattern (K-W, $p < 0.01$) (Fig. 9b). Catch-per-tow and diversity were intermediate in the other 3 years.

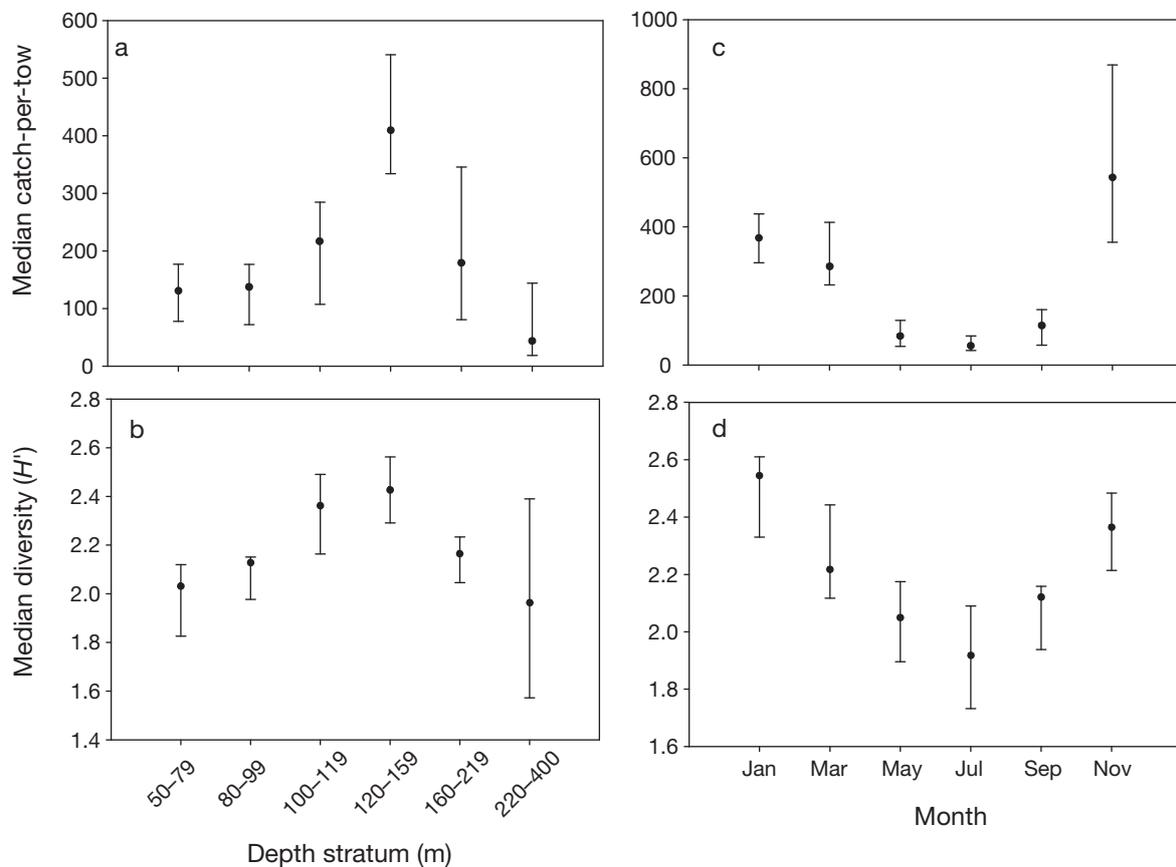


Fig. 4. (a) Median catch-per-tow (untransformed) and (b) median diversity (H') of transformed catch data by depth (Strata 1–6); (c) median catch-per-tow (untransformed) and (d) median diversity (H') of transformed catch data by month in 1989. Error bars indicate 95% confidence limits of medians

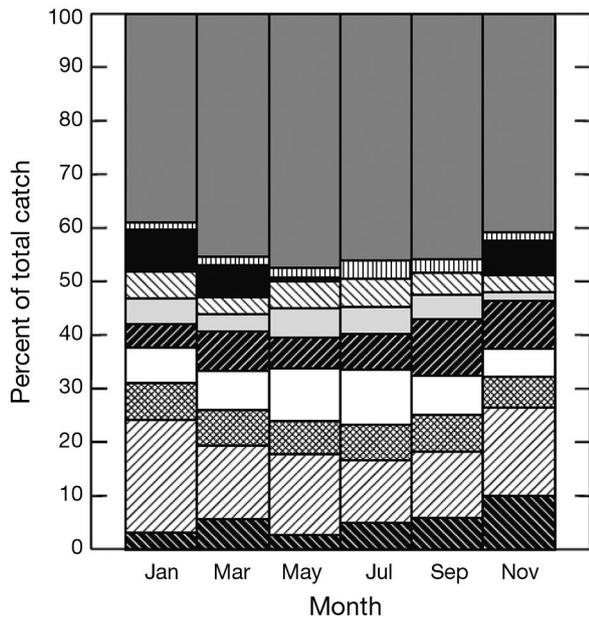
V' was >0.95 for all years. The lower catch-per-tow and diversity in 1991 was primarily the result of very low catches and few species in the 120 to 159 m and 160 to 219 m depth strata. Available netsounder data from 1991–1994 indicated that the time the net was on the bottom was generally shorter in 1991 than in 1993 and intermediate in 1992 and 1994.

Ranked MRPP analysis revealed strong differences in community structure by depth during March 1989–1994 and statistically significant but much smaller differences in community structure by year (Table 2). These results were nearly identical when presence/absence data were used for the comparisons. Pairwise comparisons among years, when all depths were combined, indicated that 5 out of the 6 greatest differences were among pairs of years that included either the year of highest catch-per-tow, 1990, or the year of lowest catch-per-tow, 1994 (Table 4). When each depth stratum was evaluated separately, interannual differences were significant at all depths; the greatest pairwise difference among years was between 1990 and 1994. This

suggests that the differences in community structure among years were not simply due to changes at one particular depth.

Part of the explanation for the small differences among years is a change in species composition. Flatfish accounted for approximately 50% of catch-per-tow in 1989–1991 and accounted for nearly 60% of catch-per-tow in 1992–1994 (Fig. 10). The ~10% difference among these time periods was a result of higher catches of several relatively rare species in 1989–1991, as well as higher catches of a few numerically abundant species such as eulachon and Pacific herring *Clupea pallasii*.

Indicator species analysis identified species that were most representative of particular years in order to help explain the interannual patterns in community structure. A total of 15 species were statistically significant indicators of a particular year when all depths were aggregated (Table 5). Presence/absence data resulted in the same indicator species, with the exception of slim sculpin *Radulinus asprellus* shifting from an indicator of 1992 to an indicator of 1993. No species



- Taxa
- Pleuronectiformes
 - ▨ Stichaeidae
 - Embiotocidae
 - ▨ Agonidae
 - Cottidae
 - ▨ Scorpaenidae
 - Zoarcidae
 - ▨ Gadiformes
 - ▨ Clup-Engr-Osmer
 - ▨ Miscellaneous

Fig. 5. Species composition (% of transformed catch-per-tow) by month during 1989 for all depths combined. See Table 1 for species in each family. Clup-Engr-Osmer represents a combination of species in the families Clupeidae, Engraulidae, and Osmeridae. Gadiformes is composed of species in the families Gadidae and Merlucciidae. Pleuronectiformes is composed of species in the families Bothidae and Pleuronectidae

were indicative of 1991 or 1994, the years with the lowest catch-per-tow and diversity. Of the indicator species, 8 were associated with 1990, the year of highest catch-per-tow and diversity. Eulachon was the species with the highest indicator value for 1990, followed by Pacific herring and whitebait smelt. All 3 are pelagic species that are occasionally caught in very high numbers in bottom trawls. Most of the indicator species for 1990 were most closely associated with outer shelf depth strata between 100 and 159 m (Table 5).

Three indicator species were associated with 1992, the year with the 2nd highest catch-per-tow. The species with the highest indicator value for March 1992 was Pacific tomcod, followed by speckled sanddab *Citharichthys stigmaeus*. Speckled sanddab was caught both in the shallowest stratum as juveniles and in deeper strata as small pre-juveniles that had recently settled from the plankton. In 1992, speckled sanddab was an indicator species because of its presence in the deeper strata (Table 5).

DISCUSSION

Assemblages of small benthic fishes along the central Oregon coast were primarily structured by depth and secondarily by season. Stations on the mid-shelf generally clustered together, as did stations on the outer shelf and continental slope. While a number of species were important components of 2 or more station clusters (Table 3), groups of co-occurring species generally corresponded to the depth gradient of station clusters (Fig. 6). Assemblages based on large-mesh

Table 2. Results of multi-response permutation procedure (MRPP) for depth, season, and transect groupings in 1989 and for year and depth, based on March Foulweather transect samples 1989 to 1994. The MRPP A-statistic is chance-corrected within-group agreement and compares within-group homogeneity to random expectation. Results were based on both catch-per-tow and presence/absence data

Factor	A-Statistic		p	Pair-wise comparisons
	Catch-per-tow	Presence/absence		
Depth in 1989, all months and transects combined (6 strata: 50–79 m, 80–99 m, 100–119 m, 120–159 m, 160–219 m, 220–400 m)	0.344	0.314	<0.01	Smallest differences are between adjacent strata
Depth in combined March 1989–1994 Foulweather transect samples (50–79 m, 80–99 m, 100–119 m, 120–159 m, 160–219 m, 220–400 m)	0.403	0.396	<0.01	Smallest differences are between adjacent strata
Season in 1989, all depths and transects combined (6 months: January, March, May, July, September, November)	0.118	0.103	<0.01	Smallest differences are within a winter group (November, January, March) and within a summer group (May, July, September)
Transect in 1989, all months and depths combined (Netarts [north], Foulweather [central], Heceta [south])	0.015	0.016	<0.01	Although statistically significant, differences among all 3 transects are extremely small (A-statistic indicates difference only 1.5% above random expectation)
Year (6 years of March samples on Foulweather transect, 1989–1994)	0.088	0.087	<0.01	Greatest differences are for 1990 and 1994. See Table 4

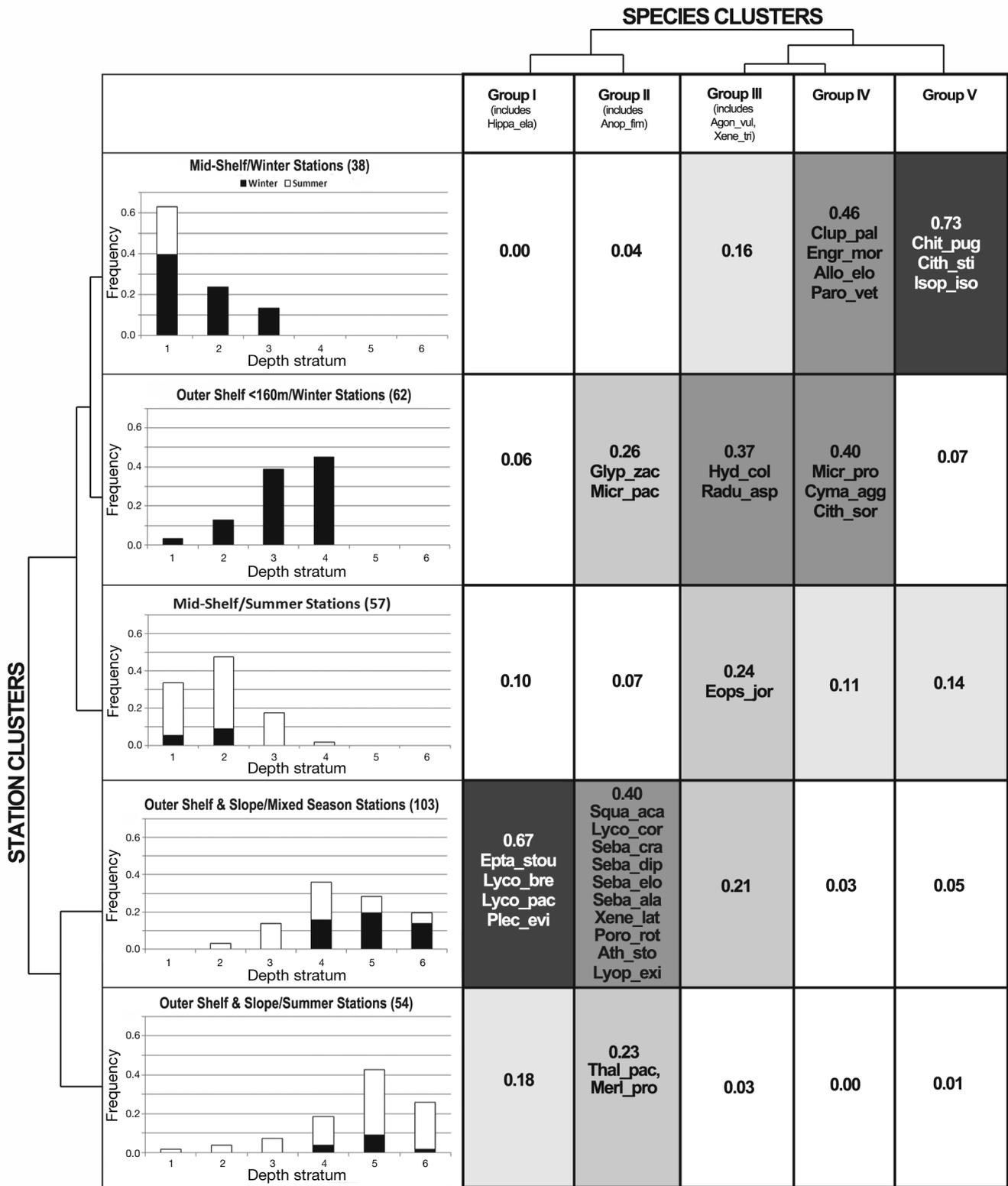
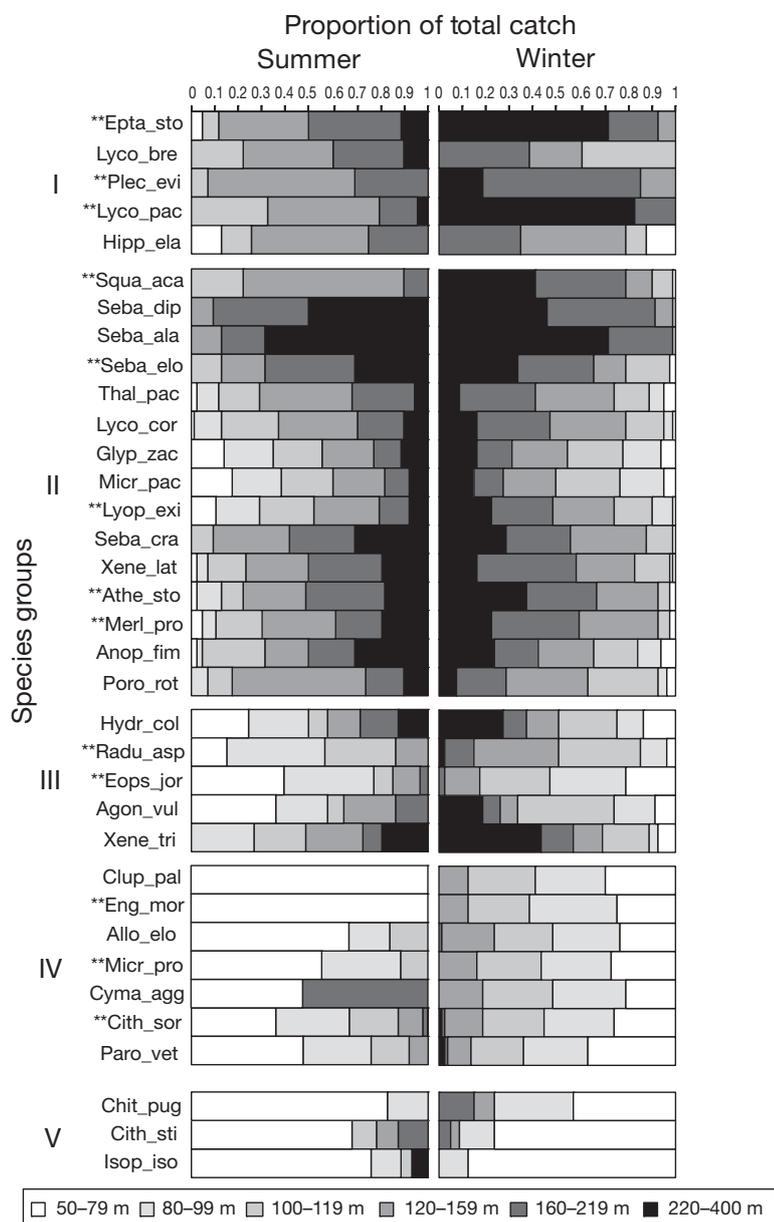


Fig. 6. Two-way hierarchical cluster analysis of 314 stations and 35 species sampled in 1989. The station dendrogram is pruned with 18% of information remaining and the species dendrogram is pruned with 33% of information remaining. Numbers in cells and relative shading represent the percentage of a species cluster's occurrence in a station cluster. Significant indicator species for each station cluster are displayed in cells. Species that were not significant indicators of any station groups are listed with the species group label. See Table 1 for explanation of species abbreviations. Depths of strata (1–6) are as in Fig. 4

Table 3. Most important species in the 5 station groups identified through hierarchical cluster analysis for 1989 sampling. Roman numerals represent species clusters shown in Fig. 6. Numbers in parentheses are ranks based on catch-per-tow followed by ranks based on frequency of occurrence. Species abbreviations are explained in Table 1

Mid-shelf/winter	Outer shelf <160 m/ winter	Mid-shelf/ summer	Outer shelf and slope/mixed season	Outer shelf and slope/summer
IV. Cith_sor (1,1)	IV. Cith_sor (1,1)	IV. Cith_sor (1,1)	II. Lyop_exi (1,1.5)	II. Thal_pac (1,1)
IV. Allo_elo (2,4)	II. Glyp_zac (2,2.5)	II. Glyp_zac (2,2)	II. Glyp_zac (3,1.5)	II. Merl_pro (2,2)
IV. Paro_vet (4,2)	IV. Cyma_agg (3,2.5)	II. Lyop_exi (3,3.5)	II. Thal_pac (2,5)	II. Seba_dip (3.5,3.5)
IV. Cyma_agg (3,5)	II. Lyop_exi (4,4)	IV. Paro_vet (4,3.5)	II. Micr_pac (5,3)	II. Lyop_exi (3.5,5)
IV. Micro_pro (5,3)	II. Thal_pac (5,7)	II. Micr_pac (5,5)	II. Lyco_cor (4,4)	II. Seba_cra (5,3.5)
II. Glyp_zac (6,8)	II. Micr_pac (7,5.5)	III. Radu_asp (6,6)	II. Xene_lat (6,7)	II. Glyp_zac (7,6)
V. Cith_sti (7.5, 6.5)	IV. Micr_pro (8, 5.5)	IV. Micr_pro (7,7)	II. Seba_cra (7,6)	II. Lyco_cor (6,7.5)
II. Micr_pac (9, 6.5)	III. Radu_asp (10,8.5)	III. Eops_jor (8,8)	II. Merl_pro (8,9)	II. Athe_sto (8,7.5)
V. Isop_iso (7.5, 9)	II. Lyco_cor (9,11)	II. Thal_pac (9, 9.5)	II. Athe_sto (11,8)	II. Seba_ala (9,10.5)
IV. Clup_pal (10,10)	IV. Paro_vet (11,10)	V. Cith_sti (10, 9.5)	II. Seba_dip (9,10.5)	II. Xene_lat (10.5,9)



bottom trawl surveys in the Oregonian province have also correlated most strongly with depth (e.g. Jay 1996, Lee & Sampson 2000, Juan-Jordá et al. 2009), as have those based on a limited number of studies using smaller nets (Day & Pearcy 1968, Pearcy 1978) and studies from other parts of the world (e.g. California: Allen 2006, northwest Atlantic: Mahon & Smith 1989, northeast Atlantic: Magnussen 2002, northwest Pacific: Fujita et al. 1995, southwest Mediterranean: Moranta et al. 1998, southwest Pacific: Connell & Lincoln-Smith 1999, northeast Pacific: Mueter & Norcross 1999, northeast Mediterranean: Labropoulou & Papaconstantinou 2000; but see also: northwest Mediterranean: Gaertner et al. 2005).

There was a general gradation from assemblages dominated by flatfishes on the middle continental shelf to assemblages dominated by Pacific hake, eulachon, bottom-associated rockfishes, sablefish, and eelpouts on the outer shelf and upper continental slope off Oregon. Collections with large-mesh trawls in the Oregonian province generally do not reveal this transition, and instead indicate a greater importance of species such as Pacific hake and

Fig. 7. Depth distribution of species by season during 1989. Blocks of different shades represent the percentage of total catch (normalized by stratum effort) within each depth stratum. Asterisks (**) indicate species that are significant indicators of shallower depth strata in the summer than in the winter, based on indicator species analysis. Species groups are the same as in Fig. 6, and species abbreviations are explained in Table 1

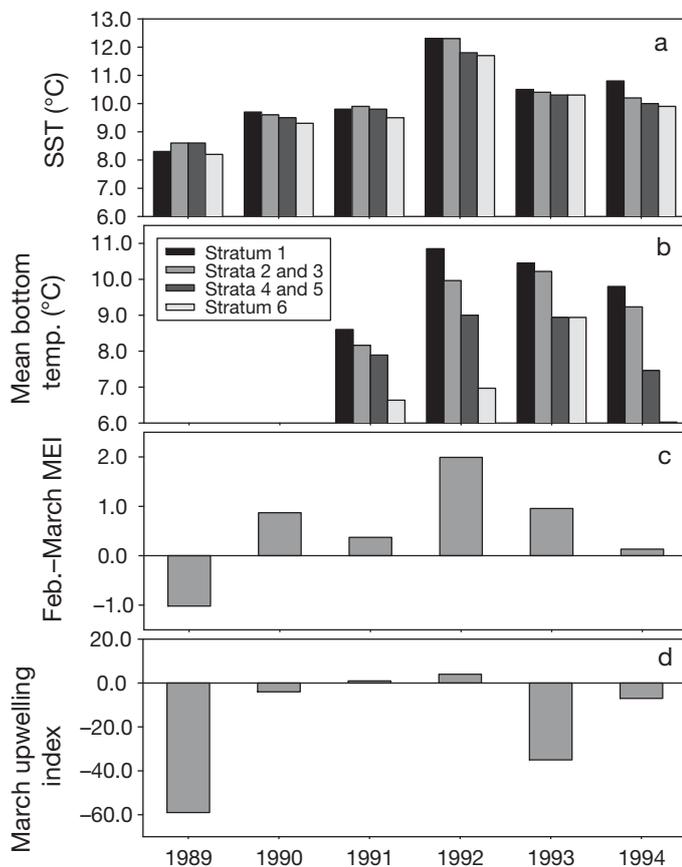


Fig. 8. Summary of March 1989–1994 environmental variables: (a) Mean sea surface temperature (SST), (b) mean bottom temperature, (c) Multivariate El Niño-Southern Oscillation Index (MEI) for February and March, and (d) March upwelling at 45°N expressed as $m^3 s^{-1} 100 m coast^{-1}$. Bottom temperatures not available for 1989 and 1990. Depth strata described in Table 2. MEI expressed as standardized departure from first principal component on the covariance matrix. Positive values represent warm El Niño conditions and upwelling, and negative values represent cold La Niña conditions and downwelling

various rockfish species on the mid-shelf and a greater importance of large adult flatfish such as Dover sole and arrowtooth flounder *Atheresthes stomias*, on the outer shelf and slope (e.g. Alton 1972, Jay 1996). These differences are probably due to the greater efficiency catching those species and life stages with large-mesh trawls and the greater efficiency of our small-mesh shrimp trawl for catching juvenile flatfishes that use the middle shelf as a nursery.

Many species were at greater depths during winter than during summer, and 4 out of 5 of the identified station groups were most closely associated with a single season. The shift in seasonal distribution has previously been described for some species off Oregon (e.g. Demory 1971), but the range of affected taxa in the present study indicates that, at least for smaller individuals, this is a broader phenomenon than previously

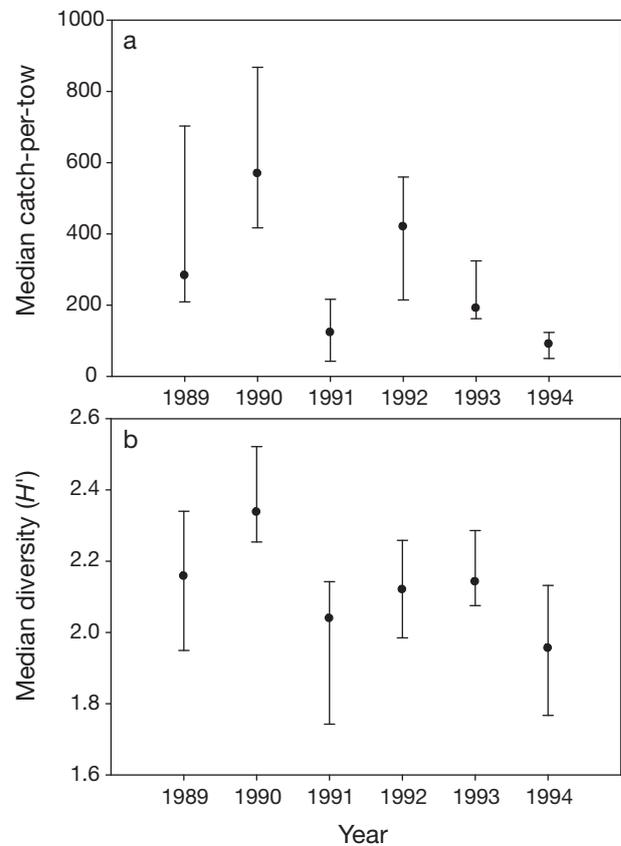


Fig. 9. (a) March median catch-per-tow (untransformed) of most common species and (b) March median diversity of transformed catch data from all depths 50 to 400 m, March 1989–1994. Error bars indicate 95% confidence limits of medians

Table 4. Pairwise comparison by year of multi-response permutation procedure (MRPP) A-statistic values for March 1989–1994 stations along the Foulweather transect. The MRPP A-statistic is chance-corrected within-group agreement and compares within-group homogeneity to random expectation. A-statistic values ≥ 0.05 are in **bold**. * $p < 0.05$

	1989	1990	1991	1992	1993
1989	–				
1990	0.028	–			
1991	0.032*	0.067*	–		
1992	0.045*	0.042*	0.059*	–	
1993	0.021	0.060*	0.046*	0.028*	–
1994	0.073*	0.120*	0.039*	0.052*	0.049*

considered. Because many species appeared to shift distribution together, there was a relatively small influence of season on community structure, compared to the influence of depth. Large-mesh trawl studies in the Oregonian province generally have been conducted only during summer months and so have not addressed seasonal changes in community structure. An excep-

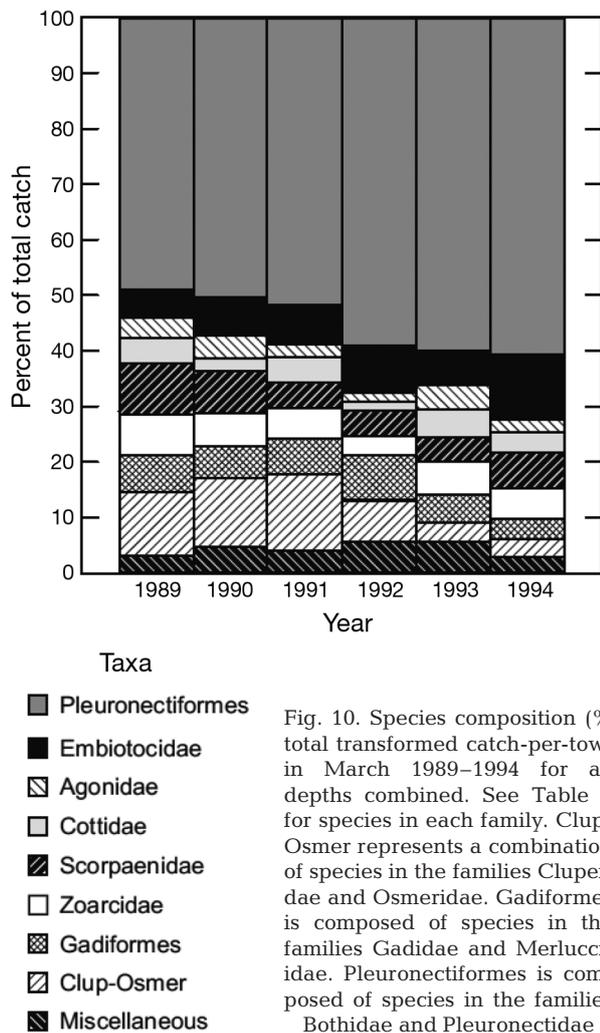


Fig. 10. Species composition (% total transformed catch-per-tow) in March 1989–1994 for all depths combined. See Table 1 for species in each family. Clup-Osmer represents a combination of species in the families Clupeidae and Osmeridae. Gadiformes is composed of species in the families Gadidae and Merlucciidae. Pleuronectiformes is composed of species in the families Bothidae and Pleuronectidae

tion is Lee & Sampson (2000), who found a significant but minimal correlation of species composition with month, compared to depth, but noted a distinct seasonal change in species composition over the mid-shelf that was consistent with the movement of deepwater species onto the shelf during summer. Limited observations with smaller nets also support our observations. Demory (1971) described summer inshore movements of small individuals (<140 to 180 mm, depending on species) of 6 species of flatfish along the Oregon coast. The shift in distribution was on the order of 37 to 73 m in depth for these species. Pearcy (1978) also found a significant depth–season interaction for the distribution of small flatfishes and a few other species off Oregon, caused by larger catches at outer shelf stations in winter than in summer. Most studies from other areas have not evaluated seasonal changes in demersal fish community structure or have found only minor effects of season, compared to depth (e.g. Connell & Lincoln-Smith 1999, Labropoulou & Papaconstantinou

2000). Hyndes et al. (1999) did find a significant effect of season on community structure at the 5 to 35 m depth range because of a combination of ontogenetic movements, spawning migrations, and movement to feeding areas. A targeted measure of the depth–season interaction should be an important component of future work.

Changes in the seasonal distribution of small individuals of several species may be related to physical or biological variables. Because a wide range of taxa are affected, this probably represents a response to broad-scale factors. Colder low-oxygen water moves onto the continental shelf during the summer upwelling season and small fish may move further inshore to remain in warmer oxygenated water. Dissolved oxygen may be a particularly important factor since hypoxic conditions have been observed extending inshore to the inner continental shelf within the study area in recent years (Grantham et al. 2004, Chan et al. 2008; authors' pers. obs. of dead invertebrates at 4 of our stations in September 1989) and reduced oxygen levels can affect feeding and growth (e.g. Tallqvist et al. 1999, Stierhoff et al. 2006).

Temperature may be a less important factor since differences among isobaths on the middle shelf appear small (Huyer 1977). Also, spring nursery areas for juvenile Dover sole were found at the same depth in each year between 1991 and 1994, despite a 2 to 3°C difference in bottom temperature (Toole et al. 1997), indicating a relatively small influence of temperature on their distribution. The summer inshore distribution of affected species also indicates that sediment is not a major factor in structuring assemblages on the Oregon shelf, since it does not change seasonally, and generally grades from coarse (sand) to fine (mud) with increasing depth. This is consistent with Pearcy's (1978) finding of little influence of sediment type on small fish assemblages off Oregon at stations with similar depths and different sediment types. Sediment is important in structuring some demersal fish communities (e.g. Mueter & Norcross 1999), but this seems to be limited to areas with heterogeneous sediments at similar depths.

Biological factors that may influence the more inshore summer distribution include higher primary production within 10 to 20 km of shore during the upwelling season (Landry et al. 1989), which would increase prey for epibenthic feeders (e.g. Pacific tomcod, smelts, speckled sanddab, Pacific sanddab, and petrale sole; Wakefield 1984) and also result in higher food production for infaunal feeders (Townsend & Cammen 1988, Juan-Jordá et al. 2009). A more inshore distribution of small fishes may also limit competition with, or predation by, larger adults returning to the continental shelf following offshore winter spawning.

Table 5. Indicator species for March 1989–1994 stations on the Foulweather transect, for all depths combined and for 4 depth ranges. No indicator species were identified for 1994. Numbers in parentheses are mean indicator values from randomized groups. See Table 1 for species definitions

Depth strata	Year	Species
All depths	1989	Lycor_cor (12.6)
		Seba_cra (7.3)
	1990	Thal_pac (9.4)
		Clup_pal (8.6)
		Allo_elo (8.3)
		Xene_lat (7.9)
		Athe_sto (7.6)
		Hydr_col (7.5)
		Seba_ala (6.3)
		Raja_bin (4.2)
1992	Micr_pro (12.3)	
	Cith_sti (9.0)	
1993	Ammo_hex (5.4)	
	Radu_asp (9.9)	
50–79 m	1992	Xene_tri (7.5)
		Ammo_hex
80–99 m	1990	Allo_elo
		Micro_pro
100–119 m	1992	Glyp_zac
		Thal_pac
120–159 m	1990	Allo_elo
		Cyma_agg
	1991	Athe_sto
		Lyop_exi
	1990	Clup_pal
		Seba_elo
	1992	Athe_sto
		Lyop_exi
		Micr_pro
		Xene_lat
1993	Cyma_agg	
	Cith_sti	
	Paro_vet	
	Hydr_col	
160–219 m	1990	Xene_lat
		Lyop_exi
	1992	Cith_sti
220–400 m	1989	Cith_sti
		Seba_elo
	1990	Xene_lat
		Glyp_zac
1992	Cith_sor	
	Cith_sti	
1993	Merl_pro	

We found that catch-per-tow decreased across the 50 to 400 m depth range during the summer, compared to the winter (Fig. 4c). Our observation is contrary to that of Alton's (1972) large-mesh trawl survey, in which biomass between 91 and 411 m was higher during summer than during winter. He attributed the higher catches during summer months to the winter movement of adults of several species into deep-water spawning

areas on the continental slope and to the latitudinal migration of Pacific hake to the Oregon coast during summer months. Our results are also contrary to the small-mesh beam trawl survey of Pearcy (1978), who did not observe a seasonal change in total abundance on the Oregon shelf. The reasons for lower summer catch-per-tow in our study are unclear but could be due to movement of small fish out of the study area, perhaps due to local hypoxia, mortality of spring-settling juvenile recruits, or a seasonal change in net efficiency and catchability. Because limited netsounder data indicated variations in the length of time that the net was on the bottom during each tow, it is possible that some differences in catch-per-tow represented increased effort rather than changes in abundance.

March community structure was similar among years, in spite of environmental conditions ranging from the cold La Niña of 1989 to the warm El Niño of 1992. The minor difference in species composition among years was primarily a result of changes in the relative proportion of smelt and herring, which are sometimes caught in large numbers in individual tows. Relatively large catches of these species occurred in 1989–1991, compared to 1992–1994, with a proportional reduction in flatfish species in those years. Because these small pelagic species are short-lived (e.g. most eulachon return to freshwater to spawn at age 3 or 4; Wilson et al. 2006), the change in species composition between the first 3 and last 3 years may have been in response to a change in recruitment of these pelagic species. The more stable proportional composition of most other species may be due to collection of multiple age classes of most species, which would reduce the influence of year-to-year variations in recruitment strength, or due to synchrony in recruitment of many species. In contrast, pelagic fish communities in this region show substantial interannual variation in response to changing ocean conditions (Brodeur et al. 2005, Phillips et al. 2009).

Relatively stable demersal fish community structure, at least within the scale of a decade, has been noted in previous studies. For example, Jay (1996) found that most assemblages of large groundfish on the Pacific coast continental shelf and upper slope were encountered over the entire 15 yr period of his study. Lee & Sampson (2000) found remarkable stability in the structure of commercially caught groundfish assemblages over the 1987–1993 period, given the range of environmental conditions and the significant removals of some species by fisheries. Filtering or dampening of interannual recruitment variability by the presence of species with multiple age classes may in part account for this relative stability (e.g. Spencer & Collie 1997). Within decade coherence in large-scale oceanographic and climatic variables may also encourage stability of

community structure on this time scale. Changes in groundfish community structure appear to primarily occur over multi-decadal scales unless there is a strong environmental (e.g. climate change; Dulvy et al. 2008) or human-caused perturbation (e.g. fisheries; Levin et al. 2006, Collie et al. 2008).

One of the principles of ecosystem-based fishery management is that 'multiple scales interact within and among ecosystems' (NMFS 1999). Most of the information used for management of groundfish fisheries in the northern Oregonian province, including descriptions of the related community structure, is derived from commercial fisheries logbooks or from National Marine Fisheries Service (NMFS) summer surveys conducted with large-mesh groundfish trawls that target marketable adult fish (e.g. Rogers & Pikitch 1992, Jay 1996, Lee & Sampson 2000, Tolimieri & Levin 2006, Juan-Jordá et al. 2009). The current study used a smaller-mesh trawl and encompassed a more limited geographical area, but also included expanded seasonal coverage during 1989. The year-round sampling in 1989 allowed us to describe an important seasonal shift in depth distribution that affects a broader range of species than has been previously reported. The fish in this study were small, with mean lengths <20 cm for most species, and included juveniles and small adults of commercially important species. Of the non-commercial species, 19 were important in our analysis (Table 1), none of which were included in the analyses of Rogers & Pikitch (1992), Jay (1996), or Lee & Sampson (2000), while Juan-Jordá et al. (2009) included 1 and Tolimieri & Levin (2006) included 4. Similarly, we did not include a number of common species reported in the other studies, presumably because our trawl was less efficient at catching larger and more mobile species. Even for the commercially important species, mean lengths of 11 common species in our study averaged 45% shorter (15 to 40% depending upon species) than in Weinberg's (1989) contemporaneous large-mesh trawl survey in the same geographical area. In spite of the differences in gear selectivity and age and size of sampled fish, some results from our study were similar to results from large-mesh trawl surveys, while other results shed additional insights on community structure and considerations for ecosystem-based management. A full understanding of the soft-bottom demersal fish community structure in this geographic region will require consideration of information from collections based upon a range of gear types, in different seasons and under varying annual hydrographic conditions.

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LITERATURE CITED

- Allen MJ (2006) Continental shelf and upper slope. In: Allen LG, Pondella DJ, Horn MS (eds) The ecology of marine fishes: California and adjacent waters. University of California Press, Berkeley, CA, p 167–202
- Allen MJ, Smith GB (1988) Atlas and zoogeography of common fishes in the Bering Sea and Northeastern Pacific. NOAA Tech Rep NMFS 66
- Alton MS (1972) Characteristics of the demersal fish fauna inhabiting the outer continental shelf and slope off the northern Oregon coast. In: Pruter AT, Alverson DL (eds) The Columbia River estuary and adjacent ocean waters. University of Washington Press, Seattle, WA, p 583–634
- Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecol* 26:32–46
- Blaxter JHS (1988) Pattern and variety in development. In: Hoar WS, Randall DJ (eds) Fish physiology, Vol 11A. Academic Press, New York, NY, p 1–58
- Bradford MJ (1992) Precision of recruitment predictions from early life stages of marine fishes. *Fish Bull* 90:439–453
- Briggs JC (1974) Marine zoogeography. McGraw-Hill, New York, NY
- Brodeur RD, Fisher JP, Emmett RL, Morgan CA, Casillas E (2005) Species composition and community structure of pelagic nekton off Oregon and Washington under variable oceanographic conditions. *Mar Ecol Prog Ser* 298:41–57
- Brodeur RD, Peterson WT, Auth TD, Soulen HL, Parnel MM, Emerson AA (2008) Abundance and diversity of coastal fish larvae as indicators of recent changes in ocean and climate conditions in the Oregon upwelling zone. *Mar Ecol Prog Ser* 366:187–202
- Brown MB, Forsythe AB (1974) Robust tests for the equality of variances. *J Am Stat Assoc* 69:364–367
- Brown GW, Mood AM (1951) On median tests for linear hypotheses. *Proc 2nd Berkeley Symp on Math Statist and Prob*, University of California Press, Berkeley, CA, p 159–165
- Carey AG (1972) Ecological observations on the benthic invertebrates from the central Oregon continental shelf. In: Pruter AT, Alverson DL (eds) The Columbia River estuary and adjacent waters. University of Washington Press, Seattle, WA, p 422–443
- Chan F, Barth JA, Lubchenco J, Kirincich A, Weeks H, Peterson WT, Menge BA (2008) Emergence of anoxia in the California Current large marine ecosystem. *Science* 319: 920
- Collie JS, Wood AD, Jeffries HP (2008) Long-term shifts in the species composition of a coastal fish community. *Can J Fish Aquat Sci* 65:1352–1365
- Connell SD, Lincoln-Smith MP (1999) Depth and structure of assemblages of demersal fish: experimental trawling

- along a temperate coast. *Estuar Coast Shelf Sci* 48: 483–495
- Day DS, Percy WG (1968) Species associations of benthic fishes on the continental shelf and slope off Oregon. *J Fish Res Board Can* 25:2665–2675
- Demory RL (1971) Depth distributions of some small flatfishes off the northern Oregon-southern Washington coast. *Res Rept Fish Comm Oregon* 3:44–48
- Donohoe CJ (2000) Metamorphosis, growth, and settlement of Pacific sanddab (*Citharichthys sordidus*) to a continental shelf nursery, inferred from otolith microstructure. PhD dissertation, Oregon State University, Corvallis, OR
- Dufrene M, Legendre P (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol Monogr* 67:345–366
- Dulvy NK, Rogers SI, Jennings S, Stelzenmüller V, Dye SR, Skjoldal HR (2008) Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. *J Appl Ecol* 45:1029–1039
- Francis RC, Hixon M, Clarke E, Murawski S, Ralston S (2007) Ten commandments for ecosystem-based fishery scientists. *Fisheries* 2:217–233
- Fujita T, Inada T, Ishito Y (1995) Depth-gradient structure of the demersal fish community on the continental shelf and upper slope off Sendai Bay, Japan. *Mar Ecol Prog Ser* 118:13–23
- Gaertner JC, Bertrand JA, de Sola LG, Durbec JP, Ferrandis E, Souplet A (2005) Large spatial scale variation of demersal fish assemblage structure on the continental shelf of the NW Mediterranean Sea. *Mar Ecol Prog Ser* 297: 245–257
- Grantham BA, Chan F, Nielsen KJ, Fox DS and others (2004) Upwelling-driven nearshore hypoxia signals ecosystem and oceanographic changes in the northeast Pacific. *Nature* 429:749–754
- Houde ED (2008) Emerging from Hjort's shadow. *J Northwest Atl Fish Sci* 41:53–70
- Huyer A (1977) Seasonal variation in temperature, salinity, and density over the continental shelf off Oregon. *Limnol Oceanogr* 22:442–453
- Huyer A, Wheeler PA, Strub PT, Smith RL, Letelier L, Kosro PM (2007) The Newport Line off Oregon—studies in the North East Pacific. *Prog Oceanogr* 75:126–160
- Hyndes GA, Platell ME, Potter IC, Lenanton RCJ (1999) Does the composition of the demersal fish assemblages in temperate coastal waters change with depth and undergo consistent seasonal changes? *Mar Biol* 134:335–352
- Jay CV (1996) Distribution of bottom-trawl assemblages over the continental shelf and upper slope of the U.S. west coast, 1977–1992. *Can J Fish Aquat Sci* 53:1203–1225
- Juan-Jordá MJ, Barth JA, Clarke ME, Wakefield WW (2009) Groundfish species associations with distinct oceanographic habitats in the Northern California Current. *Fish Oceanogr* 18:1–19
- Kruse GH, Huyer A (1983) Relationships among shelf temperatures, coastal sea level, and the coastal upwelling index off Newport, Oregon. *Can J Fish Aquat Sci* 40:238–242
- Kruskal JB, Wallis WA (1952) Use of ranks in one-criterion variance analysis. *J Am Stat Assoc* 47:583–621
- Krygier EE, Percy WG (1986) The role of estuarine and offshore nursery areas for young English sole, *Parophrys vetulus* Girard, of Oregon. *Fish Bull* 84:119–132
- Labropoulou M, Papaconstantinou C (2000) Community structure of deep-sea demersal fish in the North Aegean Sea (northeastern Mediterranean). *Hydrobiologia* 440: 281–296
- Landry MR, Postel J, Peterson W, Newman J (1989) Broad-scale distributional patterns of hydrographic variables on the Washington/Oregon continental shelf. In: Landry ML, Hickey B (eds) *Coastal oceanography of Oregon and Washington*. Elsevier, Amsterdam, p 1–40
- Lee YW, Sampson DB (2000) Spatial and temporal stability of commercial groundfish assemblages off Oregon and Washington as inferred from Oregon trawl logbooks. *Can J Fish Aquat Sci* 57:2443–2454
- Levin PS, Holmes EE, Piner KR, Harvey CJ (2006) Shifts in a Pacific Ocean fish assemblage: the potential influence of exploitation. *Conserv Biol* 20:1181–1190
- Madansky A (1988) *Prescriptions for working statisticians*. Springer-Verlag, New York, NY
- Magnussen E (2002) Demersal fish assemblages of Faroe Bank: species composition, distribution, biomass spectrum and diversity. *Mar Ecol Prog Ser* 238:211–225
- Mahon R, Smith RW (1989) Demersal fish assemblages on the Scotian Shelf, Northwest Atlantic: spatial distribution and persistence. *Can J Fish Aquat Sci* 46(S1):s134–152
- McCune BM, Grace JB (2002) *Analysis of ecological communities*. MjM Software Design, Gleneden Beach, OR
- McCune B, Mefford MJ (1999) *PC-ORD, multivariate analysis of ecological data, users guide*. MjM Software Design, Gleneden Beach, OR
- Mielke PW, Berry KJ, Johnson ES (1976) Multi-response permutation procedures for a priori classifications. *Commun Stat A Theory Meth* 5: 1409–1424
- Moranta J, Stefanescu C, Massuti E, Morales-Nin B, Lloris D (1998) Fish community structure and depth-related trends on the continental slope of the Balearic Islands (Algerian Basin, western Mediterranean). *Mar Ecol Prog Ser* 171: 247–259
- Mueter FJ, Norcross BL (1999) Linking community structure of small demersal fishes around Kodiak Island, Alaska, to environmental variables. *Mar Ecol Prog Ser* 190:37–51
- Myers RA, Cadigan NG (1993) Density-dependent juvenile mortality in marine demersal fish. *Can J Fish Aquat Sci* 50:1576–1590
- NMFS (National Marine Fisheries Service) (1999) *Ecosystem-based fisheries management. A report to Congress by the Ecosystems Principles Advisory Panel*. US Dept of Commerce, Silver Spring, MD
- Parrish RH, Nelson CS, Bakun A (1981) Transport mechanisms and reproductive success of fishes in the California Current. *Biol Oceanogr* 1:175–203
- Percy WG (1978) Distribution and abundance of small flatfishes and other demersal fishes in a region of diverse sediments and bathymetry off Oregon. *Fish Bull* 76:629–640
- Percy WG, Hosie MJ, Richardson SL (1977) Distribution and duration of pelagic life of larvae of Dover sole, *Microstomus pacificus*; rex sole, *Glyptocephalus zachirus*; and petrale sole, *Eopsetta jordani*, in waters off Oregon. *Fish Bull* 75:173–183
- Phillips AJ, Brodeur RD, Suntsov AV (2009) Micronekton community structure in the epipelagic zone of the northern California Current upwelling system. *Prog Oceanogr* 80:74–92
- Pielou EC (1977) *Mathematical ecology*. John Wiley & Sons, New York, NY
- Pikitch EK, Santora C, Babcock EA, Badun A and 13 others (2004) *Ecosystem-based fishery management*. Science 305:346–347
- Rogers JB, Pikitch EK (1992) Numerical definition of groundfish assemblages caught off the coasts of Oregon and Washington using commercial fishing strategies. *Can J Fish Aquat Sci* 49:2648–2656
- Romsos C, Lanier A, Agapito M, Goldfinger C (2008) Oregon surficial geological habitat, Version 3. Active Tectonics

- and Seafloor Mapping Lab, College of Ocean and Atmospheric Sciences, Oregon State University, Corvallis, OR <http://pacoos.coas.oregonstate.edu/MarineHabitatViewer/Viewer.aspx>
- Runge EW (1966) Continental shelf sediments, Columbia River to Cape Blanco, Oregon. PhD dissertation, Oregon State University, Corvallis, OR
- Shanks AL, Eckert GL (2005) Population persistence of California Current fishes and benthic crustaceans: a marine drift paradox. *Ecol Monogr* 75:505–524
- Shannon CE, Weaver W (1949) The mathematical theory of communication. University of Illinois Press, Urbana, IL
- Sneath PHA, Sokal RR (1973) Numerical taxonomy: the principles and practices of numerical classification. W. H. Freeman, San Francisco, CA
- Spencer PD, Collie JS (1997) Patterns of population variability in marine fish stocks. *Fish Oceanogr* 6:188–204
- Stierhoff KL, Targett TE, Miller K (2006) Ecophysiological responses of juvenile summer and winter flounder to hypoxia: experimental and modeling analysis of effects on estuarine nursery quality. *Mar Ecol Prog Ser* 325:255–266
- Tallqvist M, Sandberg-Kilpi E, Bonsdorf E (1999) Juvenile flounder, *Platichthys flesus* (L.), under hypoxia: effects on tolerance, ventilation rate and predation efficiency. *J Exp Mar Biol Ecol* 242:75–93
- Tolimieri N, Levin PS (2006) Assemblage structure of Eastern Pacific groundfishes on the U.S. continental slope in relation to physical and environmental variables. *Trans Am Fish Soc* 135:317–332
- Toole CL, Markle DF, Donohoe CJ (1997) Settlement timing, distribution, and abundance of Dover sole (*Microstomus pacificus*) on an outer continental shelf nursery ground. *Can J Fish Aquat Sci* 54:531–542
- Townsend DW, Cammen L (1988) Potential importance of the timing of spring plankton blooms to benthic-pelagic coupling and recruitment of juvenile demersal fishes. *Biol Oceanogr* 5:215–229
- Wakefield WW (1984) Feeding relationships within assemblages of nearshore and mid-continental shelf benthic fishes off Oregon. MS thesis, Oregon State University, Corvallis, OR
- Weinberg KL (1994) Rockfish assemblages of the middle shelf and upper slope off Oregon and Washington. *Fish Bull* 92:620–632
- Wilson MF, Armstrong RH, Hermans MC, Koski K (2006) Eulachon: a review of biology and an annotated bibliography. Alsk Fish Sci Cent Proc Rep 2006-12, National Marine Fisheries Service, Seattle, WA

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