

Abstract—Fjord estuaries are common along the northeast Pacific coastline, but little information is available on fish assemblage structure and its spatiotemporal variability. Here, we examined changes in diversity metrics, species biomasses, and biomass spectra (the distribution of biomass across body size classes) over three seasons (fall, winter, summer) and at multiple depths (20 to 160 m) in Puget Sound, Washington, a deep and highly urbanized fjord estuary on the U.S. west coast. Our results indicate that this fish assemblage is dominated by cartilaginous species (spotted ratfish [*Hydrolagus colliei*] and spiny dogfish [*Squalus acanthias*]) and therefore differs fundamentally from fish assemblages found in shallower estuaries in the northeast Pacific. Diversity was greatest in shallow waters (<40 m), where the assemblage was composed primarily of flatfishes and sculpins, and lowest in deep waters (>80 m) that are more common in Puget Sound and that are dominated by spotted ratfish and seasonally (fall and summer) by spiny dogfish. Strong depth-dependent variation in the demersal fish assemblage may be a general feature of deep fjord estuaries and indicates pronounced spatial variability in the food web. Future comparisons with less impacted fjords may offer insight into whether cartilaginous species naturally dominate these systems or only do so under conditions related to human-caused ecosystem degradation. Information on species distributions is critical for marine spatial planning and for modeling energy flows in coastal food webs. The data presented here will aid these endeavors and highlight areas for future research in this important yet understudied system.

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Season- and depth-dependent variability of a demersal fish assemblage in a large fjord estuary (Puget Sound, Washington)

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Estuaries are highly productive habitats that support a diversity of species, but have suffered because of growing human demands (Kennish, 2002; Lotze et al., 2006). Recognition of declining fish, marine mammal, and seabird populations and the need to consider the multiplicity of causative agents for these declines and their ecological consequences have prompted an interest in adopting ecosystem-based approaches for management, whereby knowledge of ecological interactions, such as trophodynamic control and competition is used to inform policy decisions (Pikitch et al., 2004). Our ability to implement more holistic management approaches, however, can be limited by a lack of basic information on the distribution and abundance of species that a system comprises and how these vary over time and space. This information is particularly lacking for fjord estuaries that are common features along the northeast Pacific coastline. Fjord estuaries differ from other estuaries by possessing a deep inner basin that is separated from continental shelf waters by a shallow sill near the mouth of the estuary. Although some of these ecosystems are remote and show little sign of degradation, commercial and recreational fishing, aquaculture, shoreline development, pollution, and logging are degrading a growing number of them.

Puget Sound, WA, is the southernmost fjord estuary in the northeast Pacific and supports major ur-

ban centers with a combined human population of 4 million (PSAT¹). Over the past 150 years Puget Sound has been commercially fished and subject to increasing rates of habitat loss, eutrophication, pollution, and, more recently, acidification. Presently, commercial fishing for groundfish is not permitted, but some species (e.g., *Sebastes* spp., lingcod [*Ophiodon elongates*]) are targeted by recreational fishermen. Although an ecosystem-based approach is clearly relevant for Puget Sound, there is a paucity of published information on how the demersal fishes of Puget Sound use different habitats, and thus a need for studies on assemblage structure. Identifying major patterns of assemblage variability along different habitat gradients has practical implications not only for modeling energy flows, but for devising monitoring schemes that can adequately quantify interannual changes in population abundance (Greenstreet et al., 1997; Thompson and Mapstone, 2002). Although project and agency reports provide some descriptive analyses on Puget Sound fish communities, peer-reviewed literature on demersal fish distributions from other deep fjords in the northeastern Pacific are rare.

¹ PSAT (Puget Sound Action Team). 2007. State of the Sound. 2007. Publication no. PSAT 07-01, 96 p. Office of the Governor, Olympia, State of Washington. [Available at: <http://www.psp.wa.gov/documents.php>, accessed February 2011.]

Here we evaluated depth- and season-related changes in the demersal fish assemblage structure over a 10-month period in the Central Basin—the largest and deepest of four sub-basins within Puget Sound. We anticipated strong spatial gradients in community composition on the basis of typical patterns of demersal fish assemblages in other ecosystems (e.g., Mueter and Norcross, 1999) and also hypothesized that species might exhibit seasonal patterns of habitat use that would be reflected in community structure. First, we evaluated differences in assemblage diversity metrics across depths and seasons. Second, we performed taxon-based multivariate analyses on the fish assemblage and explicitly tested whether assemblage structure was related to season and depth. Finally, we performed a size-based analysis, examining variability in the distribution of biomass across body size classes (biomass spectra) to identify whether the prevalence of small-body or large-body individuals also changed with depth and season. The value of examining biomass spectra is grounded in the observation that trophic level generally increases with body size in aquatic systems (Kerr, 1974; Jennings et al., 2001), and the relative importance of different body size classes to the overall flow of energy in the food web can be revealed by biomass spectra (Haedrich and Merrett, 1992). The patterns revealed by each of these approaches were subsequently compared.

Materials and methods

Data collection

The demersal fish assemblage was sampled by bottom trawl during 18–22 October 2004, 10–14 March, and 7–11 July 2005 along the eastern coastline of the largest subbasin within Puget Sound, the Central Basin (Fig. 1). The Central Basin is separated from the Strait of Georgia and Whidbey Basin by a sill (~60 m depth) at Admiralty Inlet and by Possession Sound to the north, respectively, and from Southern Basin by a sill at Tacoma Narrows (Fig. 1). We identified six sampling stations located in low-relief regions and amenable to bottom trawls spaced 5–10 km apart (high relief, hard bottom habitats are not common in this region of Puget Sound). At each station, we sampled four sites at depths of 20, 40, 80, and 160 m. In October we sampled stations 1–4, sampling all four depths. To increase the spatial coverage of the survey in March, we visited stations 1, and 3–6, but only sampled at 40 and 160 m. Lastly, in July we visited stations 1, 3, 4, 5, and 6, and sampled all four depths. In this manner we were able to increase the spatial coverage of the survey while maintaining overlap with the previous season. We modified our survey when

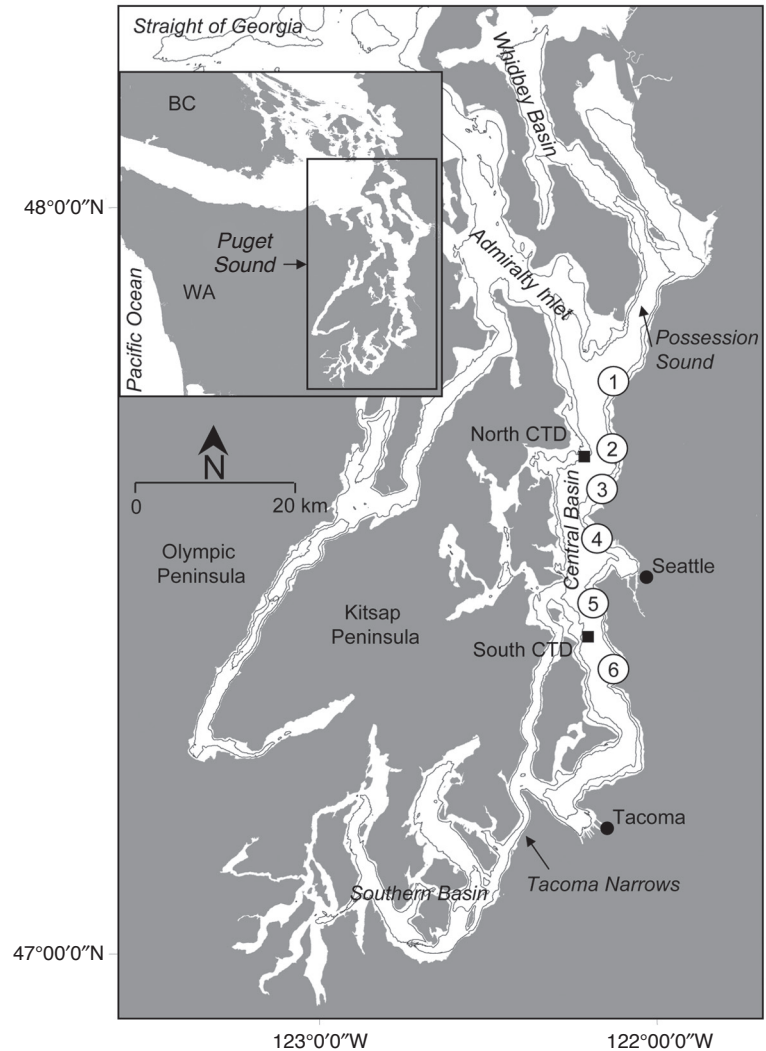


Figure 1

Demersal fish assemblages were sampled with bottom trawls at six stations (indicated by the circled numbers) in the Central Basin of Puget Sound, WA. At each station, depths at 20, 40, 80, and 160 m were sampled. Sampling occurred in October 2004 and March and July 2005. Isobaths at 40 and 160 m are indicated. Sampling sites where conductivity-temperature-density instruments (CTDs) were deployed by the King County Puget Sound Marine Monitoring Program to determine temperature and salinity are denoted by square symbols.

necessary because of limitations in boat and crew time and because of the absence of prior information on which we could base our survey.

Sampling was performed during daylight hours with a 400-mesh Eastern otter bottom trawl lined with 3.2-cm mesh in the codend. The net had a head rope and foot rope of 21.4 m and 28.7 m, respectively, and the gear was towed across the seafloor for 400–500 m at 2.5 knots. Catch was sorted to species, weighed, enumerated, and subsampled for length composition of fish. Catch was standardized to biomass density (g/m^2) by using measurements of the area swept by the net. The area

swept was calculated by multiplying the tow distance by the net opening width, the latter calculated from an empirical relationship between depth and net width.

To compare differences in salinity and temperature among depths, months, and latitude we obtained data from the King County Puget Sound Marine Monitoring Program which monthly monitors water quality at two stations in the northern and southern regions of the survey area (Fig. 1). Data were collected with a conductivity-temperature-density instrument (CTD) consisting of an SBE 3 temperature sensor, SBE 4 conductivity sensor, and SBE 29 pressure sensor (SeaBird Electronics Inc., Bellevue, WA) and were binned at 0.5-m intervals. CTD sampling occurred within 10 days of trawl sampling.

Statistical analysis

More than 200 species of fish have been documented in Puget Sound, but many of these are rare or sparsely distributed such that an intensive sampling effort would be required to sufficiently describe the distribution patterns of all species. Instead, we focused our research on the commonly occurring species that accounted for the bulk of the demersal fish biomass and therefore represent the most significant fish in the food web. To calculate diversity metrics for comparisons, rare species that occurred in fewer than 10% of the sampled trawls were removed from the data set; the exclusion of rare species permitted a coarse-scale evaluation of differences in the common components of the assemblage. Differences in species richness (N) and diversity (Shannon-Wiener diversity index, H' ; Krebs, 1989) across depths and among months were examined by using two-way analysis of variance (ANOVA). Standard two-way ANOVA requires that treatment levels be fully replicated across both main factors (in this case, depth and month). Because we lacked samples from depths of 20 m and 40 m in March, we performed two sets of tests. In the first set we included samples from all four depths, but only from October and July. In the second, we included samples from all three months, but only from 40 and 160 m. Initial examination of the data indicated normal or near-normal distributions, therefore data transformations were not called for because ANOVA is robust to minor departures from normality (Zar, 1984). In instances where either of the main factors was significant, Tukey's honestly significant difference (HSD) tests were used to identify which depth and month levels differed.

In the above analysis, both N and H' are simple and widely used measures of diversity that describe the number or relative biomass of species at each sample but ignore similarity in species composition among samples. In contrast, canonical correspondence analyses (CCA) are used to explicitly evaluate multivariate patterns of species biomass among sample sites. Essentially, CCA is a multivariate extension of multiple regression where species and sites are simultaneously ordinated in a manner that maximizes the variance related to a set of explanatory (constraining) variables

(ter Braak, 1986). As with multiple regression, the inertia, or variance explained, by a given model can be determined and the significance of the explanatory variable tested (Legendre and Legendre, 1998). In instances where two or more sets of explanatory variables are of interest (in this case, month and depth), partial CCA can be employed to isolate the effect of each variable (Legendre and Legendre, 1998). The technique is analogous to partial regression, where the response variable (species biomass) is first constrained by one of the explanatory variables (either month or depth, expressed as factors with dummy variable coding). The resulting residuals are then constrained by the second explanatory variable. Effectively, the first explanatory variable is treated as a confounding variable and its effect is "cleansed" from the data set. The assemblage pattern related solely to the second explanatory variable can then be isolated and explored (Legendre and Legendre, 1998). An advantage of CCA over standard univariate tests of species biomass (e.g., ANOVA) is that the method simultaneously depicts the strength and direction of species responses to predictor variables by the position and spread of species in ordinate space. The approach therefore offers insights into species associations that are not readily obtained by univariate methods (Legendre and Legendre, 1998).

We applied partial CCA to the data set alternating depth and month as the confounding and explicit explanatory variables, respectively. We recognized that the habitat of most fishes changes with body size (Werner and Gilliam, 1984) and therefore we divided species with abundant, small size classes (individuals less than 30% of maximum recorded total length [TL] that occurred in at least 10% of the sites sampled) into small and large size classes (greater than 30% of maximum recorded TL were categorized as large) and we treated them as distinct species in the analysis. An exception was made for spiny dogfish, which possessed a bimodal size distribution that separated at approximately 500 mm or 47% of the maximum recorded TL.

Owing to the lack of samples from 20- and 80-m depths in March, we performed partial CCA (one each for depth and month), using 1) samples collected from all three months, but from 40 and 160 m only; and 2) for all four depths from October and July only for a total of four partial CCA tests. We identify the data included in each univariate and multivariate analysis by labeling tests as "all-months" or "October+July," respectively. The analysis was split to avoid ambiguity that may have arisen from performing partial CCA on data lacking full treatment replication across factor levels (Anderson and Gribble, 1998).

To increase the robustness of each CCA only species that occurred in at least 20% of the sites sampled were included. The variance explained by a global CCA model (month+depth) was used in conjunction with results from the partial CCA to identify variance components that were uniquely and jointly explained by each predictor (Borcard et al., 1992; Anderson and Gribble, 1998). The significance of each predictor in the global and

partial CCA models was tested by comparing a pseudo F statistic to a null distribution generated by permuting the species-site matrix 5000 times (Legendre and Legendre, 1998).

The analysis of biomass spectra paralleled our analyses of the biomass of assemblage species. Length-frequency information for each species was used to divide species biomass into \log_2 body size classes. The total sum of biomass (all species) in each size class was then normalized by dividing the biomass by the antilog body size interval of each respective size class, as is commonly done in analyses of biomass spectra (Kerr, 1974; Sprules et al., 1983). In subsequent partial CCA, the size class biomass \times site matrix was treated as the response variable.

To determine whether the analyses should account for spatial autocorrelation, we tested residuals resulting from the global species biomass and biomass spectra CCA models for spatial dependence, using a multi-scale direct ordination technique. The method entails performing a constrained ordination on the global model CCA residuals with an explanatory matrix that is coded for geographic distance (Wagner, 2004). We used a grain-size equivalent to 0.1° latitude that resulted in four distance classes. Results were nonsignificant for species biomass and biomass spectra models, indicating that spatial structure at the assemblage level was not detectable. We therefore disregarded spatial dimensions and pooled samples by depth and season in subsequent analyses. During the exploratory stage of our analysis, univariate and multivariate tests that were performed with biomass densities resulted in conclusions similar to those obtained with numerical densities. We chose to limit our analyses to biomass densities to avoid redundancy and because the importance of a species to energy flow in a food web is more readily (although not perfectly) approximated by information on its biomass. We considered all statistical tests significant at the $P=0.05$ level.

Results

We captured 23,100 individual fish in our survey that represented 62 species from 23 different families. Of these, 32 species occurred in more than 10% of the trawls. In general, small size classes (<30% of maximum recorded length) for individual species were rare and only English sole (*Parophrys vetulus*), and spiny dogfish (*Squalus acanthias*) were abundant enough for inclusion in the analysis as separate size classes. Water conditions were relatively homogenous throughout the area surveyed. Temperature and salinity values differed by less than 1°C and 0.2, respectively, between the northern and southern CTD stations for each depth and month combination (Table 1). Differences in temperature and salinity among depths were small in October and March but were more evident in July; waters 20 m deep were warmer and fresher by 1.3° and 0.8°C , respectively (Table 1).

Table 1

Temperature ($^\circ\text{C}$) and salinity measurements obtained with conductivity-temperature-density (CTD) casts from the northern (N) and southern (S) regions of the area surveyed in Central Basin, Puget Sound. Data were obtained within ten days of trawl sampling. Although stations at 20 and 80 m were not sampled in March, water properties are provided to aid comparisons among sampling months.

Month	Depth (m)	Temperature		Salinity	
		N	S	N	S
October	20	12.1	12.1	30.3	30.5
	40	11.9	12.0	30.5	30.6
	80	11.7	11.8	30.6	30.7
	160	11.4	11.5	30.7	30.8
March	20	8.7	8.5	29.6	29.5
	40	8.7	8.5	29.7	29.6
	80	8.7	8.4	29.9	29.9
	160	8.8	8.3	30.1	29.8
July	20	12.8	13.0	29.6	29.6
	40	12.1	12.1	29.8	29.8
	80	11.5	11.4	30.0	30.0
	160	11.5	11.4	30.4	30.4

Overall, spotted ratfish (*Hydrolagus colliei*), spiny dogfish, and flatfish were the dominant taxonomic groups in the survey. Biomass patterns observed at each depth and month combination are depicted in Figure 2. Shallow waters (20 and 40 m) were dominated by flatfishes, which composed between 64% and 83% of the fish assemblage biomass in all three months. In deep water, assemblage biomass was nearly double that found in shallow waters (80 and 160 m; Fig. 2). In total, spotted ratfish composed approximately 80% of the fish assemblage at 160 m in all three months (Fig. 2). Spiny dogfish were found primarily at depths of 80 and 160 in October, were nearly absent from the survey in March (two individuals were captured), and present at all depths in July, with the highest biomasses occurring at depths of 80 and 160 m (Fig. 2).

Diversity metrics

Variation in species richness (N) was observed across depths in both October+July (ANOVA, $F_{[3,32]}=3.9$, $P=0.01$) and all-months tests (ANOVA, $F_{[1,26]}=103.7$, $P<0.001$) where N at 40 m was higher than at 160 m (Fig. 3). *Post hoc* analyses of the October+July test indicated that N at 160 m was significantly lower than at 80 m, but that both of these depths did not differ from N at 20 and 40 m (Fig. 3). Similar patterns were observed for species diversity (H'), with significant differences across depth for both the October+July and all-months tests (ANOVA, $F_{[1,32]}=18.4$, $P<0.001$ and $F_{[1,26]}=137.3$, $P<0.001$, respectively; Fig. 3). In both all-months and

October+July tests H' at 160 m was significantly lower than that observed at shallower depths (Fig. 3).

N did not differ significantly across months (ANOVA, $F_{[1,32]}=1.7$, $P=0.18$ and $F_{[1,26]}=0.3847$, $P=0.68$ in October+July and all-months tests, respectively) and there was no significant interaction between depth and month (ANOVA, $F_{[3,32]}=2.3$, $P=0.08$ and $F_{[2,26]}=1.4$, $P=0.26$ in October+July and all-months tests, respectively). In contrast, H' in the October+July test differed significantly by month (ANOVA, $F_{[1,32]}=13.4$, $P<0.001$), as well as the interaction between depth and month (ANOVA, $F_{[3,32]}=8.3275$, $P<0.001$). Overall, H' was high-

er in October than in July and the interaction term appears to be related to a strong seasonal change in H' at 80 m (Fig. 3). Month and the interaction between month and depth were not significant in the test for all-months (ANOVA, $F_{[1,26]}=2.0$, $P=0.15$ and $F_{[1,26]}=1.7$, $P=0.2$, respectively).

Taxon-based analysis

Depth was a significant predictor of assemblage structure in all-months and in October+July CCA tests, and explained 44% ($F_{[1,27]}=19.1$, $P<0.001$) and 34% ($F_{[3,33]}=6.1$, $P<0.001$) of the variances, respectively. Season explained a smaller proportion of the variance (5%) in the October+July CCA test ($F_{[1,33]}=2.7$, $P<0.05$) and was not a significant predictor in the all-months test ($F_{[1,27]}=1.9$, $P<0.18$). Temporal shifts in depth distributions were negligible at the assemblage level; the joint variance explained by season and depth was zero for October+July and all-months analyses.

The resulting tri-plots for each partial CCA (based on weighted averages of the species scores) simultaneously depict the centroid of the sites coded for the constraining variables and the position (eigenvectors) of the species forming the response matrix. Examination of the depth partial CCA tri-plots for October+July and all-months analyses, indicated that the first CCA axis primarily separated shallow (20 and 40 m) and deep (80 and 160 m) fish communities (Fig. 4). The spread of the variable centroids indicates the relative differences in species composition among the respective depth and month factors (distant centroids are more dissimilar in species composition than close centroids). Species centered near the origin of the tri-plot have little to no association with the predictor variables included in the analyses, but those furthest from the origin have higher loadings, the strongest associations with the CCA axis, and contribute the most to differentiating sites that separate along the same axis. For the October+July samples, the second CCA axis also separated the 80- and 160-m fish assemblages (Fig. 4). Partial CCA results for the October+July and all-months samples confirmed that 160 m was dominated by spotted ratfish and small spiny dogfish, but that Pacific hake (*Merluccius productus*), rex sole (*Glyptocephalus zachirus*), and dover sole (*Microstomus pacificus*) also typified that depth (Fig. 4). Furthermore, species that were associated with both 80 and 160 m included large spiny dogfish, and quillback rockfish (*Sebastes maliger*), brown rockfish (*Sebastes auriculatus*), blackbelly eelpout (*Lycodes pacificus*), Pacific tomcod (*Microgadus proximus*), walleye pollock (*Theragra chalcogramma*), shiner perch (*Cymatogaster aggregata*), pile perch (*Rhacochilus vacca*), black tip poacher (*Xeneretmus latifrons*), slender sole (*Lyopsetta exilis*), and plainfin midshipman (*Porichthys*

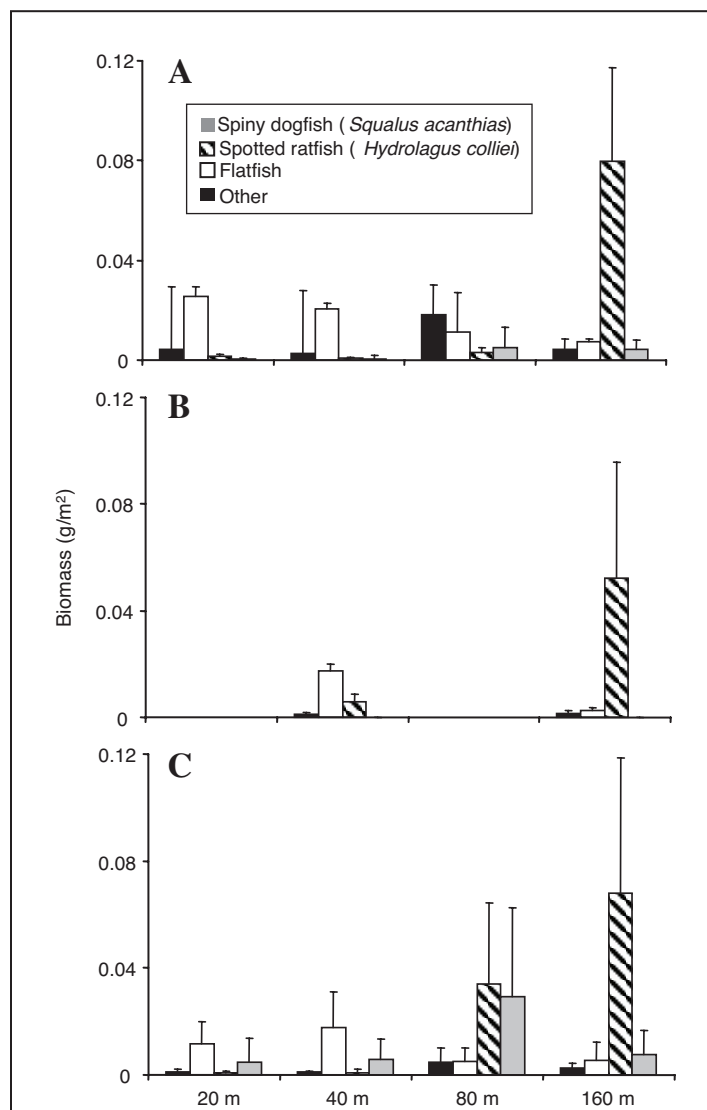


Figure 2

Average biomass of the major fish groups in the demersal fish assemblage observed at different depths from the Central Basin, Puget Sound in (A) October 2004, (B) March 2005, and (C) July 2005. Error bars indicate standard deviation. For October, March, and July, 4, 4, and 5 sites were sampled at each depth, respectively.

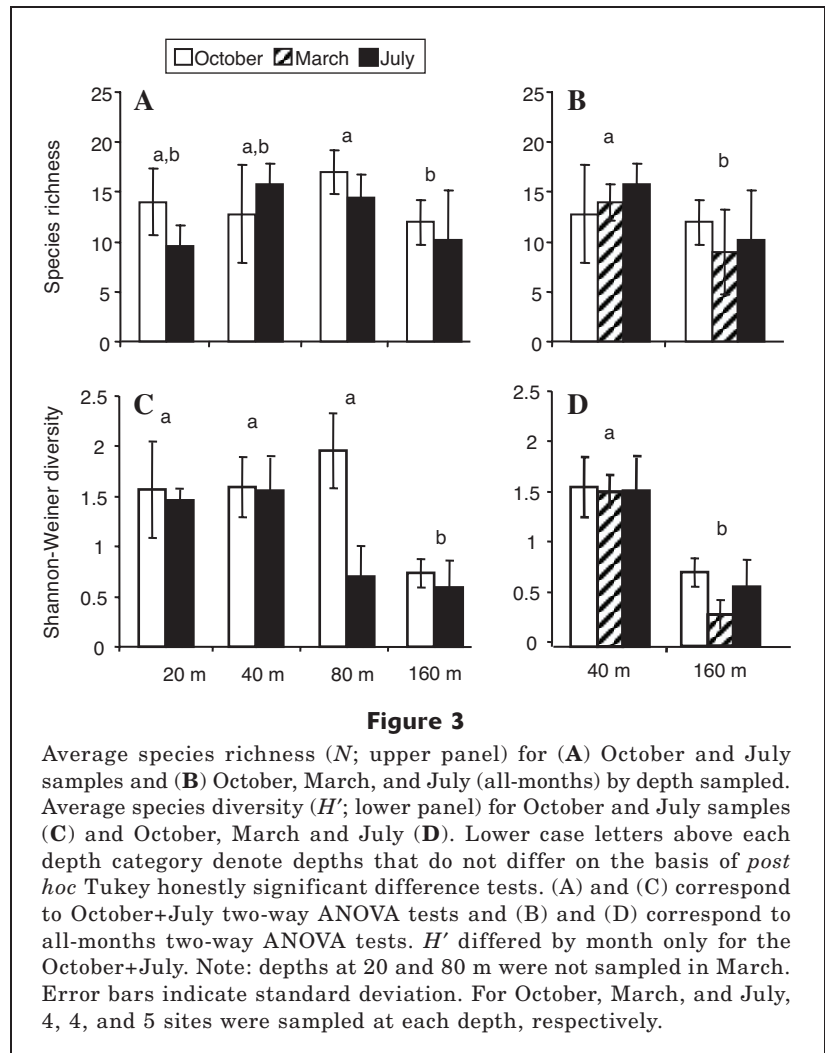
notatus; Fig. 4). In shallow waters (20 and 40 m) several flatfishes dominated including small and large English sole, rock sole (*Lepidopsetta bilineata*), C-O sole (*Pleuronichthys coenosus*), Pacific sanddab (*Citharichthys sordidus*), and sand sole (*Psettichthys melanostictus*) among other species (Fig. 4).

In the October+July analyses, temporal changes in assemblage structure were largely driven by species that were found primarily at depths of 80 m. The biomass of shiner perch, pile perch, walleye pollock, and Pacific tomcod was highest in October and the biomass of large spiny dogfish and slender sole was highest in July (Fig. 4). At depths of 20 and 40 m, the biomass of small English sole and C-O sole was highest in October and the biomass of staghorn sculpin (*Leptocottus armatus*) and sand sole was highest in July. The biomass of species that typified the 160-m depths changed little between October and July (e.g., spotted ratfish, dover sole, rex sole, and Pacific hake; Fig. 4). In the all-months analysis, species with higher biomass in March included C-O sole, sand sole, great sculpin, and rock sole (Fig. 4).

Size-based analysis

Body sizes encountered in the survey spanned eleven size classes, ranging from 2 to 2048 g. Overall, biomass spectra were nonlinear in appearance and approximately parabolic for most depth and season combinations (Fig. 5). For that reason metrics describing linear biomass size spectra (intercept, slope) were not estimated. Deep waters were dominated by individuals larger than 32 g, whereas shallow waters contained relatively more individuals that were less than 128 g (Fig. 5). Temporal differences were most apparent at depths of 80 m where biomass was concentrated in body size classes greater than 128 g in July and at 40 m that contained peak biomass levels in the 16-g body size class in March. Overall, 28% and 29% of the biomass spectra variance was associated with depth in both all-months ($F_{[1,10]}=5.4, P<0.001$) and October+July tests ($F_{[3,10]}=2.3, P<0.001$), respectively. Month explained a smaller but significant proportion of variance in the October+July test (11%; $F_{[1,10]}=2.1, P<0.001$) and was not a significant predictor in the all seasons test ($F_{[1,33]}=2.1, P=0.09$). Variance explained jointly by season and depth was again zero.

In the October+July analyses, the first CCA axis accounted for 20.9% of the total variation and separated the shallow (20 and 40 m) and deep assemblages (160 m). The second axis accounted for 10.3% of the variance and distinguished 80 m from the other depths. The



largest size class (2048 g) was associated with depths of 80 m, and the next three largest size classes (256, 512, and 1024 g) were associated with depths of 160 m (Fig. 6). In contrast, the smallest size classes (4, 8, and 16 g) were affiliated with depths of 20 and 40 m. The remaining intermediate body size classes were near the origin of the ordination plot and not closely associated with any of the depths. The analysis of all-months tests reiterated these patterns (Fig. 6). Tracking the arrival of dogfish, the size classes with the strongest temporal responses were also the largest size classes (1024 and 2048 g) which exhibited higher abundances in July (Fig. 6). In October, biomass in the smallest size classes (2, 8, and 16 g) was relatively higher.

Discussion

Fjord systems such as Puget Sound typically possess steep bathymetries and deep basins that result in deep-water habitat relatively close to shore. As expected, the demersal fish assemblage in Puget Sound varied

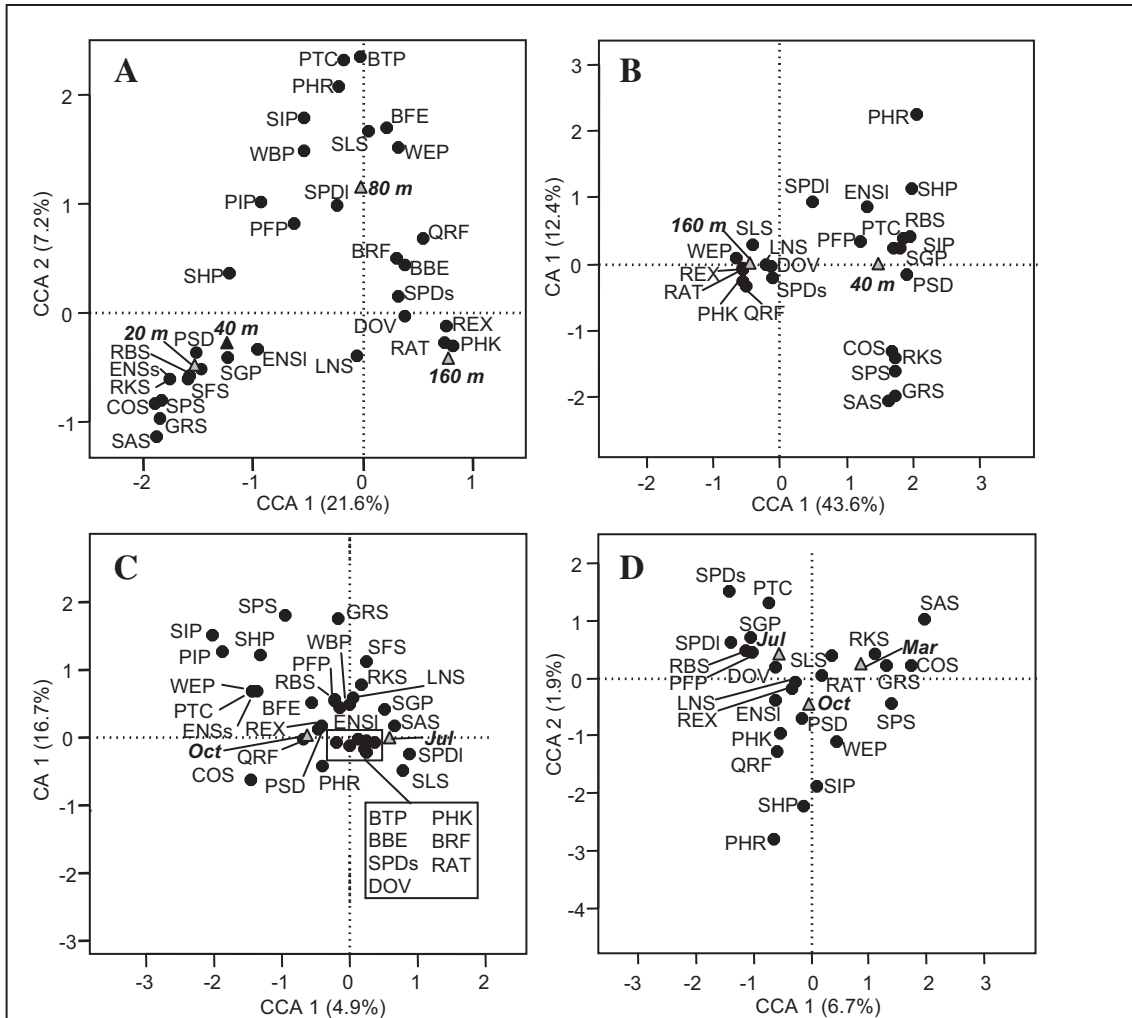
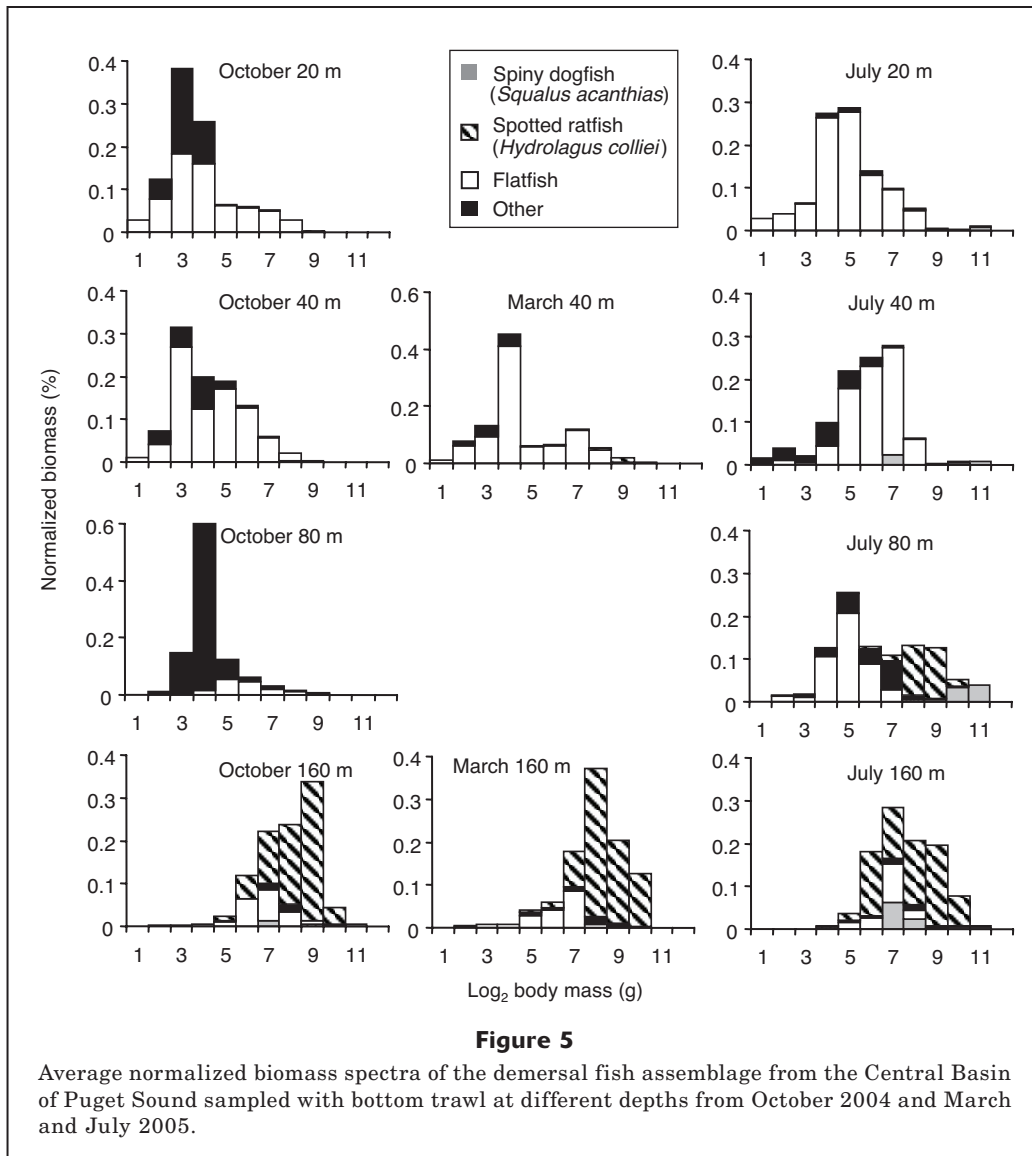


Figure 4

Species-based partial canonical correspondence analysis (CCA) tri-plots for fall+summer and all-seasons analyses in which depth (A, B) and season (C, D) are the constraining variables, respectively. In the tri-plots, the site centroids coded for each constraining factor are indicated by triangles. The proximity of factor centroids in ordination space to one another corresponds to their respective similarity in average species composition. Species that have strong loadings (large eigenvectors) are distant from the tri-plot origin and contribute the most to differentiating factor centroids that separate along the same axis. The eigenvalue or variance associated with each axis is indicated by parentheses. In cases where the constraining factor consisted of only two groups as in (B) and (C) only one CCA axis was generated. To aid interpretation two dimensional plots were generated by plotting the CCA (x-axis) against the residual axis (y-axis) derived from standard correspondence analysis (CA) performed on the remaining community variance. Species codes: BFE=bigfin eelpout (*Lycodes cortezianus*); BBE=blackbelly eelpout (*Lycodes pacificus*); BTP=blacktip poacher (*Xeneretmus latifrons*); BRF=brown rockfish (*Sebastes auriculatus*); COS=C-O sole (*Pleuronichthys coenosus*); DOV=Dover sole (*Microstomus pacificus*); ENSl and ENSs for English sole (*Parophrys vetulus*) large and small, respectively; GRS=breat sculpin (*Myoxocephalus polyacanthocephalus*); LNS=longnose skate (*Raja rhina*); PHK=Pacific hake (*Merluccius productus*); PHR=Pacific herring (*Clupea pallasii pallasii*); PSD=Pacific sanddab (*Citharichthys sordidus*); PTC=Pacific tomcod (*Microgadus proximus*); PIP=pile perch (*Rhacochilus vacca*); PFP=plainfin midshipman (*Porichthys notatus*); QRF=quillback rockfish (*Sebastes maliger*); REX=rex sole (*Glyptocephalus zachirus*); RKS=rock sole (*Lepidopsetta bilineata*); RBS=roughback sculpin (*Chitonotus pugetensis*); SAS=sand sole (*Psettichthys melanostictus*); RAT=spotted ratfish (*Hydrolagus colliciei*); SGP=sturgeon poacher (*Podothecus accipenserinus*); SFS=sailfin sculpin (*Nautichthys oculo-fasciatus*); SIP=shiner perch (*Cymatogaster aggregata*); SLS=slender sole (*Lyopsetta exilis*); SPS=speckled sanddab (*Citharichthys stigmaeus*); SPDI and SPDs=spiny dogfish (*Squalus acanthias*) large and small, respectively; SHP=staghorn sculpin (*Leptocottus armatus*); WEP=walleye pollock (*Theragra chalcogramma*); WBP=whitebarred prickleback (*Poroclinus rothrocki*).

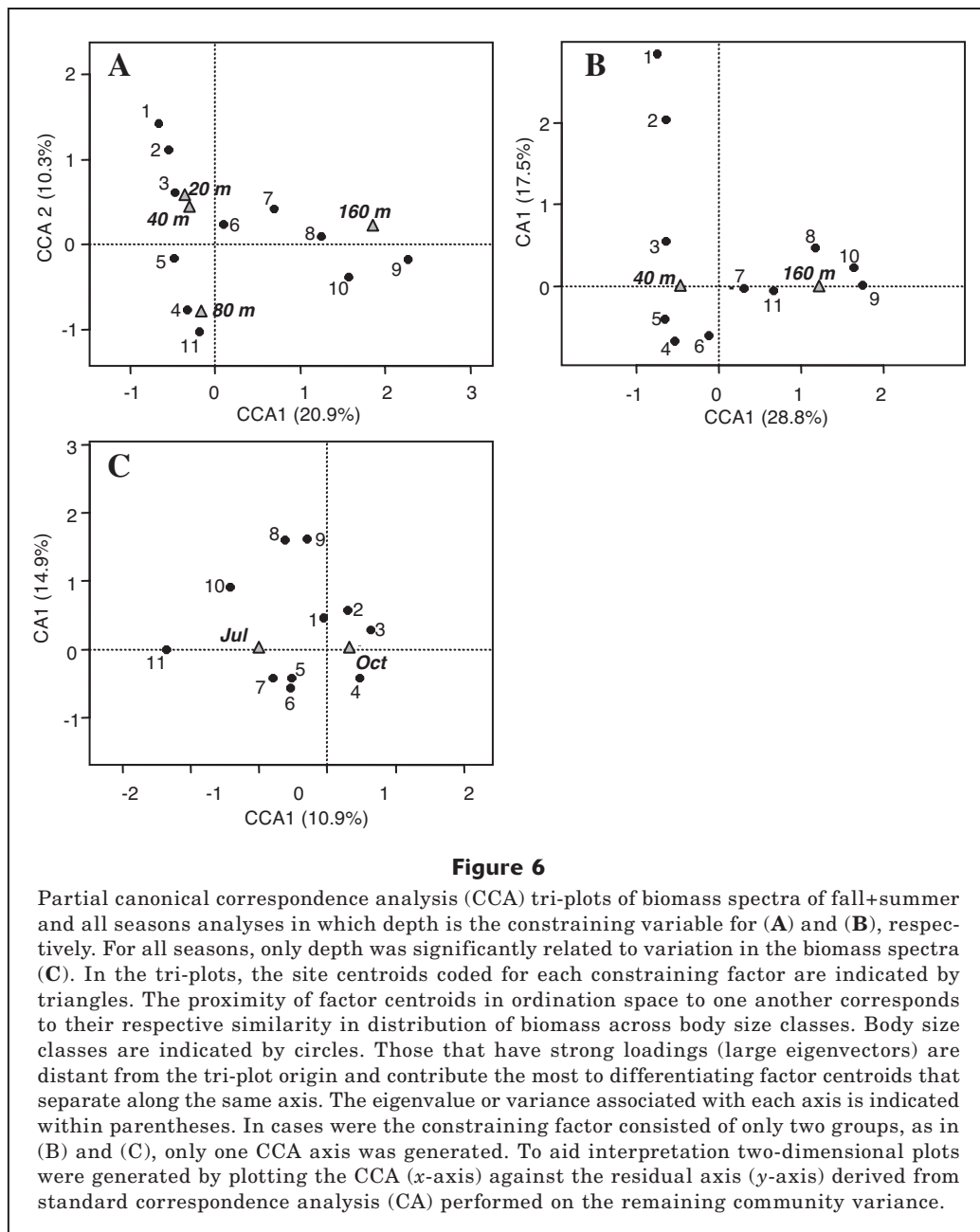


substantially across depths and among seasons, but was unusual in that chondrichthyans (spotted ratfish and spiny dogfish) made up a majority of the fish biomass. Fish assemblages in estuaries on the outer coast of Washington, Oregon, and California are dominated by teleosts (e.g., Armor and Herrgesell, 1985; Bottom and Jones, 1990; De Ben et al., 1990), and this finding shows that demersal fish assemblages in Puget Sound differ fundamentally from shallower estuarine systems.

Total assemblage biomass at depths of 80 and 160 m principally comprised spotted ratfish year round and spiny dogfish seasonally. Deepwater habitat is widespread in the Central Basin (average depth: 120 m; Burns, 1985), making these two species the dominant species, in biomass, in the area surveyed. An abundance of spotted ratfish has also been noted in deep waters immediately adjoining Puget Sound (Palsson et al.²), but what remains poorly understood is whether spotted

ratfish are common in northeastern Pacific fjords or whether they are superabundant only in Puget Sound. Spotted ratfish are primarily benthic feeders, feeding on polychaetes and bivalves and occasionally on small fishes (Quinn et al., 1980), which indicates that they potentially are competitors to benthic feeding flatfishes (Reum and Essington, 2008). In addition, they are preyed upon by large elasmobranchs (e.g., sixgill sharks [*Hexanchus griseus*], spiny dogfish). There is presently insufficient information to evaluate whether the high abundance of spotted ratfish is a secondary effect of shifts in food web structure, or whether other envi-

² Palsson, W. A., S. Hoffmann, P. Clarke, and J. Beam. 2003. Results from the 2001 transboundary trawl survey of the southern Strait of Georgia, San Juan Archipelago and adjacent waters, 117 p. Washington State Dept. Fish and Wildlife, Olympia, WA.



ronmental features of Puget Sound promote their high abundance. Historical abundance records of spotted ratfish in Puget Sound are available in agency and project reports and indicate that they have been a common component of the food web at least since the 1930s, but it is difficult to extract trends from these data because of the lack of standardization of sample sites and gears. Future comparisons with less impacted fjords may offer insight into whether cartilaginous species naturally dominate in these systems or do so only under conditions related to human-caused ecosystem degradation. Despite our poor understanding of long-term changes in the Puget Sound fish community, the high abundance

of ratfish in the area surveyed indicate that they likely constitute a significant node in the Puget Sound food web and are therefore deserving of further study.

Spiny dogfish was the most abundant demersal piscivore and may have a particularly important influence on assemblage structure in Puget Sound and other coastal ecosystems. Spiny dogfish have a diverse diet, feeding on Pacific herring, flatfish, spotted ratfish, salmonids, as well as a wide range of benthic and pelagic invertebrates (Reum and Essington, 2008; Beamish and Sweeting, 2009). Large mobile predators such as spiny dogfish play an important role by linking different communities through predation and may stabilize

communities by dampening oscillations in prey populations through behavioral mechanisms such as switching prey (McCann et al., 2005). Moreover, understanding how large predators use different habitats is important for estimating prey mortality rates and system energy flows (Bax, 1998). Information on spiny dogfish movement patterns in Puget Sound is limited to tagging studies from the 1940s and 1970s. Results from these studies indicate that approximately 70% of the spiny dogfish population resides in the Sound and the adjoining Strait of Georgia for multiple years, while the remaining dogfish are transient (McFarlane and King, 2003). Spiny dogfish on the outer Washington and British Columbia coasts are known to exhibit seasonal latitudinal migrations, but seasonal movements of dogfish tagged within Puget Sound and the Strait of Georgia are less clear (McFarlane and King, 2009; Taylor and Gallucci, 2009) and remain the subject of ongoing research. It is unknown whether spiny dogfish migrate in the winter to other subbasins within Puget Sound, to habitats shallower than 20 m, or whether they simply feed higher in the water column, disassociating with the benthos. There is evidence that catch rates of spiny dogfish in monitoring surveys have declined since the mid 1980s (Palsson, 2009) and that growth and size-at-maturity have also undergone substantial shifts (Taylor and Gallucci, 2009). Characterizing movement patterns and population dynamics will clarify the impact of spiny dogfish on nearshore food webs.

As demonstrated in Puget Sound, fjordal fish assemblages vary markedly in space and time, and this variation has practical implications for modeling energy flows and interspecific interactions such as predation and competition. Food web models can foster ecosystem based management because they offer a framework for summarizing system knowledge and permit the simulation of alternative management scenarios. However, food web models for Puget Sound (as well as any other temperate system) parameterized by using fish abundances from one season alone may misrepresent the importance of different feeding modes and mischaracterize patterns of trophic links in the fish assemblage (Greenstreet et al., 1997). In addition, stark differences between deep and shallow assemblages in terms of total biomass and species composition indicate strong spatial structuring in the likelihood and intensity of interactions among species, which may be a more general feature of fjord estuaries with similar deep basin bathymetrics. The data presented here, when coupled with diet information, provide a basis for determining the parameters of trophodynamic models that account for spatial and temporal variability in the fish assemblage (e.g., Pauly et al., 2000).

The use of three separate methods for analyzing differences in the demersal fish assemblage allowed us to investigate whether our interpretation of assemblage variation differed depending on the method. All three methods indicated significant differences between shallow (20, 40, and 80 m) and deep waters (160 m) across seasons, with the exception of N , where values from 20

and 40 m waters did not differ from values in 160 m waters. We note however, that variation in N may have been artificially reduced by our exclusion of rare species from the analysis. In contrast, species diversity, H' , which takes into account the relative biomass of each species, should be more robust to the exclusion of rare species. Results from taxon-based CCA complemented results from the diversity metrics by highlighting those species that co-varied with depth and simultaneously depicted site similarity in ordination space. Lastly, size-based analyses revealed differences in assemblage structure based on biomass spectra, a macroecological descriptor of assemblage structure (Jennings, 2005). Because body size is correlated with trophic level in aquatic systems (Kerr 1974; Jennings et al., 2001), differences in biomass spectra among assemblages may reveal fundamental differences in trophic structure (Rice, 2000; Sweeting et al., 2009). Significant depth related differences in the biomass spectra paralleled results from our taxon-based analyses and offer evidence that food web structure likely varies with depth. Combined, these approaches offer alternative prisms through which to view the demersal fish assemblage and mutually confirm important differences in assemblage structure.

As with other marine fish surveys, our results are partly contingent on the effectiveness of the sampling gear and are premised on the assumption that catchability varies little among species. To maintain comparability with past demersal fish studies in Puget Sound we intentionally sampled using trawl equipment with specifications nearly identical to those used in previous agency surveys in the region. The use of bottom trawls, however, also meant that species associated with rocky reef habitats would be excluded from our survey because the gear was suitable only for trawling in soft-bottom habitats. Moreover, large species such as six gill shark, which typically exceed 2 m in length in Puget Sound, were missed from the survey altogether. For future comparisons with other fjord systems, an effort should be made to sample regions with similar soft bottom habitats. We note that the data presented here reflect daytime distribution patterns, and diel movements of species may potentially connect deep and shallow communities. Another limitation of the present study is that our results span only a single time period and cover only a single basin in Puget Sound. Thus, we do not presume that the patterns described here will necessarily hold for all regions and be stable across time. Indeed, ample evidence from marine ecosystems points to the dynamic nature of community structure (Anderson and Piatt, 1999). Future research may very well improve our estimates of diversity and increase our understanding of temporal shifts in the Puget Sound fish assemblage.

Although depth and season were clearly important in explaining community structure and species abundances, roughly one-half of the variation in these metrics was not related to depth or season. Differences in temperature and salinity between the northern and southern CTD stations were relatively slight and differ-

ences among other parameters, such as oxygen concentration and turbidity (data not shown), showed similar patterns. Because water conditions vary little in the region surveyed they are unlikely to explain site-specific variability. Other unmeasured variables, however, such as substrate composition, sediment contamination, or shoreline and land cover characteristics in regions adjoining each sample site may potentially explain additional variance in the assemblage. We note, however, that spatial autocorrelation was not detected in the data set and indicates that spatially structured environmental variables, such as those that covary with coastal urbanization, are unlikely to explain much additional variation at least at the spatial scales embraced by our survey (Borcard et al., 1992).

Our research provides the first published assessment of seasonal variability in assemblage structure across multiple depths in the Puget Sound demersal fish assemblage and offers insight into general features of deep fjord systems. We found strong structuring of the assemblage by depth and smaller, although important, differences across seasons. These shifts were manifest in simple assemblage metrics and in multivariate taxon-based and size-based analyses. The identification of these patterns, in turn, identifies priorities for future investigators that will further our understanding of the demersal assemblage and the forces that act to shape it. Notably, we identified species that may seasonally modify the Puget Sound food web in significant ways (e.g., spiny dogfish) and we confirmed the findings of other researchers who have identified spotted ratfish as one of the most abundant fishes in the Puget Sound region (Quinnell and Schmitt³). Remarkably, research directed toward uncovering the life history and ecology of spotted ratfish has been limited (but see Quinn et al., 1980; Barnett et al. 2009). Furthermore, key species in the Puget Sound food web may be those that link habitats through movement and foraging activities. Understanding diel and seasonal-scale movement patterns will greatly improve our understanding of the Puget Sound fish assemblage.

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³ Quinnell, S., and C. Schmitt. 1991. Abundance of Puget Sound demersal fishes: 1987 research trawl survey results, 240 p. Washington State Dept. Fish and Wildlife, Olympia, WA.

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