

Abstract—Puget Sound is one of the largest and most ecologically significant estuaries in the United States, but the status and trends of many of its biological components are not well known. We analyzed a 21-year time series of data from standardized bottom trawl sampling at a single study area to provide the first assessment of population trends of Puget Sound groundfishes after the closure of bottom trawl fisheries. The expected increase in abundance was observed for only 3 of 14 species after this closure, and catch rates of most (10) of the abundant species declined through time. Many of these changes were stepwise (abrupt) rather than gradual, and many stocks exhibited changes in catch rate during the 3-year period from 1997 through 2000. No detectable change was recorded for either temperature or surface salinity over the entire sampling period. The abrupt density reductions that were observed likely do not reflect changes in demographic rates but may instead represent distributional shifts within Puget Sound.

Manuscript submitted 27 August 2012.
 Manuscript accepted 3 April 2013.
 Fish. Bull. 111:205–217 (2013).
 doi 10.7755/FB.111.3.1

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Shifts in the estuarine demersal fish community after a fishery closure in Puget Sound, Washington

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Estuaries support diverse marine communities and act as nursery areas for many coastal populations (Beck et al., 2001; Armstrong et al., 2003), but they are the most heavily affected marine ecosystems (Lotze et al., 2006; Halpern et al., 2008) because they also commonly serve as ports for shipping, support commercial and recreational fisheries, and are used as recreational areas. Because of their close link with terrestrial systems, they are susceptible to coastal eutrophication (Carpenter et al., 1998) that leads to hypoxia (Diaz, 2001; Breitburg et al., 2009), harmful algal blooms (Anderson et al., 2002), and concentrations of contaminants (Nichols et al., 1986). Because of the myriad ecosystem services they provide (Guerry et al., 2012) and the many human activities that may impair their delivery, there is a growing effort to protect and restore these ecosystems. However, assessment of the efficacy of protection measures is often hindered by the lack of long-term, standardized data and by confounding changes in many aspects of the ecosystem, such as fishery management, shoreline protection, and water quality.

Puget Sound is one of the largest and most ecologically significant estuaries in the United States, supporting a rich fauna with more than 200 fish species, 26 marine mammals, more than 100 bird species and

a high diversity of invertebrates.¹ It is the second-largest estuary (2330 km²) in the coterminous United States, and its watershed supports a large and growing human population. Land alteration and habitat loss (Levings and Thom, 1994), fishing,² and toxic contaminants (Landahl et al., 1997) have had widespread effects on this ecosystem. Currently, 8 fish species or fish stock in Puget Sound are protected under the U.S. Endangered Species Act, and many others are identified as being at risk (Musick et al., 2000). Tagging studies, genetic analyses, and differences in toxic contaminant levels all indicate that Puget Sound stocks of various fish species are distinct from coastal stocks (Day, 1976; Andrews et al., 2007; West et al., 2008; Andrews and Quinn, 2012). Notwithstanding these issues, much of the area

¹ Ruckelshaus, M. H., and M. M. McClure. 2007. Sound science: synthesizing ecological and socioeconomic information about the Puget Sound ecosystem. U.S. Dep. Commer., NOAA, National Marine Fisheries Service, Northwest Fisheries Science Center. Seattle, WA. 93 p. [Available from http://www.nwfsc.noaa.gov/research/shared/sound_science/documents/sound_science_finalweb.pdf.]

² Palsson, W. A., T. J. Northrup, and M. W. Barker. 1998. Puget Sound groundfish management plan, 48 p. Washington Department of Fish and Wildlife, Olympia, WA. [Available from <http://wdfw.wa.gov/publications/00927/>.]

in Puget Sound is deep because of its glacial origin (Burns, 1985), compared with the much shallower estuarine systems on the East Coast of North America. Therefore, the shallow biogenetic habitats that have been altered by humans—a common occurrence in estuaries—encompass a relatively small fraction of the total available habitat. The local government is working to assess the status of the Puget Sound ecosystem and to identify and implement measurable restoration goals.³ However, this planning process is hindered by a paucity of long-term data on species and community trends.⁴ Without such time series, it is difficult to assess the rate and extent of recovery that may be reached within planning timelines.

Here we present our analysis of one of the longest continual and standardized surveys of the groundfish community in Puget Sound (surveys conducted by the University of Washington) to assess the nature and extent of change that has accompanied significant restoration measures. Most significantly, the state of Washington progressively prohibited commercial trawling by closing most waters of central and southern Puget Sound in 1989, and then closing all inland marine waters to nontribal bottom trawling in 2010.² Therefore, we hypothesized that these survey data—the collection of which began in 1991—would provide an indication of rates of recovery of exploited fish stocks and community reorganization because not all species were exploited. Our time series is limited in spatial extent but provides a 20-year record of species composition and abundance of the groundfish community and, therefore, may indicate the effect of commercial trawling and enable assessment of the status of recovery.

This ecosystem affords a rare opportunity to track the recovery of groundfish populations and communities in response to a commercial fishery closure. Typically, information about fisheries effects has come from tracking changes in “no-take” marine reserves (Russ and Alcala, 1996; Babcock et al., 1999; Halpern, 2003). Although such spatial closures provide important information for identifying restoration targets, no-take areas are often smaller in area than the range of populations affected by fishing and, therefore, may not reveal the full extent of fishing effects (Claudet et al., 2008). In contrast, the commercial trawl-fishing closure in Puget Sound covered a large area that closely matches the distribution scales of resident populations. Moreover, because more than 2 decades have passed

since the closure, we have the potential to describe not only the extent but also the trajectory of population recovery. Therefore, we can ask whether recovery was monotonic as predicted by simple population models or whether, instead, it was characterized by abrupt and sustained shifts in abundance and composition that would indicate either nonlinear population or community dynamics (Doak et al., 2008; McClanahan et al., 2011) or decadal-scale environmental drivers (Mantua et al., 1997; Anderson and Piatt, 1999).

Our specific objectives were to determine 1) whether catch rates of resident Puget Sound groundfishes generally increased through time following the closure of bottom trawl fisheries, 2) the extent to which shifts in this time series may represent population fluctuations or instead represent local effects that result from distribution shifts, 3) whether dynamics are best represented by smooth trends through time or instead through more abrupt state-changes, and 4) whether observed trends in catch rates for resident Puget Sound groundfish populations may be linked to changes in environmental conditions reflected in oceanographic monitoring data.

Materials and methods

Study location and design

Catch data were derived from bottom trawl surveys conducted in Port Madison, a large bay on the west side of central Puget Sound, north of Bainbridge Island (Fig. 1; see also Andrews and Quinn [2012] for specific sampling sites) as part of a Fisheries Ecology course of the University of Washington. The study area is located in the central basin of Puget Sound, the largest of the 4 main basins that compose the inland marine waters of Washington State. The area is not industrialized, and the shoreline is primarily a natural bluff-beach formation typical of central Puget Sound with some armoring around private residences. All sampling was conducted on the third weekend in May, beginning in 1991 and continuing until 2012; sampling did not occur in 1992 and 1998.

Bottom trawl surveys consisted of single tows of ~5 min conducted at 4 fixed index sites at discrete depths (10, 25, 50 and 70 m) over 5 diel time periods: afternoon (~15:00–18:00 h), evening (~20:00–23:00 h), night (~01:00–04:00 h), morning (~06:00–09:00), and mid-day (~11:00–14:00 h). This survey design was intended to capture and account for diel shifts in onshore–offshore distribution of key species (Andrews and Quinn, 2012). Trawl paths did not overlap within sampling years but were staggered slightly. All sampling was conducted from RV *Kittiwake*. Each tow covered 0.37 km at 0.5 m/s, with a standard Southern California Coastal Water Research Project bottom trawl that had a footrope

³ Puget Sound Partnership. 2009. Puget Sound Action Agenda : Protecting and restoring the Puget Sound ecosystem by 2020, 213 p. Puget Sound Partnership, Olympia, WA. [Available from http://www.psp.wa.gov/downloads/AA2009/Action_Agenda_FINAL_063009.pdf.

⁴ Essington, T. E., T. Klinger, T. Conway-Cranos, J. Buchanan, A. James, J. Kerschner, I. Logan, and J. West. 2011. The biophysical condition of Puget Sound. In Puget Sound Science Update, p. 205–423. Puget Sound Partnership, Tacoma, WA. [Available from <http://www.psp.wa.gov/scienceupdate.php>.]

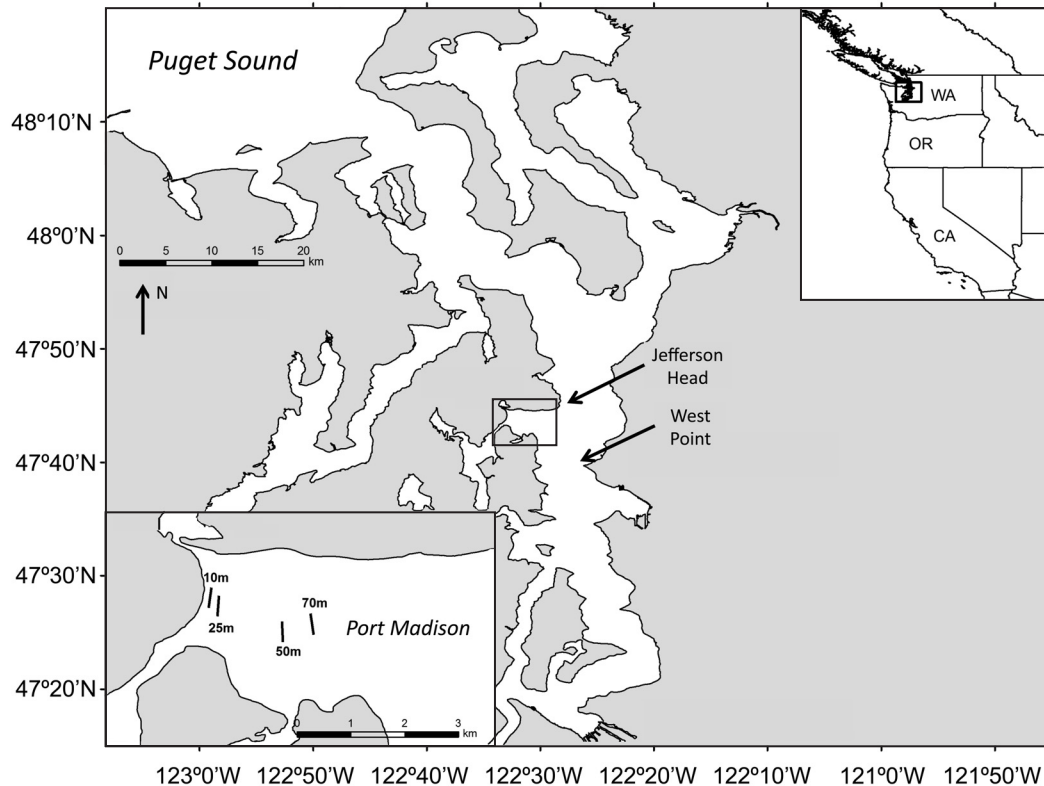


Figure 1

Map of the locations of the study area (rectangle at the center) where bottom trawl surveys were conducted in Port Madison from 1991 to 2012 and of 2 nearby monitored sites (labeled West point and Jefferson Head) where time series data on environmental conditions, such as temperature and surface salinity, were recorded. Map inset in upper-right corner shows location of Puget Sound, Washington, along the U.S. Pacific coast, and map inset in lower-left corner shows detailed view of the Port Madison study area and locations of 4 sampling sites with corresponding depths listed.

of 5 m and net width of 3.5 m during fishing.⁵ The bottom trawl was fitted with a 3.8-cm body mesh and 3.2-cm codend mesh with a 0.4-cm codend liner. The net primarily targets flatfishes but also catches small demersal fishes, such as gadids and some elasmobranchs.

Fish were identified to species on deck with the aid of dichotomous keys (Hart, 1973), but a few individuals were retained for examination in the laboratory. We measured fork length for all species except length of Spotted Ratfish (*Hydrolagus colliei*), for which precaudal length (tip of snout to second dorsal fin; Anderson and Quinn, 2012) was measured; all length measurements were made to the nearest millimeter. Consistency in field identification was facilitated by the presence of one of us (T. Quinn) for virtually every tow in the entire time series.

⁵ Eaton, C. M., and P. A. Dinnel. 1993. Development of a trawl-based criteria for assessment of demersal fauna (macroinvertebrates and fishes): pilot study in Puget Sound, Washington, 87 p. Final report to the U.S. Environmental Protection Agency. Bio-Marine Enterprises, Seattle, WA.

Environmental data

We obtained data from 2 monitoring sites on water-column characteristics (temperature and salinity profiles) for March, April, and May. The King County Water and Land Resources Division samples a location 4.4 km northeast of Port Madison called Jefferson Head, and the Washington State Department of Ecology samples a location 8.5 km southeast of Port Madison called West Point—both on a monthly basis (Fig. 1). We used data from both of these sampling programs (1990–2008 for West Point, 1992–2008 for Jefferson Head) to identify years and time periods with unusual environmental conditions on the basis of sub-mixed-layer temperature and surface salinity. Surface salinity gives a measure of seasonal runoff and, therefore, indicates seasonal weather events (years with high precipitation have low surface salinity). Sub-mixed-layer temperature is indicative of the thermal habitat experienced by groundfishes. Sub-mixed-layer temperature was used instead of bottom temperature because the latter was not always sampled. When bot-

tom temperature was sampled, it was generally within 0.7°C of sub-mixed-layer temperature (depth=20 m) for March, April, and May. We focused on data from these months because they include the time periods immediately before bottom trawl sampling and, therefore, could best indicate changes in environmental conditions that might affect catch rates. Moore et al. (2008) demonstrated strong intra-annual coherence of oceanographic properties within Puget Sound basins; therefore these data are likely representative of intra-annual environmental conditions throughout the central Puget Sound basin.

Analysis

For most years, all 20 depth×time combinations were successfully sampled, but gear malfunction and other events resulted in missing sets for some sampling sites. These missing sets constituted only 5% of the total sample design, but we wanted to account for them in deriving annual catch levels. We first ascertained whether these differences can alter annual estimates of catch rates by fitting an analysis of variance (ANOVA) for each of our study species with year, depth, time, and a depth×time interaction term. All but one species, the Shiner Perch (*Cymatogaster aggregata*), showed either a significant effect of depth, depth+time, or a depth×time interaction term.

We used a simple approach to account for the small numbers of missing sets. Rather than fitting generalized linear models to calculate a statistical “year effect,” we instead calculated an annual average catch anomaly for each year on the basis of expected catches for each time×depth combination. This approach is equivalent to fitting a generalized linear model with a time+depth+time×depth interaction term, but it has a straightforward interpretation and permitted a parallel calculation for the trawl and environmental data. We calculated the mean catch rate (number of fish/tow) for each depth×time combination for each species with data from the entire sampling period. We then calculated the catch anomaly as the difference between observed species-specific catch and the expected (mean) catch rate given the depth and time of sampling. The annual abundance index for each species was equal to the average catch anomaly over all samples conducted within a year. We used the same approach to generate temperature and salinity anomalies for each year. For each month and monitoring site, we calculated the mean temperature and salinity values from all available data, generated anomalies for each year, month, and site, and averaged these across months to derive a yearly anomaly value.

We generally tracked abundances at the species level, but, in some cases, we aggregated closely related species. Rock soles were allocated to a single species when the survey began, but subsequent genetic work indicated that the rock sole genus (*Lepidopsetta*) consists of 3 species (Orr and Matarese, 2000), 2 of

which occur in Puget Sound: Rock Sole (*Lepidopsetta bilineata*) and Northern Rock Sole (*Lepidopsetta polyxystra*). We conducted our analysis at the scale of an aggregated species group because the 2 Puget Sound species are not readily distinguished in the field and we wanted to maintain consistency throughout the time series. Further, Speckled Sanddab (*Citharichthys stigmaeus*) and Pacific Sanddab (*Citharichthys sordidus*) are morphologically similar as juveniles; for this reason, species-level identifications were not reliable. We, therefore, combined all individuals identified as either species into a species group termed “sanddab; (*Citharichthys*).”

We focused analysis on the most common species and species groups encountered with the sampling gear so that we had sufficient statistical power to detect changes in abundance through time. We set an arbitrary threshold of 200 sampled individuals over the entire time period for species to be included in the analysis. This use of a threshold eliminated species so rarely encountered that trends would not be reliable, species for which the gear was not appropriate, and samples for which species identity could not be determined (e.g., samples in very early juvenile stages). For each species, we asked whether abundance changed through time, and, if so, whether it was best described by a continuous linear increase or decrease or a discontinuous shift in the mean catch rate. The latter is consistent with regime shifts as reflected by rapid and persistent changes in population densities (Rodionov and Overland, 2005). For each time series, we used Akaike’s information criteria adjusted for a small sample size (AIC_c) to choose between 3 models: constant, linear, or change point. For each model, we assumed normally distributed residuals. We used the changepoint package (vers. 0.6; Killick and Eckley, 2011) in R software (vers. 2.13; R Development Core Team, 2011) to assess discontinuous shifts in the mean catch rate. We required that the best fitting change-point model consist of time periods spanning at least 4 years of data. In other words, estimated change points that broke the time series into increments shorter than 4 years were discarded, thus preventing the model from placing change points at the beginning or end of time series.

Because we found evidence of change points for many flatfishes, we explored the data for flatfish species in more detail. The gear captures individuals across a wide size range and range of life history stages; therefore we evaluated whether changes in catch rate could be attributed to changes in recruitment patterns. If changes in densities were driven by changes in recruitment, we would expect to see time trends of abundance for small size classes to lead trends for larger size classes. For each flatfish species, we calculated catch anomalies separately for small and large size classes (individuals below the 33rd percentile and above the 66th percentile of the cumulative length-frequency distribution, respectively). Size-at-age data are not available for most species, but for English

Table 1

Summary of total catches for species or species groups that were commonly collected during bottom trawl surveys conducted from 1991 to 2012 in Port Madison, Puget Sound, Washington. A full listing of all species collected is presented in the appendix table.

Species	Catch (number of fish)	Percentage of total
Blackbelly Eelpout (<i>Lycodes pacificus</i>)	3398	9.3
Dover Sole (<i>Microstomus pacificus</i>)	366	1.0
English Sole (<i>Parophrys vetulus</i>)	10,427	28.6
Flathead Sole (<i>Hippoglossoides elassodon</i>)	1665	4.6
Pacific Hake (<i>Merluccius productus</i>)	958	2.6
Pacific Herring (<i>Clupea pallasii</i>)	478	1.3
Pacific Tomcod (<i>Microgadus proximus</i>)	2677	7.3
Plainfin Midshipman (<i>Porichthys notatus</i>)	497	1.4
Rock soles (<i>Lepidopsetta bilineata</i> and <i>L. polyxystra</i>)	773	2.1
Sanddabs (<i>Citharichthys sordidus</i> and <i>C. stigmæus</i>)	1075	3.0
Sand Sole (<i>Psettichthys melanostictus</i>)	680	1.9
Shiner Perch (<i>Cymatogaster aggregata</i>)	1139	3.1
Slender Sole (<i>Lyopsetta exilis</i>)	2242	6.2
Spotted Ratfish (<i>Hydrolagus collieri</i>)	4068	11.2

Sole (*Parophrys vetulus*), the most common species, available aging data (senior author, unpubl. data) indicate that this procedure effectively separates age-1 individuals from those individuals aged 3 years and older.

Results

During the 20-year survey 65 fish species were sampled, and the 14 species that were sampled frequently enough (>200 individuals) to evaluate time trends accounted for more than 85% of the total catch (Table 1). Notably, 7 of these species were flatfishes (Pleuronectidae and Paralichthyidae). English Sole and Spotted Ratfish were by far the most common species, collectively, contributing more than 40% of all individuals sampled. Other common species included Blackbelly Eelpout (*Lycodes pacificus*) and Pacific Tomcod (*Microgadus proximus*).

Time series of catch anomalies were nonstationary for most species (Fig. 2). Spotted Ratfish was the only species for which no trend or apparent change in abundance over the sampling period was observed (Table 2; Fig. 2). As for changes in abundance values that were seen, a change point was identified for 9 species and a continuous linear trend was found for only 3 species. In all cases where the change-point model provided the best fit to the data, the relationship indicated a reduction in the mean catch rate in the later portion of the time series. These cases included the one for the most abundant species, English Sole, for which the mean catch anomaly shifted from +27/tow before 1998 to -7/tow afterward. In contrast, increases in the mean

catch anomaly were observed for all 3 species for which abundance trends were best described by the linear model. Trends in total catch (unstandardized) summed across all species mirrored the trends of English Sole (Fig. 2).

Many species exhibited changes in catch rates at similar time periods. Of the 9 species whose dynamics were best described by a change-point, 5 species had estimated change points between 1997 and 1999 (catches were not sampled in 1998). Three species had change points between 1999 or 2000 and 2000 or 2001. Therefore, there was evidence of a change in catch rates between 1997 and 2001 reflected by several species.

Analysis of catch-anomaly trends among different size classes of flatfishes did not support the hypothesis that trends were driven by changes in recruitment (Fig. 3). For most species, anomalies for small- and large-size fishes were synchronous with no apparent lag. On the basis of the length-frequency distribution of each species or species group, fishes were categorized as small if they fell in the 33rd percentile or lower and as large if they were assigned to the 67th percentile or higher. For instance, the catch anomalies for English Sole were nearly identical between small (age 1) and large (age 3+) size classes. Catch-anomaly trends for the rock sole species group were more consistent with recruitment shifts because catch anomalies of small rock soles declined steeply after 1997 but catch anomalies for large rock soles had a less sudden and delayed decline. For Dover Sole (*Microstomus pacificus*) and sanddabs, nearly all the variation in catch anomaly was attributed to large-size individuals; catches of small individuals changed little.

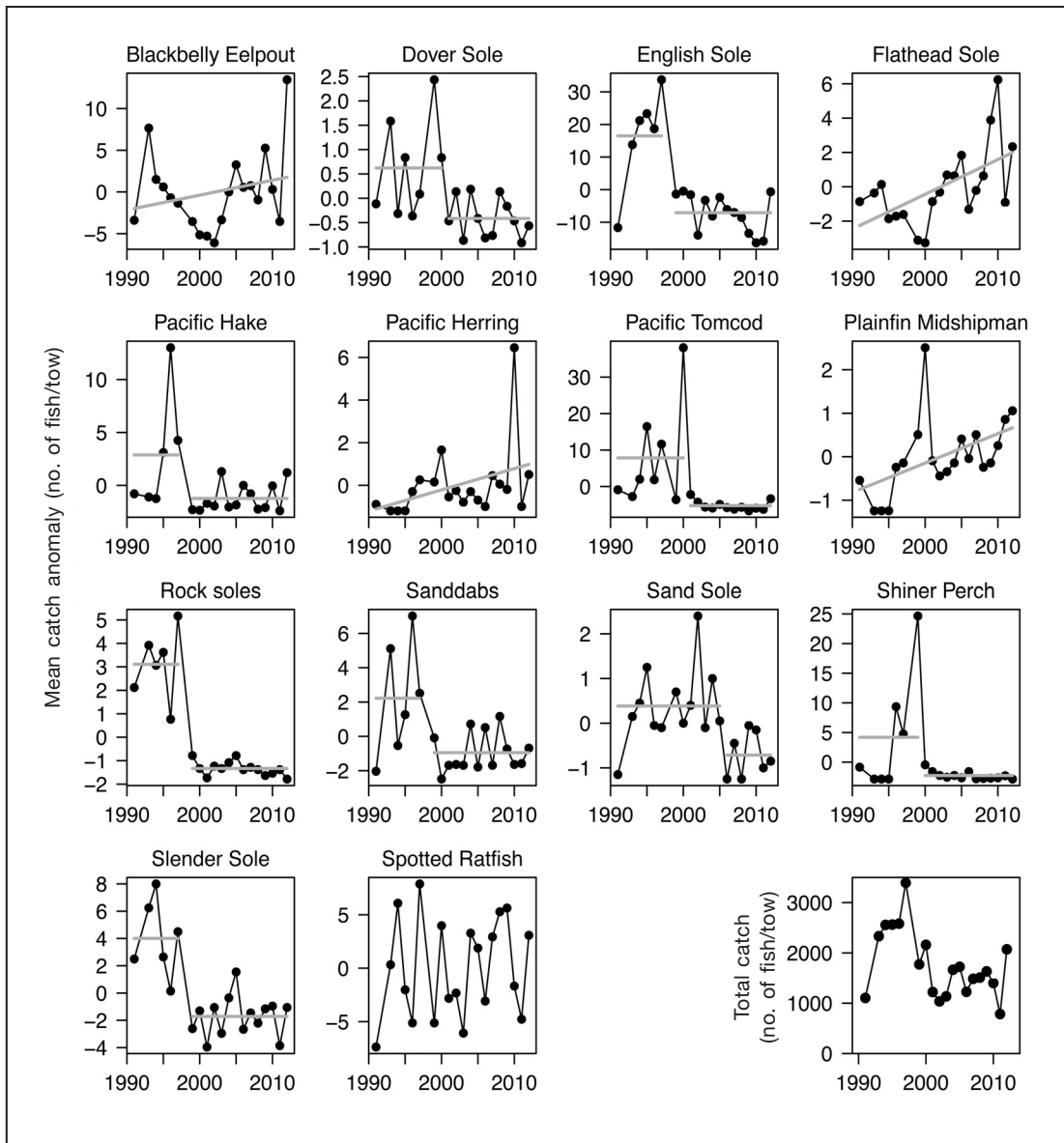


Figure 2

Time series of annual catch anomalies for 14 species or species groups commonly captured during bottom trawl surveys conducted during 1991–2012 in Port Madison, Puget Sound, Washington. Gray lines depict instances where the linear or change-point model provided the best fit to the data. Graph in the bottom right corner depicts total survey catch (unstandardized). Catch anomalies are the yearly averaged differences between each trawl tow and the average catch rate (number of fish) for all tows collected at the same depth and time of day.

Time series of anomalies in sub-mixed-layer temperature and surface salinity were generally consistent with each other between the 2 monitored sites (Fig. 4). The data indicated exceptionally warm years in 1992, 1994, 1998, 2003, and 2004 and cool years in 1993, 1999–2002, and 2008. For each of the 2 sites, temperature time series indicated neither a distinct shift near 1997–1999 nor any other change point or linear trend (Table 3). The time series of surface salinity for the West Point

site was generally more variable than the time series for the Jefferson Head site, yet both time series showed the same years as exceptionally high or low. At both sites, 1992, 2001, 2004, and 2008 were high-salinity years and 1991 and 1997 were low-salinity years. There was no indication of a linear trend or change point in the surface salinity at West Point (Table 3), but the surface salinity at Jefferson Head showed a positive linear trend (change of roughly 0.04 ppt/year).

Table 2

Comparison of 3 models of changes in catch rates of species or species groups commonly collected during bottom trawl surveys conducted from 1991 to at Port Madison, Puget Sound, Washington. Akaike's information criteria adjusted for small sample size (AIC_c) was used to choose between the models compared: constant (no change), linear (change through time), or change point (abrupt change at a single point in time, with no temporal change elsewhere). Values indicate a difference in AIC_c for each species from lowest AIC_c among all species. No result is given for species for which the change-point model estimated a breakpoint in the first 4 or last 4 years of the time series and, therefore, these species could not be considered in change-point model comparisons.

Species	ΔAIC_c		
	Constant	Linear	Change point
Blackbelly Eelpout (<i>Lycodes pacificus</i>)	1.98	0.00	–
Dover Sole (<i>Microstomus pacificus</i>)	31.07	12.95	0.00
English Sole (<i>Parophrys vetulus</i>)	65.77	26.91	0.00
Flathead Sole (<i>Hippoglossoides elassodon</i>)	28.70	0.00	–
Pacific Hake (<i>Merluccius productus</i>)	21.37	16.74	0.00
Pacific Herring (<i>Clupea pallasii</i>)	9.62	0.00	–
Pacific Tomcod (<i>Microgadus proximus</i>)	30.74	19.15	0.00
Plainfin Midshipman (<i>Porichthys notatus</i>)	19.94	0.00	–
Rock soles (<i>Lepidopsetta bilineata</i> and <i>L. polyxystra</i>)	154.96	82.95	0.00
Sanddabs (<i>Citharichthys sordidus</i> and <i>C. stigmaeus</i>)	30.06	18.88	0.00
Sand Sole (<i>Psettichthys melanostictus</i>)	28.72	23.23	0.00
Shiner Perch (<i>Cymatogaster aggregata</i>)	15.22	11.95	0.00
Slender Sole (<i>Lyopsetta exilis</i>)	82.67	38.21	0.00
Spotted Ratfish (<i>Hydrolagus colliei</i>)	0.00	0.23	–

Discussion

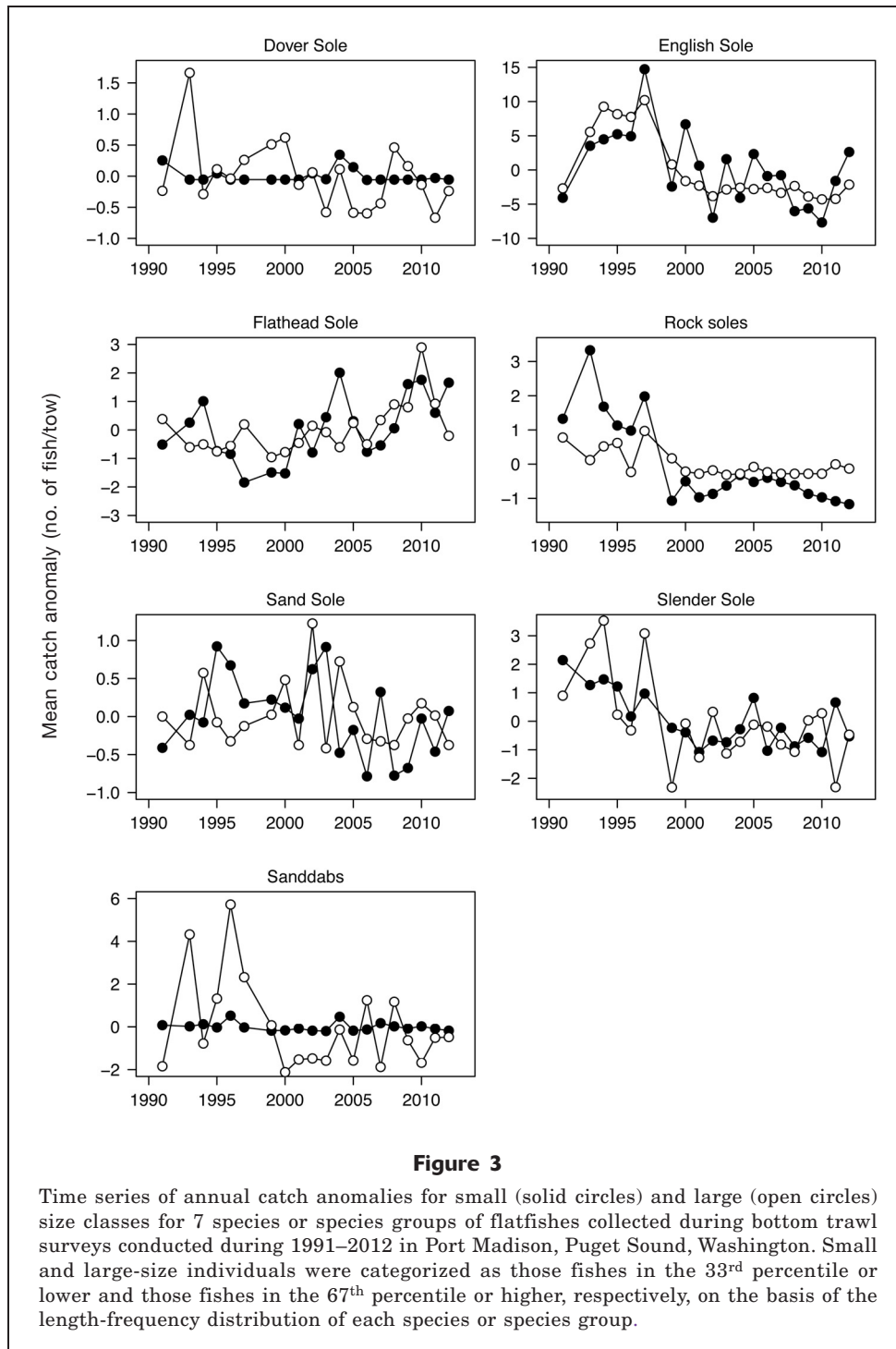
We hypothesized that the data from Port Madison would reveal trends of increasing abundance in resident groundfish populations in Puget Sound after the cessation of commercial bottom trawling and, thereby, would indicate rates and magnitudes of recovery. Before the ban on commercial trawling in the central basin of Puget Sound, commercial catches ranged from 224 metric tons (t)/year to more than 500 t/year and, therefore, likely represented a significant source of mortality for many targeted species.⁶ Commercial fish catches through other methods (set nets, purse seines, or set lines) also have been reduced sharply.⁵ However, most species exhibited nonlinear patterns of abundance characterized by abrupt and sustained changes in relative abundance indices during the 21-year time period that the survey spanned. These abrupt abundance shifts were notable because they were most commonly in the opposite direction from our expectation and appeared to be synchronous among different common groundfish species. Moreover, these shifts did not appear to be related to demographic changes indicative of recruitment shifts, and they were not linked to temporal patterns in local water temperature and salinity.

Currently, no recruitment time series are available for demersal fishes in Puget Sound.

There are several possible explanations for the synchronous reduction in catch rates of groundfish species that occurred in the late 1990s to early 2000s. The first is loss or impairment of habitat that resulted in emigration out of the survey area. Most of these groundfish species reside on soft-bottom habitats (sand or mud) and do not rely on biogenic habitats, such as eelgrass beds, that are particularly vulnerable. However, Nichols (2003) reported an increase in abundance of common prey items of English Sole in Port Madison and in nearby areas from the early 1960s to the early 1990s. It is possible that this trend reversed after this time period, although direct data are needed to evaluate this hypothesis. Alternatively, trawling itself may have altered physical habitat and benthic infaunal communities (Auster et al., 1996); cessation of this activity may have promoted a community of less-preferred prey for these fish predators. Little information, however, is available on bottom habitat or infaunal community dynamics to test any of these hypotheses.

Alternatively, the second explanation is that changes in catch rates in Port Madison may reflect expansions and contraction of population ranges, possibly as a consequence of changes in population densities (MacCall, 1990). However, the sharp decreases in abundance that we witnessed suggest a decline in densities throughout Puget Sound and a contraction to other habitats. This implication is not supported by data from bottom trawl

⁶ Schmitt, C. S., S. Quinnell, M. Rickey, and M. Stanley. 1991. Groundfish statistics from commercial fisheries in Puget Sound, 1970–1988. Progress Report No. 285, 315 p. Washington Department of Fisheries, Olympia, WA.

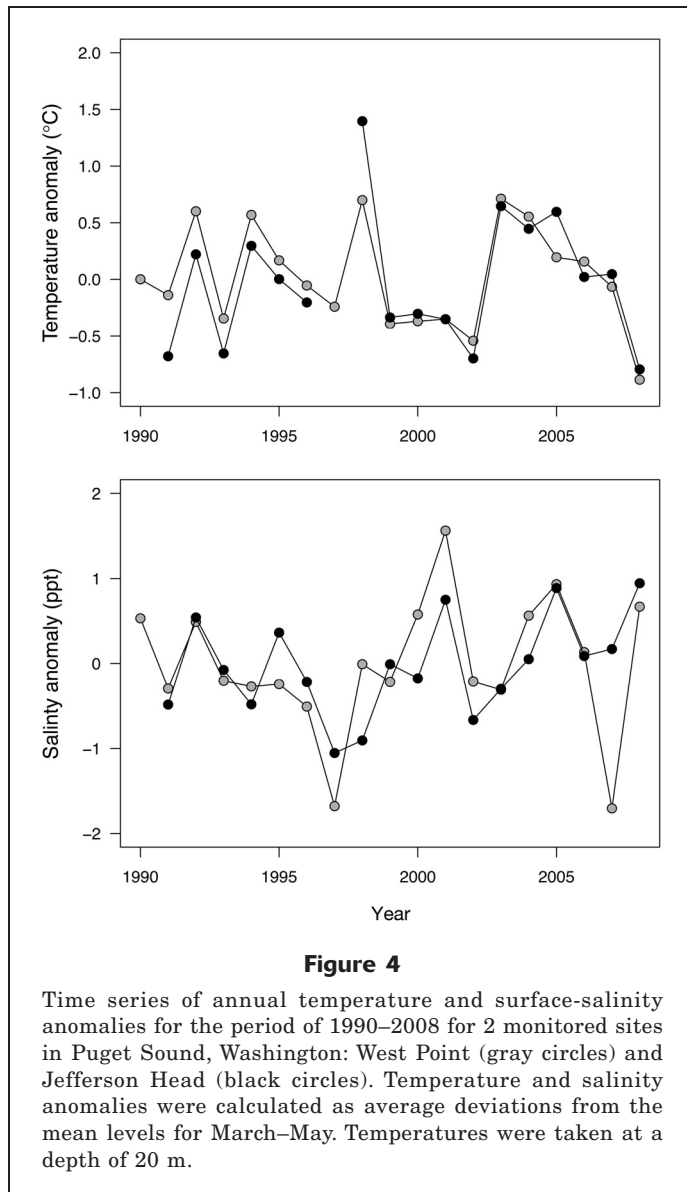


surveys that cover a wider area and that generally indicate greater groundfish densities through the 1990s.⁷

Third, decreases in catch rates could be explained by changes in predator abundance in this region that may

⁷ Palsson, W. 2010. Personal commun. NOAA Fisheries, Alaska Fisheries Science Center, Seattle, WA. 98115.

impose increased mortality or result in distributional shifts of prey species (Heithaus et al., 2008). Demersal fish species in Puget Sound are consumed by elasmobranchs, such as Spiny Dogfish (*Squalus acanthias*) and Bluntnose Sixgill Shark (*Hexanchus griseus*), and marine mammals, such as the harbor seal (*Phoca vitulina*; Bromaghin et al., 2013; Howard et al., 2013) and



California sea lion (*Zalophus californianus*), but we are unaware of any abrupt changes in predator densities in Port Madison to explain these patterns. Jeffries et al. (2003) reported a monotonic increase in harbor seal abundance in Puget Sound from the late 1970s to the 1980s that was followed by little change in abundance during the mid- to late 1990s.

Fourth, groundfish densities can be sensitive to water quality, especially to oxygen concentrations at the seafloor that result in distributional shifts to normoxic conditions (Breitburg et al., 2009; Essington and Paulsen, 2010), and chronic hypoxia exposure could diminish productivity of groundfish prey (Diaz and Rosenberg, 1995). There is no consistent sampling for dissolved oxygen in Port Madison to evaluate this hypothesis, but the exposure of this area to strong tidal

currents and subsequent high mixing likely mean that this area is not particularly prone to low dissolved oxygen (Nichols, 2003). Moore et al. (2008) did not detect a change in water temperatures throughout Puget Sound from 1993 to 2002; therefore, changes are unlikely a result of a shift in temperature on a scale larger than Puget Sound.

Several important limitations of our data warrant specific discussion. First, our bottom trawl sampling—although highly standardized in time, space, and method—may not be representative of the entire Puget Sound. Indeed, one of our main conclusions is that shifts in densities of demersal fish species more likely were indicative of distributional shifts than of population shifts. Also, the opening of the bottom trawl was small and, therefore, likely had low selectivity for large-size groundfishes (e.g., >50 cm). Additionally, because sampling was restricted to a standardized and limited time of year, the data cannot account for seasonal changes (Reum and Essington, 2011) and may not reflect trends apparent in different seasons.

Our environmental data were collected from monitoring sites near the study area for bottom trawl surveys, and bottom temperature was not always recorded. We used sub-mixed-layer temperature as a proxy for bottom temperature, which appeared to be robust for years in which bottom data were available. Bottom water temperature may deviate from temperature of the shallower sub-mixed layer because of water exchange between Admiralty Inlet, the Strait of Juan de Fuca, and the coastal Pacific Ocean. However, because deepwater dynamics reach equilibrium over time scales of months, they reflect local, seasonal environmental conditions (e.g., air temperature, freshwater runoff) (Ebbesmeyer and Barnes, 1980) and, therefore, are useful for interannual comparisons. Despite these limitations, this study presents the first long-term standardized assessment of the groundfish community in Puget Sound and, therefore, can provide a baseline for expanded sampling efforts.

A large body of research on estuarine fishes focuses on the roles of estuaries as nursery habitats, the value of protecting specific critical habitats, and descriptions of patterns of juvenile survival and growth. Estuaries are often viewed as critical habitats that support coastal fish populations (Beck et al., 2001), and nearshore habitat features, such as eelgrass beds, are commonly identified as key features of estuarine habitats (Levin and Stunz, 2005). Although loss of eelgrass beds has been identified as a threat in Puget Sound, their importance to the groundfish species examined here is unknown. In well-studied estuarine ecosystems, extensive time series of fish abundance indices have permitted exploration of the roles of density dependence, overwinter survival, predation, and growth-dependent mortality on year-class strength of fishes (Hurst and Conover, 1998; Buckel et al., 1999; Kim-

Table 3

Comparison of 3 models for changes in environmental time series data collected at 2 monitoring sites—West Point and Jefferson Head—in Port Madison, Puget Sound, Washington, near sampling sites at which bottom trawl surveys were conducted from 1991 to 2012. Akaike's information criteria adjusted for small sample size (AIC_c) was used to choose between the models: no change ("constant"), linear change ("linear"); or abrupt change ("change point"). Separate models were run for each monitoring site.

	Constant	Linear	Change point
Temperature			
West Point	0.00	0.62	2.85
Jefferson Head	0.00	2.41	2.85
Surface salinity			
West Point	0.00	2.41	2.85
Jefferson Head	7.89	0.00	10.81

merer et al., 2000; Taylor et al., 2009). The processes that regulate juvenile survivorship and fish population dynamics in Puget Sound are not easily discerned because of a paucity of long-term monitoring data.

Conclusions

Catch rates of resident groundfishes from a study area in Puget Sound indicated that a synchronous and abrupt decline in densities occurred in the late 1990s, counter to expectations formed on the basis of the cessation of commercial bottom trawling that preceded our sampling. Available evidence suggests that these declines may have resulted from a distributional shift rather than a demographic shift, although an analysis of data sets that span a spatial extent wider than our study area in Port Madison is needed to test this hypothesis. Therefore, considerable additional analyses are needed to address the response of species and food webs to fishing and to determine how localized closures, such as marine protected areas, may promote recovery of species. Further, there is a need to relate density shifts to environmental and biological changes (e.g., climatic drivers, human-induced habitat shifts, or trophodynamics). Finally, the unexpected shifts in localized catch rates in this study indicate a need for caution when time series are used in evaluating long-term shifts in population and community structure without consideration of whether the data are representative of entire populations.

Acknowledgments

We thank Charlie Eaton, the owner and operator of the RV *Kittiwake*, for the 2 decades of careful vessel operation and logistic assistance. Sampling took place as

field research for the Fisheries Ecology class at the School of Aquatic and Fishery Sciences, University of Washington (UW), and funding for vessel charter was provided by the teaching program. We thank the numerous teaching assistants and even more numerous students in the class over the years for their help with sorting and measuring fishes. Additional funding for the data analysis was provided by the SeaDoc Society, Lowell Wakefield Endowment, the UW Climate Impacts Group, and the Puget Sound Gatekeepers Alliance. We thank Wayne Palsson and 3 anonymous reviewers for helpful comments on the manuscript. We thank Chantel Wetzel for conducting preliminary analysis.

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Appendix table

Complete list of species or taxonomic groups collected in Port Madison, Puget Sound, Washington during the period of 1991–2001, with total number of specimens collected, length range, and number of years that each was collected. * indicates that the maximum length could not be determined because of ambiguous identification of morphologically similar species. All lengths are fork length, except for Spotted Ratfish (precaudal length was measured for this species).

Species	Total number	Min. length (mm)	Max. length (mm)	Number of years
English Sole (<i>Parophrys vetulus</i>)	10,427	11	470	20
Spotted Ratfish (<i>Hydrolagus colliei</i>)	4067	80	550	20
Blackbelly Eelpout (<i>Lycodes pacificus</i>)	3398	33	997	20
Pacific Tomcod (<i>Microgadus proximus</i>)	2677	16	480	20
Slender Sole (<i>Lyopsetta exilis</i>)	2242	20	340	20
Flathead Sole (<i>Hippoglossoides elassodon</i>)	1665	60	342	20
Shiner Perch (<i>Cymatogaster aggregata</i>)	1139	10	*	16
Pacific Hake (<i>Merluccius productus</i>)	958	69	565	19
Speckled Sanddab (<i>Citharichthys stigmaeus</i>)	853	55	340	19
Rock soles (<i>Lepidopsetta bilineata</i> and <i>L. polyxystra</i>)	773	74	415	20
Sand Sole (<i>Psettichthys melanostictus</i>)	680	76	450	20
Plainfin Midshipman (<i>Porichthys notatus</i>)	497	58	326	17
Pacific Herring (<i>Clupea pallasii</i>)	478	75	320	17
Dover Sole (<i>Microstomus pacificus</i>)	366	45	381	19
Pacific Sanddab (<i>Citharichthys sordidus</i>)	222	48	352	18
Walleye Pollock (<i>Theragra chalcogramma</i>)	174	22	490	8
Pile Perch (<i>Rhacochilus vacca</i>)	170	95	211	12
Rex Sole (<i>Glyptocephalus zachirus</i>)	142	50	250	16
Snake Prickleback (<i>Lumpenus sagitta</i>)	99	50	395	16
Roughback Sculpin (<i>Chitonotus pugetensis</i>)	89	50	145	14
Shortfin Eelpout (<i>Lycodes brevipes</i>)	86	29	80	10
Pacific Staghorn Sculpin (<i>Leptocottus armatus</i>)	60	73	258	15
Tubesnout (<i>Aulorhynchus flavidus</i>)	33	64	165	11

Appendix table (cont.)

Complete list of species or taxonomic groups collected in Port Madison, Puget Sound, Washington during the period of 1991–2001, with total number of specimens collected, length range, and number of years that each was collected. * indicates that the maximum length could not be determined because of ambiguous identification of morphologically similar species. All lengths are fork length, except for Spotted Ratfish (precaudal length was measured for this species).

Species	Total number	Min. length (mm)	Max. length (mm)	Number of years
Brown Rockfish (<i>Sebastes auriculatus</i>)	33	65	325	12
C-O Sole (<i>Pleuronichthys coenosus</i>)	29	110	305	10
Slim Sculpin (<i>Radulinus asprellus</i>)	22	80	160	9
Starry Flounder (<i>Platichthys stellatus</i>)	19	110	410	12
Northern Anchovy (<i>Engraulis mordax</i>)	19	73	190	8
North Pacific Spiny Dogfish (<i>Squalus suckleyi</i>)	12	290	460	3
Bay Goby (<i>Lepidogobius lepidus</i>)	9	59	100	7
Sturgeon Poacher (<i>Podothecus accipenserinus</i>)	8	75	166	5
Longnose Skate (<i>Raja rhina</i>)	8	365	640	7
Copper Rockfish (<i>Sebastes caurinus</i>)	8	56	300	2
Sablefish (<i>Anoplopoma fimbria</i>)	6	320	400	1
Northern Spearnose Poacher (<i>Agonopsis vulsa</i>)	6	87	174	4
Eulachon (<i>Thaleichthys pacificus</i>)	6	89	150	4
Big Skate (<i>Raja binoculata</i>)	6	125	1050	3
Soft Sculpin (<i>Psychrolutes sigalutes</i>)	5	25	45	3
Snailfishes (family Liparidae)	6	24	35	5
Chinook Salmon (<i>Oncorhynchus tshawytscha</i>)	5	78	96	2
Blacktip Poacher (<i>Xeneretmus latifrons</i>)	5	140	184	1
Pacific Sand Lance (<i>Ammodytes hexapterus</i>)	4	59	145	2
Butter Sole (<i>Isopsetta isolepis</i>)	4	75	258	3
Sailfin Sculpin (<i>Nautichthys oculoasciatus</i>)	3	120	121	3
Quillback Rockfish (<i>Sebastes maliger</i>)	3	82	230	3
Curlfin Sole (<i>Pleuronichthys decurrens</i>)	3	161	260	2
Red Brotula (<i>Brosmophycis marginata</i>)	3	220	305	1
Bigfin Eelpout (<i>Lycodes cortezianus</i>)	3	260	280	1
Surf Smelt (<i>Hypomesus pretiosus</i>)	2	86	125	2
Pacific Pompano (<i>Peprilus simillimus</i>)	2	110	149	2
Pacific Cod (<i>Gadus macrocephalus</i>)	2	420	610	2
Great Sculpin (<i>Myoxocephalus polyacanthocephalus</i>)	2	220	395	2
Tadpole Sculpin (<i>Psychrolutes paradoxus</i>)	1	30	30	1
Pygmy Poacher (<i>Odontopyxis trispinosa</i>)	1	161	161	1
Pink Salmon (<i>Oncorhynchus gorbuscha</i>)	1	66	66	1
Padded Sculpin (<i>Artedius fenestralis</i>)	1	125	125	1
Northern Ronquil (<i>Ronquilus jordani</i>)	1	165	165	1
Longspine Combfish (<i>Zaniolepis latipinnis</i>)	1	230	230	1
Cabezon (<i>Scorpaenichthys marmoratus</i>)	1	410	410	1
Brown Irish Lord (<i>Hemilepidotus spinosus</i>)	1	90	90	1
American Shad (<i>Alosa sapidissima</i>)	1	274	274	1