

**Abstract**—In response to declining biomass of Northeast Pacific groundfish in the late 1990s and to improve the scientific basis for management of the fishery, the Northwest Fisheries Science Center standardized and enhanced their annual bottom trawl survey in 2003. The survey was expanded to include the entire area along the U.S. west coast at depths of 55–1280 m. Coast-wide biomass and species richness significantly decreased during the first eight years (2003–10) of this fishery-independent survey. We observed an overall tendency toward declining biomass for 62 dominant taxa combined (fishery target and nontarget species) and four of seven subgroups (including cartilaginous fish, flatfishes, shelf rockfishes, and other shelf species), despite increasing or variable biomass trends in individual species. These decreases occurred during a period of reduced catch for groundfish along the shelf and upper slope regions relative to historical rates. We used information from multiple stock assessments to aggregate species into three groups: 1) with strong recruitment, 2) without strong recruitment in 1999, and 3) with unknown recruitment level. For each group, we evaluated whether declining biomass was primarily related to depletion (using year as a proxy) or environmental factors (i.e., variation in the Pacific Decadal Oscillation). According to Akaike's information criterion, changes in aggregate biomass for species with strong recruitment were more closely related to year, whereas those with no strong recruitment were more closely related to climate. The significant decline in biomass for species without strong recruitment confirms that factors other than depletion of the exceptional 1999 year class may be responsible for the observed decrease in biomass along the U.S. west coast.

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## Variations in eastern North Pacific demersal fish biomass based on the U.S. west coast groundfish bottom trawl survey (2003–2010)

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Over the past 20 years, a number of changes have occurred in the Northeast Pacific groundfish fishery with low abundance observed for multiple species (Field and Fox, 2006; Levins et al., 2006). Historically catch and annual exploitation rates increased from the 1950s through the 1980s and then declined rapidly. Between 1999 and 2002, nine important fish stocks in the eastern North Pacific off the U.S. west coast were declared overfished, at which time the Pacific Fishery Management Council (PFMC) introduced a series of regulatory measures to reduce fishing pressure. Management actions included reducing total allowable catch and fleet size, and closure of large areas of the upper continental shelf to fishing (PFMC, 2008a). In response to management concerns the NOAA Northwest Fisheries Science Center (NWFSC) also expanded and standardized the annual west coast groundfish bottom trawl survey to provide enhanced scientific information for managers. Since 2003, the Northwest Fisheries Science Center (NWFSC) has conducted a comprehensive fishery-independent bottom trawl survey covering the entire coast from the U.S.–Canada to the U.S.–Mexico borders, at depths of 55 to 1280 m (Keller et al., 2008). This groundfish survey follows strict sampling protocols with standardization of vessels, fishing gear,

deployment methods, catch sampling practices, and geographic extent from 2003 onward (Stauffer, 2004).

Here we summarize variations in biomass indices for species collected during the 2003–10 fisheries-independent west coast groundfish bottom trawl survey. We evaluate if an observed decline in biomass of demersal fish (target and nontarget species) from 2003 through 2010 can be attributed primarily to recruitment (i.e., depletion after strong recruitment events for multiple species in the late 1990s) or to climate variability (i.e., poor environmental conditions).

The 2003–10 survey time series covers a period within the California Current system characterized by 1) reduced catch and exploitation of groundfish species relative to historical rates (Worm et al., 2009; Hilborn et al., in press); 2) the population effects of a very strong 1998–99 year class observed for many west coast groundfish species (e.g., Pacific hake [*Merluccius productus*], English sole [*Parophrys vetulus*], <http://www.pcouncil.org/>, accessed June 2011); and 3) a phase shift in the Pacific Decadal Oscillation (PDO), an El Niño-like pattern of Pacific climate variability linked to productivity (Mantua et al., 1997). The PDO is detected as warm or cool surface waters in the western Pacific Ocean, north of 20°N, that shift phases on a scale of about

10 to 30 years. During a “warm” or “positive” phase, part of the eastern Pacific Ocean warms and productivity of waters off the U.S. west coast declines; during a “cool” or “negative” phase, the opposite pattern occurs (Schwing et al., 2009).

The aim of this study was to evaluate the importance of depletion after strong recruitment versus environmental effects on declining biomass observed during groundfish surveys in the western U.S. shelf system. We used data from 24 stock assessments conducted since 2005 (<http://www.pcouncil.org/>, accessed September 2011). With information contained in the assessments we separated 62 dominant species into three groups: those with strong recruitment during the late 1990s–early 2000s, those without a strong recruitment during this period, and those with unknown year-class strength. For each group and the overall biomass indices for all groups we evaluated regression models between demersal fish biomass (2003 through 2010) along the U.S. west coast versus year (as a proxy for gradual depletion after recruitment of exceptional year classes to the fishery) and the PDO index, an ecosystem-level indicator of climate variability. For each comparison, the most appropriate model for describing the relationship with biomass was determined. A similar analysis was undertaken for species richness. We additionally present information on frequency of occurrence (number of positive hauls) and depth distribution by species.

## Materials and methods

### Survey design and methods

The NWFSC conducted annual bottom trawl surveys of groundfish resources off the U.S. West Coast using standardized procedures from 2003 through 2010 (Keller et al., 2008). Surveys occurred May through October from the area off Cape Flattery, Washington (lat. 48°10'N), to the U.S.–Mexico border (lat. 32°30'N) at depths of 55–1280 m (Fig. 1). The entire geographic extent of the survey was covered twice each year by two west coast commercial fishing vessels (20 to 28 m in length) per pass. Each year sampling extended from late May through late July for the first period and mid-August through late October for the second. A stratified random sampling design was used, in which the surveyed region was subdivided into ~13,000 cells of equal area (1.5 nmi longitude by 2.0 nmi latitude) (Fig. 1). An average of 700 primary cells was randomly selected each year, stratified by geographic location and depth. The geographic allocation was based on a simple north–south division at 34°30'N lat. (Point Conception, California) with 80% of the effort in the northern portion of the survey and 20% in the southern range. The survey area was further stratified into depth zones as follows: north of Point Conception, 40% of the cells were in the shallow depth zone (55–183 m), 30% at mid-depths (184–549 m), and 30% in the deep stratum (550–1280 m); and south of Point Conception, 25% were in the shallow depth zone,

45% at mid-depth, and 30% in the deep stratum. Four chartered west coast fishing vessels were assigned an equal portion of stations to sample per year except in 2004 when only three vessels were used.

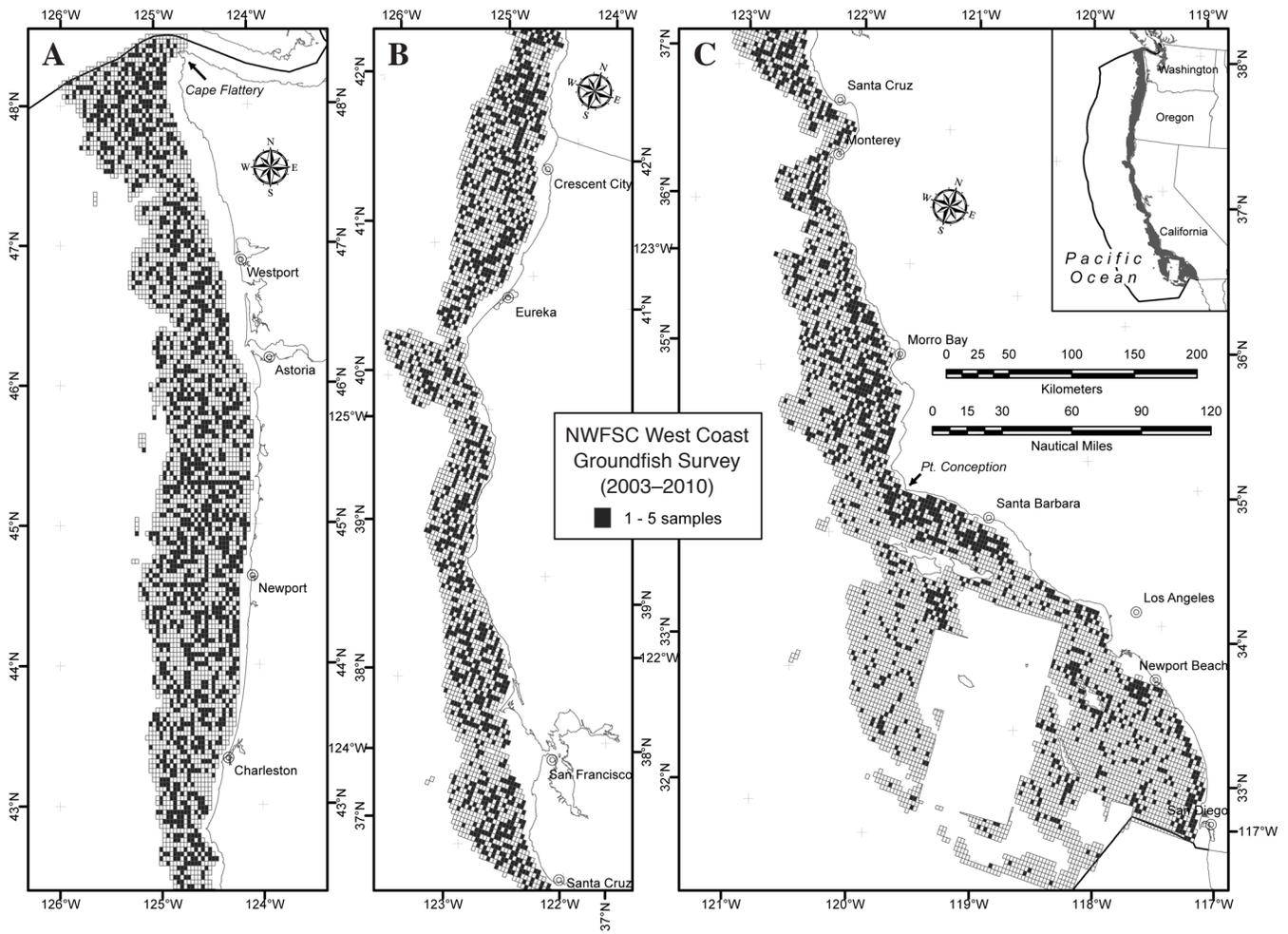
Vessels were equipped with customized Aberdeen-style nets with a small mesh (3.8 cm stretched measure) liner in the codend, a 25.9-m headrope, and a 31.7-m foot rope. All fishing operations were conducted in strict compliance with national and regional protocols detailed in Stauffer (2004). Simrad Integrated Trawl Instrumentation (ITI, Kongsberg Simrad Mesotech Ltd., Port Coquitlam, B.C., Canada<sup>1</sup>) was used to monitor and record net performance and position for each haul. A differential global positioning system (DGPS) navigation unit (Northstar 500, Northstar Technologies, Acton, MA) was used to monitor towing speed during each haul. Standard survey haul positions were estimated from DGPS data—generally the mid-point between the net touchdown and net liftoff positions. Average net speed over ground and distance fished were calculated from the position data for the trawl and actual bottom time (Keller et al., 2008).

Samples were collected by trawling within the randomly selected cells (Fig. 1) for a target fishing time of 15 minutes at a target speed of 1.13 m sec<sup>-1</sup> (2.2 knots). All fish and invertebrates were sorted to species (or the lowest possible taxon), and then weighed by using an electronic, motion-compensated scale (Marel, Reykjavik, Iceland). Abundance was not analyzed in this study because not all individuals were counted. Total abundance is estimated from biomass and the two cannot be considered independent without analysis of the variability of mean weights. That analysis is beyond the scope of the present study. Near bottom temperature (°C) and depth (m) were measured during each trawl with an SBE 39 temperature and pressure recorder (Sea-Bird Electronics, Inc., Bellevue, WA) attached to the head rope. Mean tow depths were computed as the average of all depth recordings from the center 80% of the trawl duration (net touch down to lift off). Only tows judged to be acceptable (based on postcollection analysis of bottom contact, net performance, and other metrics; Stauffer, 2004) were included in the data analyses.

### Analyses of catch

To limit this analysis to the most reliably sampled species, we initially examined catch for 310 individual fish species summed over the 2003–10 period. When graphed by species in order of descending catch, no obvious break was apparent and therefore we included all demersal species with an overall catch greater than 450 kg. This break point included the 62 most abundant species in the survey and incorporated 45 of the demersal groundfish species present in the Pacific Fishery Management Council Pacific Coast groundfish

<sup>1</sup> Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.



**Figure 1**

Geographical extent of the Northwest Fisheries Science Center's West Coast Groundfish Bottom Trawl Survey and the location of stations (shaded) trawled one to five times from 2003 through 2010. (A) Stations off Washington and Oregon. (B) Stations off northern California. (C) Southern California stations. The Cowcod (*Sebastes levis*) Conservation Area in Southern California was excluded from the experimental design because it is closed to fishing for groundfish species.

fishery management plan (PFMC, 2008b), as well as two important benthic invertebrates and 15 non-fished species. The break point also represented a greater than 10% difference in catch relative to the next most abundant species. Species-specific catch per unit of effort (CPUE,  $\text{kg ha}^{-1}$ ) was calculated for each tow on the basis of area swept. Area swept was computed from the mean net width for each tow multiplied by the distance fished. Mean CPUE was calculated for each stratum (depth and geographic region, including those with zero catch), by species. Species-specific biomass indices ( $\bar{b}$ , in metric tons [t]) were computed by multiplying the mean CPUE by the appropriate stratum area and then summing the strata biomasses. The estimate of the variance of the biomass was the sum of the variances of the strata involved:

$$\text{Var}(\bar{b}) = \sum_{i=1}^n \left( \text{Var}(\overline{\text{CPUE}}_i) \times A_i^2 \right),$$

with  $n$  equal to the number of strata, and  $A$  equal to the area of each stratum ( $\text{km}^2$ ). Standard errors (SE) for the annual species-specific biomass indices were calculated using standard statistical techniques (Cochran, 1977).

To examine variation in biomass over time, species groups were initially designated on the basis of either taxonomy or depth (e.g., shelf and slope rockfishes). Subsequently we examined relationships between biomass and both year and the PDO index using groups designated by the presence, absence, or unknown occurrence of a strong recruitment during the mid to late 1990s and early 2000s. In all cases biomass was summed over the appropriate group and variance was calculated as previously described. For those species included in the 2003–10 biomass analyses, we also calculated mean depth (m) by averaging station values weighted by catch for each species in each year (Hsieh et al., 2008).

## Recruitment versus PDO indices

Stock assessments for 24 of the 62 species in the analyses have been published by the PFMC since 2005 (available at <http://www.pcouncil.org/groundfish/stock-assessments/safe-documents/2011-safe-document/>, accessed September 2011) and provide information on the number of recruits by year. We examined stock assessments for each species to determine whether strong recruitment events occurred during the period from the mid to late 1990s through 2002. Annual recruitment strength is generally modeled in the assessments as random deviations about a stock-recruitment (S-R) relationship. These deviations and the central tendency of the S-R curve are informed by all other sources of available information (i.e., observed lengths, weights, age, and trend information from fishery-dependent and independent sources) and will reflect predation intensity, climate, and other influences (Methot, 2011). For this analysis, we defined strong recruitment as 1.7–5 times greater than the average recruitment during the 10 to 14 years before the most recent assessment.

We subsequently subdivided the 62 species included in our study into three groups: those with strong recruitment during the late 1990s, those without strong recruitment during this period, and those with unknown recruitment levels. We summed the biomass indices for all species within each group and the overall biomass indices for all three groups and regressed these summed values versus year. We reasoned that declining biomass indices would be more tightly tied to time for those species with elevated recruitment as the resulting exceptionally strong cohorts declined due to natural and fishing-induced mortality in the early 2000s.

Biomass indices for the aggregated subgroups and overall were also compared with the PDO, a widely used index of climate variability for the California Current system. The PDO is an index based on patterns of variation in sea surface temperature of the North Pacific from 1900 to the present (Mantua et al., 1997; Schwing et al., 2009). Although derived from sea surface temperature data, the PDO index is well correlated with other environment factors, including sea level pressure, winter air temperature, wind shear, and precipitation, as well as other Pacific climate indices (ENSO [El Niño-Southern Oscillation] and MEI [multivariate ENSO index]). For comparison with the annual survey data, monthly PDO values were averaged annually (November to October) to include the survey period each year (Mantua<sup>2</sup>).

## Species richness

Coast-wide estimates of species richness were calculated as area-weighted mean number of fish species taken per trawl sample. Estimates were stratified by survey year (2003–10), depth (55–183 m, 184–549 m,

and 550–1280 m), and geographic region (one degree latitudinal increments from 32° to 49°N) for all fish species. Estimates were built upon the number of distinct fish species reported for each trawl sample. Mean species counts were determined for each stratum and weighted by the proportion of stratum area within the total area. Annual species richness estimates were computed as the sum of these area-weighted species counts within the area of interest (per depth range or coast-wide) and survey year. Species richness variance within each area was similarly estimated as the sum of stratum variances weighted by their associated squared proportion of stratum area within the total area. Standard errors of the mean were computed as the square root of the ratio of the variance estimate to the stratum count for each area (i.e., within a specific depth stratum or coast-wide). We compared species richness over time by regressing against year and also evaluated the relationship between species richness and the annual Pacific Decadal Oscillation (PDO) index. In both cases, regression analyses by depth strata and overall depth were undertaken

## Statistical analyses

For the biomass data we examined individual species, and present for comparison several aggregate groups formed by summing species coast-wide biomass indices (metric tons, t). For each species, regression analysis was used to initially investigate the relationship between annual biomass indices and year. To account for the large number of tests conducted, a sequential Bonferroni correction with a significance level of 0.05 was applied to the data (Peres-Neto, 1999). Grouping data for later analyses (initially by depth or taxonomic group to examine trends over time for aggregated data and subsequently by the presence, absence, or unknown occurrence of exceptionally large year classes after recruitment) resulted in fewer tests and no Bonferroni correction was applied. Results for biomass and species richness were statistically compared with year and the PDO index by linear and multiple regression (GLM) by using SAS for Windows (SAS Institute, Inc., Cary, North Carolina). To stabilize the variance, the natural logarithm of the response variable was used in the regression models; however, even after the transformation, annual variance estimates were highly variable for some species. Regressions weighted by the variance estimate of the annual values were therefore used to examine interactions between annual biomass indices and species richness versus year, PDO values, or both (Draper and Smith, 1981).

The Akaike information criterion (AIC) was used to choose between competing models (i.e., recruitment, environmental variability or both) when comparing biomass values, summed by groups, versus year and the PDO index (Sakamoto et al., 1986). For each group, the best model was selected on the basis of the smallest AIC value ( $AIC_{min}$ ). A similar comparison was done between species richness versus year, the PDO index, and both year and the PDO index. To determine whether a model

<sup>2</sup> Mantua, N. 2010. Personal commun. Dep. Atmospheric Sciences, Univ. Washington, Seattle, WA 98195.

other than the best model was plausible, the difference in AIC values for each model was calculated as

$$\Delta_i = AIC_i - AIC_{min.}$$

Models with  $\Delta_i < 2$  are considered equivalent to the best model ( $AIC_{min}$ ) and candidate models with  $\Delta_i > 10$  are highly unlikely to be plausible alternatives for the best model. Candidate models with  $\Delta_i$  between 3 and 7 have less support than the best model (Burnham and Anderson, 2002).

## Results

### Biomass

Between 2003 and 2010, 5271 trawls were successfully conducted as part of the groundfish survey with an annual average of 659 trawls  $\text{yr}^{-1}$  (range: 505 to 722 trawls; Fig. 1). Although an average of 265 individual fish taxa were identified each year (range: 252–310), the 60 demersal fishes and two benthic invertebrates included in this analysis comprised greater than 99% of the total catch. Annual biomass indices (t) for the 62 individual species revealed variable trends over time (2003–10) (Figs. 2 and 3). Six species exhibited significant ( $P < 0.001$ ) increases in biomass indices over time (Fig. 2A), 20 species displayed significant ( $P < 0.05$ ) or near significant ( $P < 0.10$ ) negative trends (Fig. 3, California skate [*Raja inornata*] and pygmy rockfish [*Sebastes wilsoni*] not shown), and 36 species exhibited nonsignificant trends over time. Representative examples for species with no significant trends are shown for the most abundant species within each group (Fig. 2B). Regardless of trends, both target and nontarget species occurred in each group.

Mean, minimum, and maximum depth (m), and total numbers of positive hauls over the eight year study are shown for the 62 individual species included in the analyses (Table 1). Catch for these 62 species was initially partitioned into seven groups based on taxonomy and depth (in order of decreasing biomass): flatfish (30%), other shallow to mid-depth species (20%), shelf rockfish (15%), sharks, skates, and ratfish (13%), other deep water species (9%), thornyheads (8%), and slope rockfish (5%), to examine trends over time. The weighted mean depths for shallow to mid-depth species was <500 m, and the weighted average for deep water species was >650 m. Shelf rockfish occurred at average depths ranging from 101 to 209 m, whereas slope rockfish were somewhat deeper (226–456 m). In general, rockfish were encountered in fewer hauls than other subgroups.

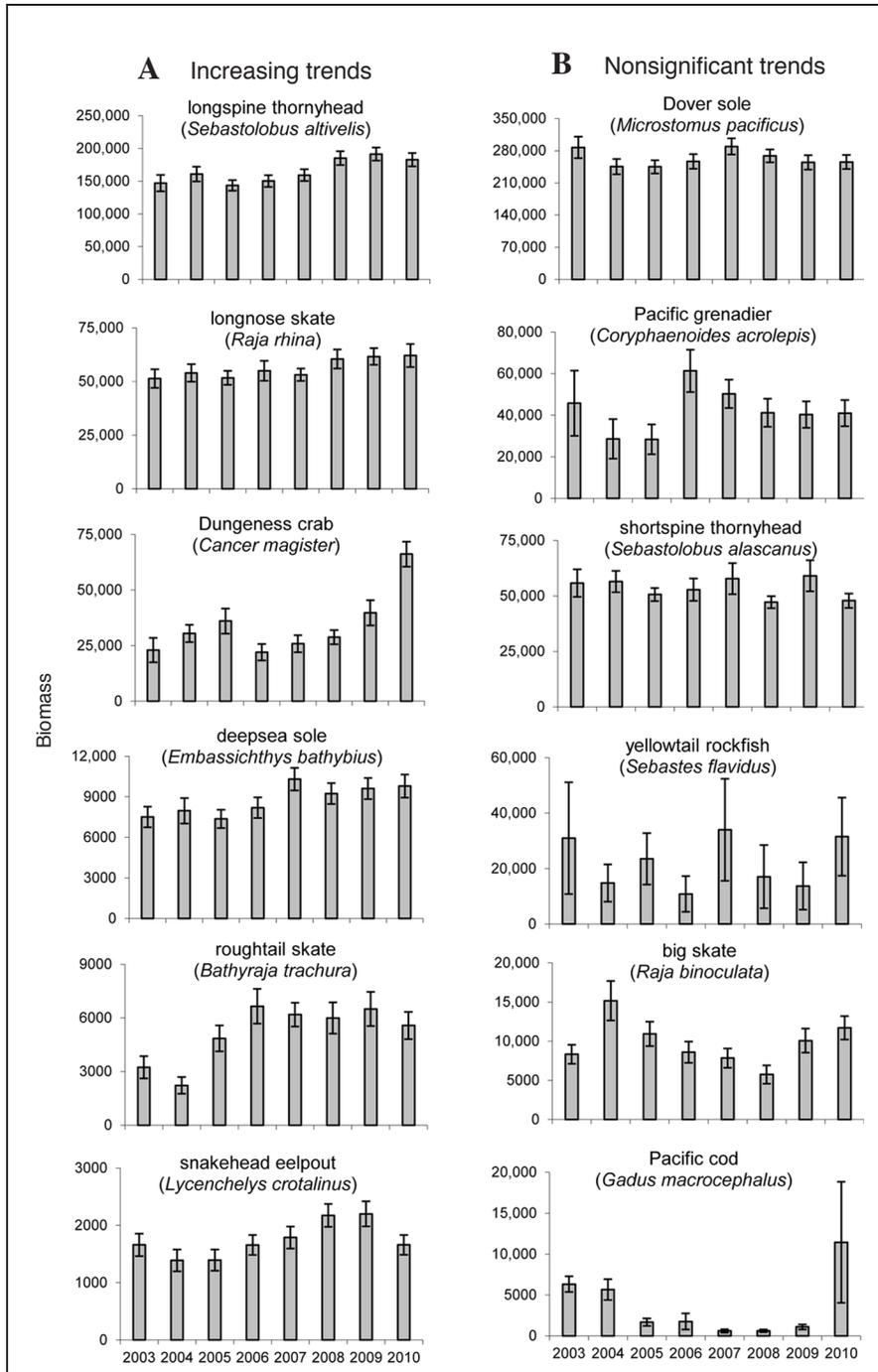
Despite variations in biomass indices at the species level, four of the seven groups initially examined here (with the exception of slope rockfish, thornyheads, and other deep water species) and overall biomass indices decreased significantly ( $P < 0.05$ ) over time (Fig. 4). Overall aggregate coastwide biomass indices for all 62

species decreased approximately 60% from 2,308,207 t in 2003 to 1,384,391 t in 2010. However the lowest biomass (1,373,473 t) was recorded in 2008 (the year of the lowest PDO and also possibly a good recruitment year) followed by slight increases in 2009 and 2010.

### Recruitment versus PDO indices

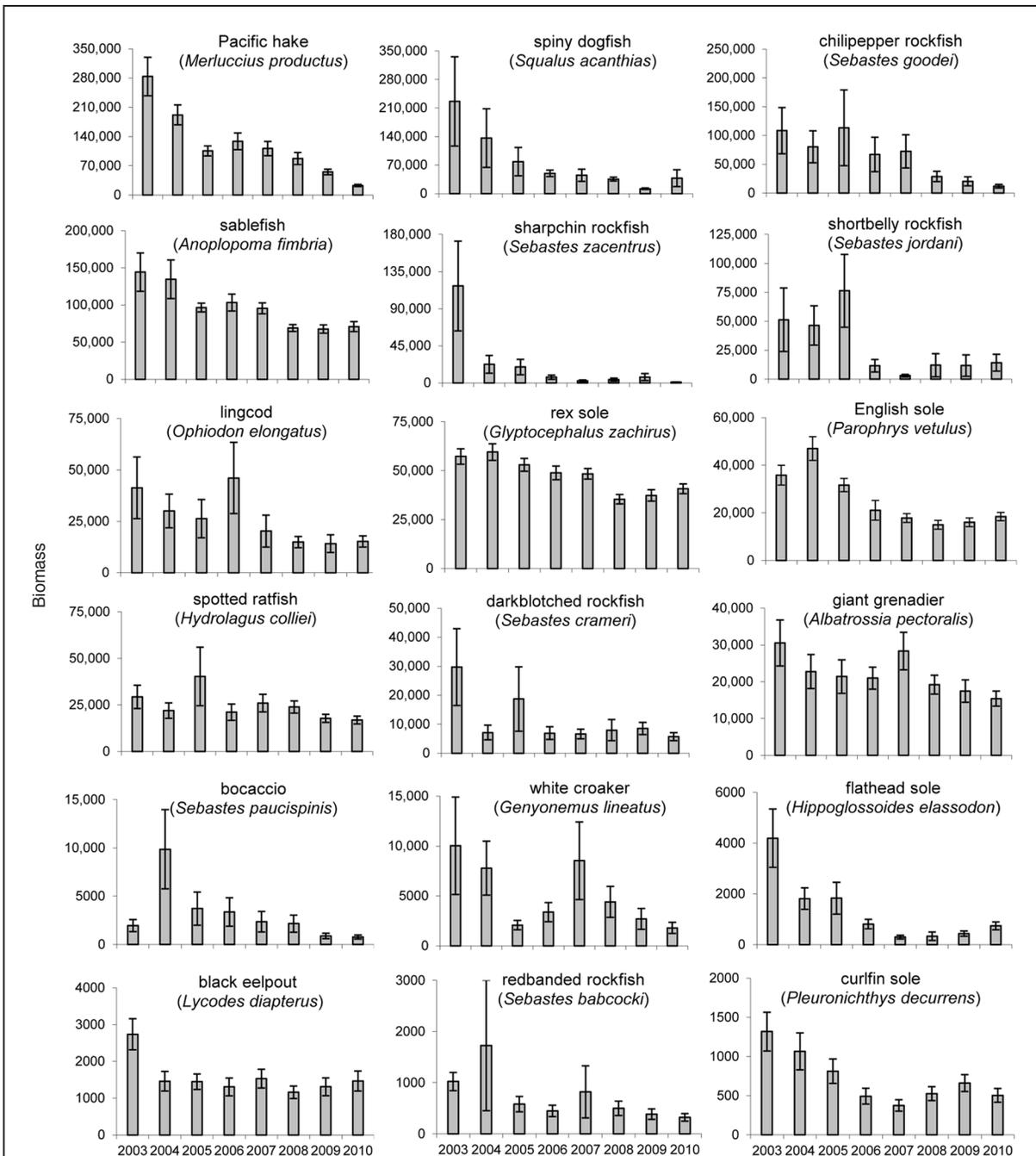
Our initial analyses based on biomass indices for species grouped taxonomically or by depth indicated that deepwater species, such as thornyheads and slope rockfish, did not significantly decrease over time (Fig. 4). However because some species within these groups either decreased significantly or displayed decreasing trends (Figs. 2 and 3), we included all 62 species when we separated demersal catch into categories based on recruitment. Our examination of 24 stock assessment models revealed that 13 species had large recruitment events occurring primarily in 1999 (arrowtooth flounder [*Atheresthes stomias*], English sole, Pacific hake, sablefish [*Anoplopoma fimbria*], bocaccio [*Sebastes paucispinis*], chilipepper rockfish [*Sebastes goodie*], splitnose rockfish [*Sebastes diploproa*], but occasionally somewhat earlier (petrale sole [*Eopsetta jordani*], longspine thornyhead [*Sebastes altivelis*]), or later (Dover sole [*Microstomus pacificus*], greenstriped rockfish [*Sebastes elongates*], darkblotched rockfish [*Sebastes crameri*], Pacific ocean perch [*Sebastes alutus*]). Eleven additional species assessed since 2005 did not display significantly larger individual recruitment levels during the period examined (spiny dogfish [*Squalus acanthias*], longnose skate [*Raja rhina*], lingcod [*Ophiodon elongatus*], blackgill rockfish [*Sebastes melanostomus*], canary rockfish [*Sebastes pinniger*], greenspotted rockfish [*Sebastes chlorostictus*], shortbelly rockfish [*Sebastes jordani*], widow rockfish [*Sebastes entomelas*] yelloweye rockfish [*Sebastes ruberrimus*], yellowtail rockfish [*Sebastes flavidus*], shortspine thornyheads [*Sebastes alascanus*]). Stock assessments have not yet been conducted on the remaining 38 species included in our analyses.

During the 1999–2010 period, when depletion of a strong year class by fisheries was expected to result in declining biomass trends, we observed variable trends in the PDO index (Fig. 5). Changes in the PDO index from 1999 to 2010 indicate that average climate in the California Current system gradually shifted from cool (1999–2001) to warm (2003–06) and back to cool (2007–10) conditions (Fig. 5). We summed biomass for each of the three groups previously described and overall (all species combined) and regressed aggregate biomass (natural log transformed) versus year and annual PDO indices (Fig. 6). We noted significant ( $P < 0.001$ ) or near-significant ( $P = 0.06$ ) inverse relationships for all groups and overall versus year (Fig. 6). For species with strong recruitment events in 1999, the trend in biomass over time was increasingly downward, whereas for those with no or unknown recruitment there was a tendency for biomass to increase in recent years (Fig. 6). All groups also demonstrated significant relationships with the annual PDO indices (Fig. 6); however, the greatest



**Figure 2**

(A) Increasing and (B) nonsignificant trends in annual, coast-wide demersal biomass indices (in metric tons, t) for 12 taxa caught in the Northwest Fisheries Science Center’s West Coast Groundfish Bottom Trawl Survey, 2003–10. Taxa are ranked from highest (top) to lowest (bottom) biomass for each category, and standard errors are shown. All six species exhibiting significant ( $P < 0.05$ ) or near-significant ( $P < 0.10$ ) increases in biomass indices over time are shown; however representative examples of species with nonsignificant trends (36 species) are shown only for the most abundant taxa for each subgroup described in Table 1.



**Figure 3**

Decreasing trends in demersal biomass indices in metric tons (t) ( $\pm$ standard error) for 18 of 20 taxa caught in the Northwest Fisheries Science Center’s West Coast Groundfish Bottom Trawl Survey, 2003–10. With the exception of California skate and pygmy rockfish, all species exhibiting significant ( $P < 0.05$ ) or near-significant ( $P < 0.10$ ) decreases in biomass indices over time are shown.

amount of variation in biomass was explained by the PDO indices for those species with no strong recruitment during the late 1990s. We used AIC to determine which model (i.e., based on year, PDO indices or combined) provided the best fit to the data for each group

(Table 2). For species with strong recruitment, the regression of biomass versus year had the minimum AIC value; for species without strong recruitment the model incorporating PDO indices provided the best fit. For both other groups (unknown recruitment and overall),

**Table 1**

Common name, scientific name, and group designations according to taxonomy or depth for 62 dominant demersal species collected during the 2003 to 2010 Northwest Fisheries Science Center West Coast Groundfish Bottom Trawl Surveys. Mean, minimum, and maximum depth, and the total number of positive hauls per species are shown for the 2003 to 2010 period. Mean values are weighted by catch per unit of effort to accurately reflect average depth.

Common name	Scientific name	Depth (m)			Hauls (No. of hauls)
		mean	min.	max.	
<b>Sharks, skates, ratfish</b>					
big skate	<i>Raja binoculata</i>	104	56	332	668
California skate	<i>Raja inornata</i>	107	56	792	517
filetail cat shark	<i>Parmaturus xaniurus</i>	489	113	1224	472
longnose skate	<i>Raja rhina</i>	265	57	1227	2934
sandpaper skate	<i>Bathyraja kincaidii</i>	284	59	1173	1631
spiny dogfish	<i>Squalus acanthias</i>	171	57	1143	1737
spotted ratfish	<i>Hydrolagus collicii</i>	185	56	1241	2521
<b>Flatfish</b>					
arrowtooth flounder	<i>Atheresthes stomias</i>	208	58	992	1726
curlfin sole	<i>Pleuronichthys decurrens</i>	94	56	440	473
Dover sole	<i>Microstomus pacificus</i>	382	56	1246	4205
English sole	<i>Parophrys vetulus</i>	130	56	480	1957
flathead sole	<i>Hippoglossoides elassodon</i>	146	62	346	332
Pacific sanddab	<i>Citharichthys sordidus</i>	107	56	491	1554
petrale sole	<i>Eopsetta jordani</i>	136	56	541	2059
rex sole	<i>Glyptocephalus zachirus</i>	235	56	937	3147
slender sole	<i>Lyopsetta exilis</i>	209	57	830	2564
<b>Shallow to mid-depth water (&lt;500 m)</b>					
bigfin eelpout	<i>Lycodes corteziianus</i>	343	57	1095	1418
black eelpout	<i>Lycodes diapterus</i>	470	82	1143	896
Dungeness crab	<i>Cancer magister</i>	139	56	835	1633
lingcod	<i>Ophiodon elongatus</i>	137	56	417	1553
Pacific cod	<i>Gadus macrocephalus</i>	133	56	285	273
Pacific hake	<i>Merluccius productus</i>	281	56	1213	2775
plainfin midshipman	<i>Porichthys notatus</i>	109	56	464	656
sablefish	<i>Anoplopoma fimbria</i>	495	57	1268	3320
white croaker	<i>Genyonemus lineatus</i>	85	56	181	302
<b>Rockfish—shelf</b>					
bocaccio	<i>Sebastes paucispinis</i>	159	56	333	263
canary rockfish	<i>Sebastes pinniger</i>	139	57	264	340
chilipepper	<i>Sebastes goodei</i>	167	56	464	656
greenspotted rockfish	<i>Sebastes chlorostictus</i>	146	62	348	303
greenstriped rockfish	<i>Sebastes elongatus</i>	156	64	474	1299
halfbanded rockfish	<i>Sebastes semicinctus</i>	115	57	440	378
pygmy rockfish	<i>Sebastes wilsoni</i>	138	64	268	95
redstripe rockfish	<i>Sebastes proriger</i>	158	66	271	120
rosethorn rockfish	<i>Sebastes helvomaculatus</i>	207	65	447	420
sharpchin rockfish	<i>Sebastes zacentrus</i>	209	76	455	307
shortbelly rockfish	<i>Sebastes jordani</i>	170	71	406	405
squarespot rockfish	<i>Sebastes hopkinsi</i>	101	59	203	80
stripetail rockfish	<i>Sebastes saxicola</i>	175	59	436	1076
swordspine rockfish	<i>Sebastes ensifer</i>	156	100	236	30
widow rockfish	<i>Sebastes entomelas</i>	195	64	399	182
yelloweye rockfish	<i>Sebastes ruberrimus</i>	149	66	250	107
yellowtail rockfish	<i>Sebastes flavidus</i>	141	60	343	315

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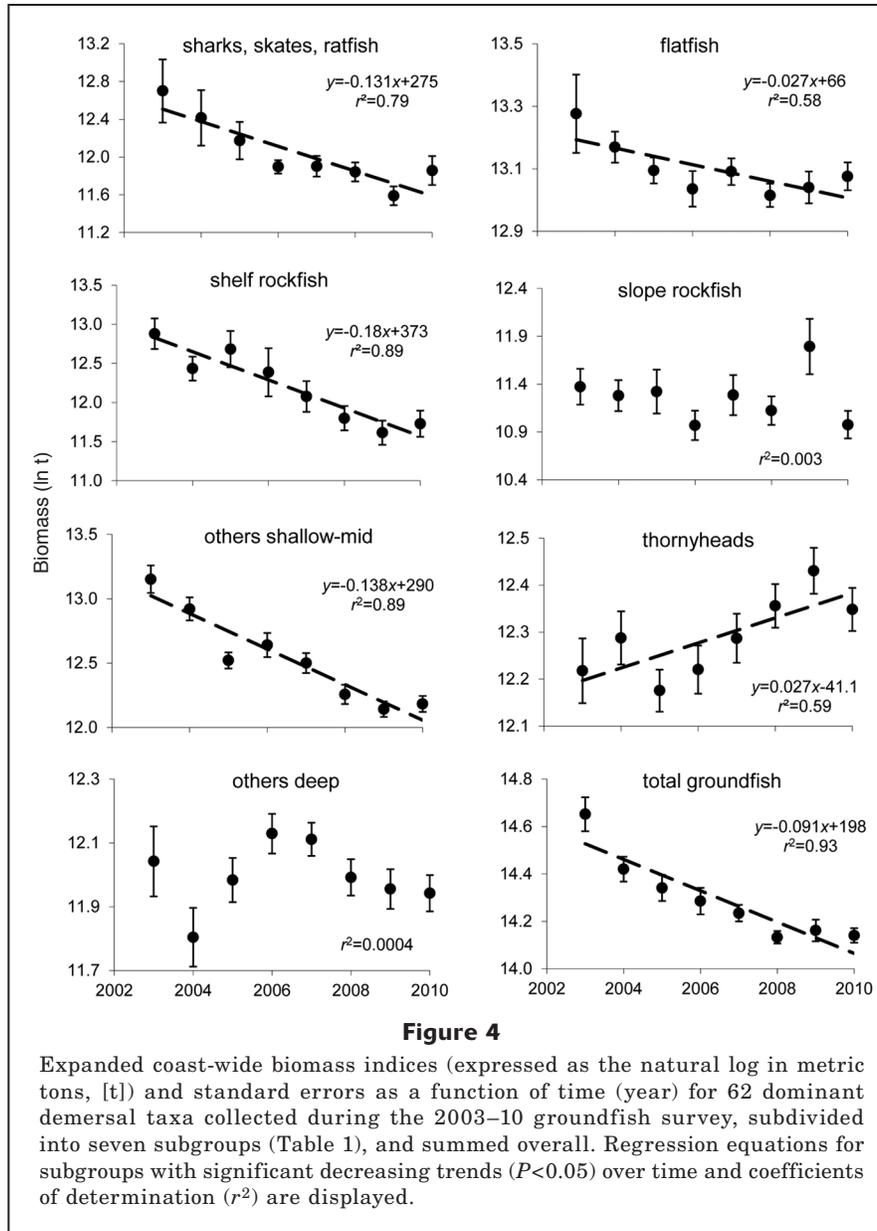
**Table 1 (continued)**

Common name	Scientific name	Depth (m)			Hauls (No. of hauls)
		mean	min.	max.	
<b>Rockfish—slope</b>					
aurora rockfish	<i>Sebastes aurora</i>	456	129	814	689
bank rockfish	<i>Sebastes rufus</i>	267	101	499	91
blackgill rockfish	<i>Sebastes melanostomus</i>	406	133	647	264
darkblotched rockfish	<i>Sebastes cameri</i>	226	84	538	920
Pacific ocean perch	<i>Sebastes alutus</i>	279	87	715	344
redbanded rockfish	<i>Sebastes babcocki</i>	269	84	550	398
rougeye rockfish	<i>Sebastes aleutianus</i>	291	124	798	253
splitnose rockfish	<i>Sebastes diploproa</i>	287	68	559	1107
<b>Thornyhead rockfish</b>					
longspine thornyhead	<i>Sebastolobus altivelis</i>	767	104	1271	1844
shortspine thornyhead	<i>Sebastolobus alascanus</i>	611	67	1268	2590
<b>Deep (&gt;650 m)</b>					
brown cat shark	<i>Apristurus brunneus</i>	672	82	1241	1717
California slickhead	<i>Alepocephalus tenebrosus</i>	909	477	1268	1097
deepsea sole	<i>Embassichthys bathybius</i>	874	276	1271	1116
giant grenadier	<i>Albatrossia pectoralis</i>	943	443	1271	838
grooved Tanner crab	<i>Chionoecetes tanneri</i>	782	64	1271	1431
Pacific flatnose	<i>Antimora microlepis</i>	931	262	1271	890
Pacific grenadier	<i>Coryphaenoides acrolepis</i>	915	313	1271	994
rougetail skate	<i>Bathyraja trachura</i>	941	107	1271	622
snakehead eelpout	<i>Lycenchelys crotalinus</i>	893	63	1264	783
twoline eelpout	<i>Bothrocara brunneum</i>	861	343	1271	898

**Table 2**

Akaike information criterion (AIC),  $P$ , coefficient of determination ( $r^2$ ), and  $\Delta_i$  for different models fitting annual biomass indices versus year, Pacific Decadal Oscillation (PDO) values, and both variables for three subgroups of demersal species determined by the occurrence of strong recruitment during the late 1990s (with recruitment:  $n=13$ , without recruitment:  $n=11$ , and unknown:  $n=38$ ) and overall ( $n=62$ ). The best model for each group is determined by the minimum AIC value (<sup>1</sup>) within each category, with lower AIC values indicating a better fit. Additionally, when  $\Delta_i$  values are  $\leq 7$  (<sup>2</sup>) there is some support for the alternative model. Similar results are shown for species richness subdivided by depth strata (shallow 55–183 m; mid-depth 184–549 m; deep 550–1280 m and overall 55–1280 m).

Models:	With year			With PDO			With year and PDO			$\Delta_i$
	AIC	$P$	$r^2$	AIC	$P$	$r^2$	AIC	$P$	$r^2$	
<b>Biomass</b>										
with recruitment	-8.9 <sup>1</sup>	0.007	0.87	-4.8	0.02	0.62	-1.7	0.008	0.93	7.2
without recruitment	2.8	0.002	0.81	-0.6 <sup>1</sup>	0.001	0.84	5.6	0.01	0.91	6.2 <sup>2</sup>
unknown recruitment	0.8	0.07	0.45	-5.1	0.01	0.70	-8.7 <sup>1</sup>	0.0002	0.99	9.5
all	-6.3	0.001	0.85	-7.5	0.002	0.81	-11.9 <sup>1</sup>	0.0001	0.99	5.6 <sup>2</sup>
<b>Richness</b>										
shallow	23.1	0.15	0.34	15.7 <sup>1</sup>	0.009	0.71	18.4	0.10	0.75	7.4
mid-depth	17.5	0.06	0.49	12.6 <sup>1</sup>	0.01	0.68	16.1	0.12	0.73	4.9 <sup>2</sup>
deep	18.7	0.28	0.19	16.0	0.20	0.20	12.8 <sup>1</sup>	0.05	0.84	5.9 <sup>2</sup>
all	15.9	0.08	0.45	7.6 <sup>1</sup>	0.004	0.80	13.4	0.08	0.79	8.3



the minimum AIC value occurred for models incorporating both year and PDO indices combined (Table 2). The  $\Delta_i$  for the four biomass models indicate that none of the models are equivalent to the best model; however, the observed  $\Delta_i \leq 7$  for two of the four groups suggest some support for alternative models (Table 2).

### Species richness

Species richness indices incorporated all fish collected during the 2003–10 surveys, including rare deep-water species and those not normally associated with the bottom. Regressions between species richness and year indicate near significant negative trends for mid-depth ( $P = 0.06$ ) and overall ( $P = 0.08$ ), but insignificant rela-

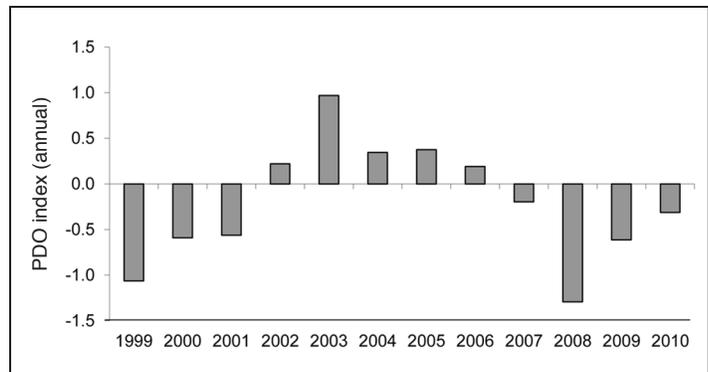
tionships for shallow and deep depth strata (Fig. 7). With the exception of the deep depth stratum ( $P = 0.20$ ), significant positive relationships ( $P < 0.01$ ) were observed between species richness and the PDO. The number of fish species present within two depth strata (shallow and mid-depth) and overall increased during the warm PDO phase. Additionally, species richness indices declined within increasing depth strata (Fig. 7).

Based on minimum AIC values, the models which provided the best fit to changes in species richness during the survey period were either models incorporating only PDO indices (shallow, mid-depth, and overall) or models incorporating both year and PDO values (deep), but not models based solely on year (Table 2).

## Discussion

The Pacific Coast groundfish fishery is exceedingly complex to manage because a wide range of species (90+), including a number of overfished and rebuilding stocks, are caught with the same trawl gear. Beginning in 2000, the PFMC initiated a series of measures designed to reduce catch along the west coast, including fleet reductions, closed areas, and catch restrictions. These measures were initiated in direct response to nine stocks being declared overfished from 1999 to 2002. Landed catch from 1980 through 2010 shows that groundfish harvests off Washington, Oregon, and California were significantly lower (rockfishes, flatfishes, sablefish) or relatively constant (Pacific hake, thornyheads) in recent years relative to historical rates (Fig. 8). This period of decreased catch corresponds to the implementation of the PFMC's management plan. And yet, despite much reduced fishing effort (and landings), overall survey indices of groundfish biomass off the western United States declined from 2003 through 2010. The PFMC's management directives also coincided with the period following expansion of the NWFSC's West Coast Groundfish Bottom Trawl Survey to annually include both the shelf region, as well as the upper continental slope waters along the entire coast (U.S.–Canada to U.S.–Mexico). We used data from this fishery-independent survey combined with information from 24 stock assessments since 2005 to attempt to unravel the causes for the decline in biomass indices despite strict adherence to fishery management plans.

Our results indicated that from 2003 through 2010 individual groundfish stocks along the U.S. west coast responded in varying ways to the newly imposed management measures, with many of the overfished species of concern exhibiting increases in spawning stock biomass (PFMC, 2008a). However, despite improvements in individual stocks there has been a gradual decline in overall groundfish biomass, measured as the sum of the biomass indices for 60 abundant groundfish and two benthic invertebrate species, as well as in major groundfish groups (e.g., sharks, flatfishes, and rockfishes). Twenty of the 62 species described here significantly decreased in observed biomass from 2003 through 2010, whereas 6 species significantly increased. Of the remaining 36 species, 20 exhibited decreasing trends and 16 exhibited increasing trends. These changes indicate that the decline in biomass is not attributable to just a few species. Similar declines in Northwest Atlantic fish stocks have previously been attributed to a variety of factors including overfishing and environmental effects (Haedrich and Barnes, 1997). Hilborn et al. (in press) noted that the dramatic decline in catch can be interpreted in two ways: as an indication of collapsing stocks caused by overfishing, or as a demonstration that management has effectively reduced catch to prevent overfishing of sensitive species. However, the continued decline in overall observed bio-



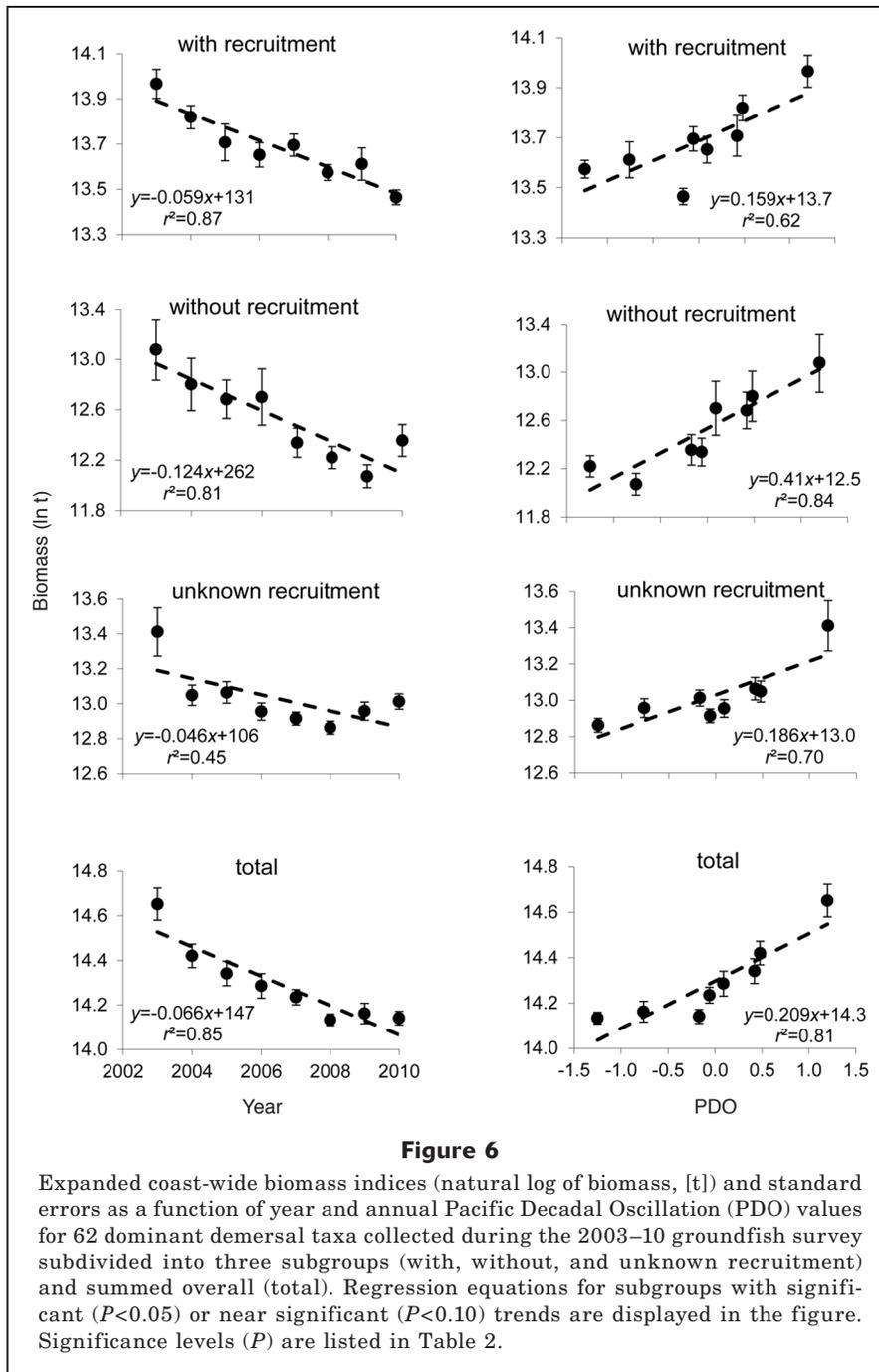
**Figure 5**

Annual variation in the Pacific Decadal Oscillation index (PDO) from January 1999 through December 2010 as it fluctuated between cool negative and warm positive phases. Annual values are the mean of the 12 months beginning in November of the year preceding the start of each annual survey and ending in October with the completion of the annual survey.

mass along the west coast suggests that reduced catch in itself may not be sufficient to prevent biomass from further decreasing when environmental conditions are poor. Hsieh et al. (2008) further concluded that fishing pressure reduces the resilience of exploited populations facing negative climatic effects.

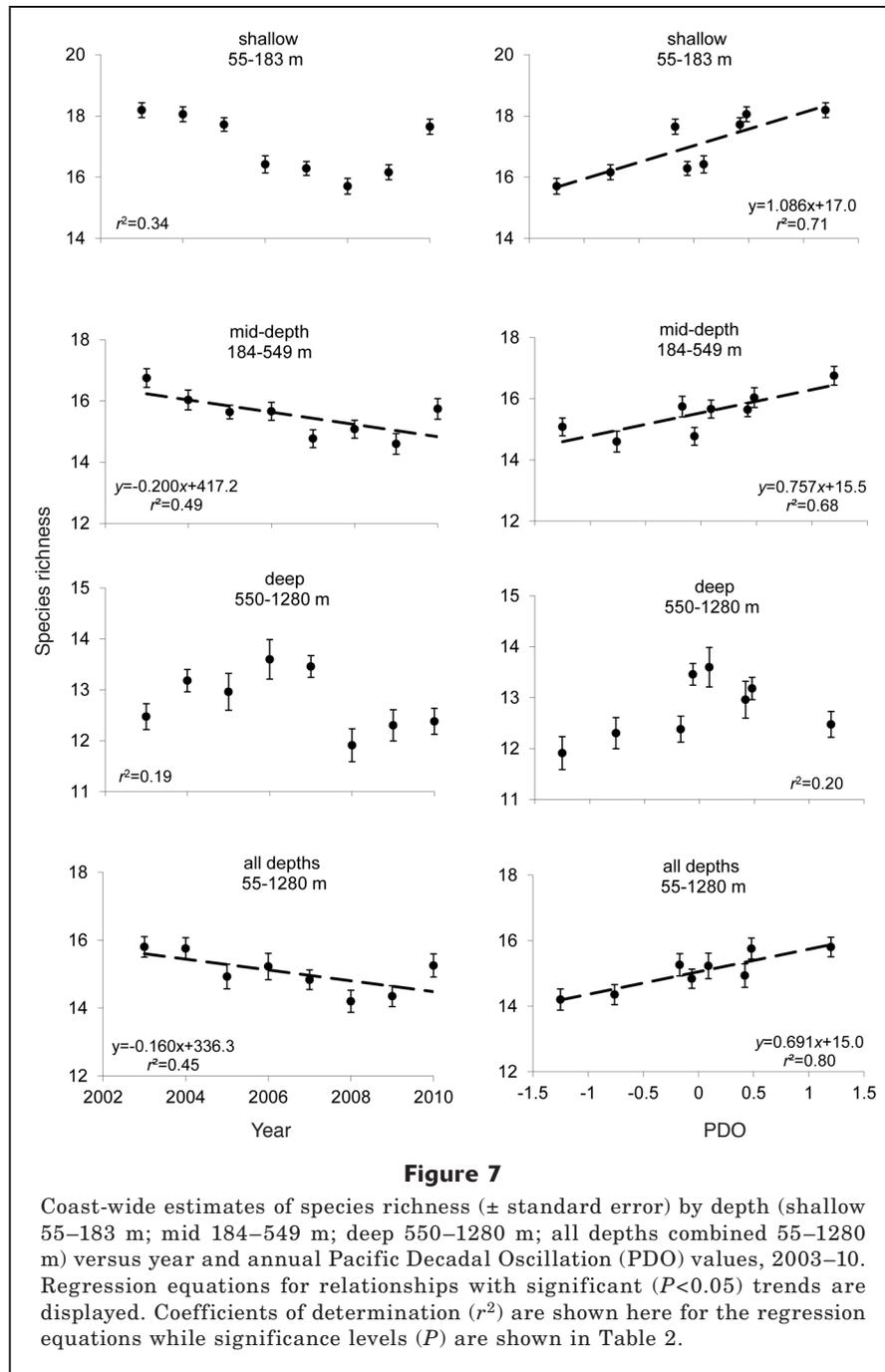
By chance our study occurred during a period after the emergence of a particularly strong 1999 year class for many groundfish species inhabiting the California Current system (Haltuch and Hicks, 2009) and a period of changing environmental conditions as indicated by variability in the annual PDO index. The observed declining survey trends are consistent with natural and fishing-induced mortality estimated for the 1999 cohort in many stock assessments, especially flatfishes, sablefish, and Pacific hake (Schirripa, 2007; Haltuch and Hicks, 2009; Stewart et al., 2011). However, the prevalence of this large year class among many west coast groundfish and its gradual depletion over the survey period (2003–10) may not be entirely responsible for the dramatic decline in overall biomass estimated with data from our west coast fishery-independent survey.

The decline in biomass may additionally be tied to environmental conditions. The annual PDO index, a measure of climate variability, declined from a high value at the start of our standardized survey (2003) to low and negative values near the end of the series examined (2007–10). Numerous studies correlate shifts in the abundance and distribution of marine fish to oscillations in ocean conditions (Francis et al., 1998; Beamish et al., 1999; Hare et al., 1999). Within the northern California Current system, changes in salmon production (Mantua et al., 1997), landed sardine catch (Smith and Moser, 2003; Norton et al., 2008), and Pacific hake distribution (Benson et al., 2002) are linked to decadal-scale fluctuations in climate. Hollowed et al. (2001) further reported that production of commercial fish stocks (32 pelagic fish and groundfish species) in



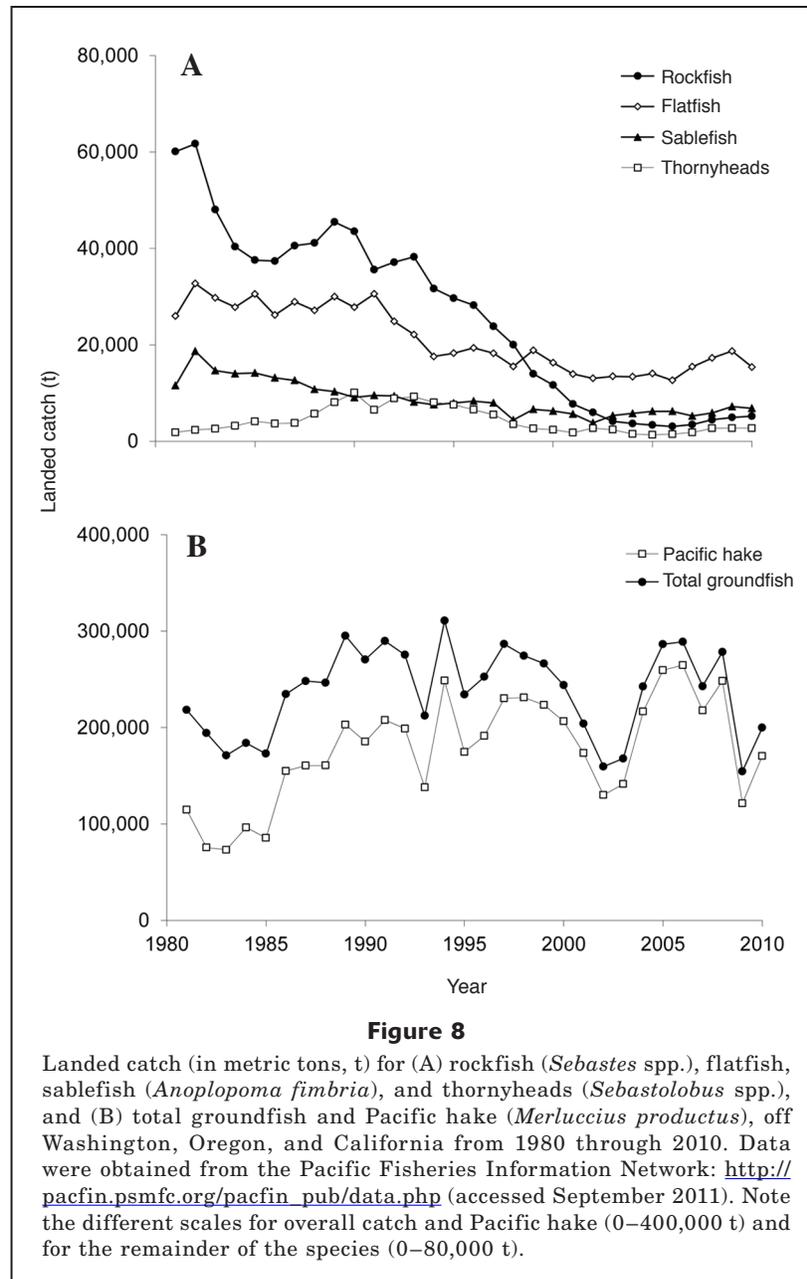
the North Pacific responded to climatic shifts. Major changes in coastal ocean productivity of the eastern Pacific are correlated with phase changes in the PDO and cold eras are associated with enhanced productivity. Warm periods are correlated with low productivity in the California current system (Brodeur and Ware, 1992; Hare and Francis, 1995) and the observed decrease in coastwide biomass could reflect the decline in biomass during the most recent warm period (2003–06) as productivity levels drop.

Results indicate that not only for individual species but also for species grouped taxonomically or by depth the change in biomass over time (2003–10) was variable. For the slope rockfish group (aurora rockfish [*Sebastes aurora*], bank rockfish [*Sebastes rufus*], blackgill rockfish, darkblotched rockfish, Pacific ocean perch, redbanded rockfish, [*Sebastes babcocki*], roughey rockfish [*Sebastes aleutianus*], and splitnose rockfish) and the deepwater species group (mean depth >650 m) composed of brown cat shark (*Apristurus brunneus*),



California slickhead (*Alepocephalus tenebrosus*), deep-sea sole (*Embassichthys bathybius*), giant grenadier (*Albatrossia pectoralis*), Pacific flatnose (*Antimora microlepis*), Pacific grenadier (*Coryphaenoides acrolepis*), rougtail skate (*Bathyraja trachura*), snakehead eelpout (*Lycenchelys crotalinus*), twoline eelpout (*Bothrocara brunneum*), and grooved Tanner crab (*Chionoectes tanneri*), no significant relationship with time was detected over the survey period. Thornyheads were the sole group to exhibit an overall positive correlation

with time (with higher biomass occurring in recent years). Shallow to mid-water species (mean depth  $< 500$  m) consisting of groups composed of cartilaginous fish, flatfish, shelf rockfish, or a mixed subgroup of fish, and overall biomass all significantly declined over time. These declines occurred despite the classification of the west coast fishery as having the lowest overall exploitation rates of ten ecosystems examined by Worm et al. (2009) and multiple management measures introduced to reduce catch.



To evaluate the decline in overall groundfish biomass indices off the western United States, despite much reduced fishing effort, we investigated two potential and perhaps overlapping factors: depletion after strong recruitment and environmental effects. Decreases in total biomass indices occur within an ecosystem when catch is greater than net population growth. To evaluate the contribution of these factors to the observed decline in biomass, we separated the species examined here into subgroups based on the presence or absence of strong recruitment during the late 1990s. We used information contained in 24 stock assessments to assign species to subgroups with strong recruitment (primarily in 1999), without strong recruitment, and with unknown

recruitment. We developed regressions models for each subgroup and overall versus year, annual PDO indices, and including both variables. We assumed that year was a good proxy for depletion of exceptionally strong cohorts as they recruited to the groundfish fishery in subsequent years (Haltuch and Hicks, 2009). For multiple species with highly successful recruitment events in 1999, there has been a gradual decline in biomass since 2003. Regression models for total biomass of these species were best fitted by time, whereas regression models for those species without strong recruitment were best fitted to variation in climate as measured by annual PDO indices. Our analysis also indicated that for models comparing summed biomass for groups with

unknown recruitment and overall, the best fit incorporated both year and PDO indices combined. We think it is important to note that for all subgroups, particularly the group without species with known strong recruitment events, there is still a significant decrease in biomass indices over time. This decrease indicates that the depletion of an exceptionally strong 1999 year class for multiple species is not the only factor contributing to decreasing biomass of west coast demersal fish species. Despite the overall decline in biomass observed in recent years, very few of the species examined here are considered overfished (NMFS, 2009) and therefore a loss of yield cannot be inferred. However, the continued decline in overall observed biomass from 2003 to 2010, despite enactment of multiple management measures and reduced catch, emphasizes the need for the state of the ecosystem to be considered when setting catch limits. During periods of low ocean productivity, a precautionary approach is advised.

During the NWFSC bottom trawl survey, random, rare, and very large tows of schooling rockfish are occasionally taken. If a tow occurs near rocky but still trawlable habitat when schooling rockfishes are present, then very large catches of rockfish are possible (Stewart, 2007). Occurrence of these large catches may prevent detection of underlying biomass trends when only a small number of years are available for analysis, as with the 2003–10 survey. Although this phenomenon appears clear for canary and widow rockfish, for species like sharpchin and redbanded rockfish, it is harder to clearly separate large rare tows from an increase or decrease in biomass, and certainly random large catches and biomass trends may be occurring at the same time (Fig. 3).

The higher productivity associated with the cool PDO phase in the California Current system may have resulted in another strong recruitment event in 2008 (Ralston<sup>3</sup>) and if cool conditions continue, the associated higher productivity could promote enhanced growth and survival of groundfish. Our data indicate that the return to cool conditions in 2007–10 was followed by a slight increase in overall biomass in 2010—an increase that suggests a time lag between cool conditions and increased demersal biomass within the California Current. Although many rockfish species are long lived and exhibit highly variable recruitment, previous studies have additionally indicated that both rockfish recruitment and juvenile growth respond to broad indicators of productivity, and that juvenile abundance is correlated with large-scale oceanographic events such as El Niño–Southern Oscillation and the PDO (Ainley et al., 1993; Laidig et al., 2007). For now we find our results interesting and recognize that the value of the groundfish survey increases with each annual increment and over time will provide additional information to unravel these relationships.

The best models to describe the variation in species richness (restricted to fish only) included the PDO indices (shallow, mid-depth, and overall) or a combination of the PDO indices and year (deep depths) but were not based on year alone. Species richness was positively correlated with the annual PDO index indicating that more species were present within the survey area and, in particular, at shallow and mid-depth strata during the warm phase of the PDO. Tolimieri and Levin (2006) and Tolimieri (2007) examined patterns of diversity in groundfish assemblages in relation to depth (200–1200 m) and latitude (33–37° N) along the U.S. Pacific Coast. They found, as we did, that species richness declined with depth (Fig. 7), but they did not examine changes over time or in relation to climate indices. However, their observation that patterns of diversity were correlated with temperature may partially support our observation of elevated species richness during the warm phase of the PDO. Tolimieri (2007) points out that latitude and depth are factors well known to correlate with diversity and assemblage structure. Both species richness and biomass decreased along the U.S. west coast for demersal groundfish as the PDO index shifted from a warm to a cool phase. Given that the swept area per haul remains constant, fewer species per haul are expected if the underlying population densities decrease; however, as demonstrated above, the densities for the 62 most abundant species exhibited variable trends from 2003 through 2010.

Mueter and Litzow (2008) provided convincing evidence of climate-linked changes in the distribution of demersal fishes in the Bering Sea (1982–2006), coupled with reorganization in community composition by latitude. They observed increases in both biomass and species richness in an area characterized by warming temperatures. Community-wide patterns indicated that taxa shifted northward and also were captured with increasing frequency at shallower stations from 1982 to 2006. Interestingly, they noted that mean species richness significantly increased within the portion of the survey area termed the “cold-pool” as it warmed over time, in a similar relationship to that observed here. Species richness along the U.S. west coast was elevated during the warmer phase of the PDO and lower during the cool phase. Changes in species richness are most likely caused by movement of species in response to environmental conditions (Trenkel and Cotter, 2009).

Understanding the mechanisms underlying the observed relationships between biomass indices, species diversity, depletion, and climate remains a challenge. However, Brodeur et al. (2008) recently related variations in the abundance of dominant ichthyoplankton in the northern California Current to oceanic and climatic indices, thus providing a link between climate and recruitment success. Both larval concentrations and diversity varied on a semidecadal basis in conjunction with fluctuations in the PDO. Zheng and Kruse (2006) found some evidence that recruitment variation in eastern Bering Sea crabs may be related to climate forcing, although interaction with groundfish predators likely

<sup>3</sup> Ralston, S. 2011. Personal commun. National Marine Fisheries Service, Southwest Fisheries Science Center, Fisheries Ecology Division. Santa Cruz, CA 95060.

contributed to recruitment success as well. Brodeur and Ware (1992) and Sugimoto and Tadokoro (1997) both demonstrated changes in zooplankton biomass and distribution coupled with changes in ocean conditions, and Lenarz et al. (1995) reported reduced primary productivity and zooplankton biomass, coupled with poor rockfish recruitment off the west coast during El Niño events. Recruitment success of salmon within the northern California Current system has previously been tied to fluctuations in the PDO index (Mantua et al., 1997). Hollowed et al. (2001) examined the timing of the PDO and ENSO and correlated changes in both with recruitment success in groups such as flatfish and gadoids, but further study is needed to confirm their findings. Like others, they caution that additional factors could also affect biomass, species richness, and distributional changes such as density-dependent habitat selection, timing of migrations, changes in local currents, catchability, and shifts between nursery and feeding grounds (Swain et al., 1994; Delworth et al., 1997; Attrill and Power, 2002; Magill and Sayer, 2002). The interactions among climate variability, currents, and the seasonal strength of upwelling and downwelling is particularly interesting given our prior research where we directly linked changes in demersal biomass and species diversity to depressed oxygen levels along the Oregon shelf (Keller et al., 2010).

At the species level, changes appear driven by climate-induced variation in primary and secondary productivity and recruitment (Beaugrand et al., 2003; Steingrund and Gaard, 2005), although the nature of the relationship has not been deciphered. We recognize that the relatively short time series examined may increase the likelihood that the results are spurious. The observed tight correlations between total and grouped groundfish biomass indices and the PDO are expected if the underlying relationship results from reduced population growth due to poor environmental conditions or if environmental conditions, such as phase shifts in regional climate (Mantua et al., 1997; Hollowed et al., 2001; Castonguay et al., 2008) are also coupled with periodic strong recruitment events, such as the emergence of the 1999 year class.

Natural mortality for species with relatively high natural mortality rates could play an additional role in declining biomass indices. However, for rockfish with low natural mortality rates, it is likely that growth would be more important than mortality during most of the time period. The relationship between the PDO and biomass indices may also be due to changes in catchability or selectivity, rather than to actual population changes. A decrease could be due to higher selection of younger fish (i.e., to peak selection around age 4 or 5 and a decline afterwards). Although understanding the mechanisms supporting the relationships observed here remains problematic, our results demonstrate the importance of incorporating environmental conditions in management decisions. Despite enactment of highly effective management measures and the occurrence of periodic strong recruitment, biomass indices declined

as oceanographic conditions changed throughout much of the survey period.

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## Literature cited

- Ainley, D. G., W. J. Sydeman, R. J. Parrish, and W. H. Lenarz.  
1993. Oceanic factors influencing distribution of young rockfish (*Sebastes*) in central California: A predator's perspective. *CalCOFI Rep.* 34:133–139.
- Attrill, M. J., and M. Power.  
2002. Climatic influence on a marine fish assemblage. *Nature* 417:275–278.
- Beamish, R. J., D. Noakes, G. A. McFarlane, L. Klyashtorin, V. V. Ivonov, and V. Kurashov.  
1999. The regime concept and natural trends in the production of Pacific salmon. *Can. J. Fish. Aquat. Sci.* 56:506–515.
- Beaugrand, G., K. Brander, J. A. Lindley, S. Souissi, and P. C. Reid.  
2003. Plankton effect on cod recruitment in the North Sea. *Nature* 426:661–664.
- Benson, A. J., G. A. McFarlane, S. F. Allen, and D. E. Dower.  
2002. Changes in Pacific hake (*Merluccius productus*) migration patterns and juvenile growth related to the 1989 regime shift. *Can. J. Fish. Aquat. Sci.* 59:1969–1979.
- Brodeur, R. D., W. T. Peterson, T. D. Auth, H. L. Soulen, M. M. Parnel, and A. A. Emerson.  
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.
- Brodeur, R. D., and D. M. Ware.  
1992. Long-term variability in zooplankton biomass in the subarctic Pacific Ocean. *Fish. Oceanogr.* 1:32–37.
- Burnham, K. P., and D. R. Anderson.  
2002. Model selection and multimodel inference: a practical information-theoretic approach, 2<sup>nd</sup> ed., 488 p. Springer, New York.
- Castonguay, M., S. Plourde, D. Robert, J. A. Runge, and L. Fortier.  
2008. Copepod production drives recruitment in a marine fish. *Can. J. Fish. Aquat. Sci.* 65:1528–1531.
- Cochran, W. G.  
1977. Sampling techniques, 2<sup>nd</sup> ed., 428 p. John Wiley & Sons, Inc., New York.
- Delworth, T. L., S. Manabe, and R. J. Stouffer.  
1997. Multidecadal climate variability in the Greenland Sea and surrounding regions: a coupled model simulation. *Geophys. Res. Lett.* 24:257–260.

- Draper, N. R., and H. Smith.  
1981. Applied regression analysis, 2nd ed., 709 p. John Wiley & Sons, Inc., New York.
- Field, J. C., and R. C. Fox.  
2006. Considering ecosystem-based fisheries management in the California Current. *Mar. Policy* 30:552–569.
- Francis, R. C., S. R. Hare, A. B. Hollowed, and W. S. Wooster.  
1998. Effects of interdecadal climate variability on the oceanic ecosystems of the NE Pacific. *Fish. Oceanogr.* 7:1–21.
- Haedrich, R. L., and S. M. Barnes.  
1997. Changes over time of the size structure in an exploited shelf fish community. *Fish. Res.* 31:229–239.
- Haltuch, M. A., and A. Hicks.  
2009. Status of the U.S. petrale sole resource in 2008. *In* Pacific Coast groundfish fishery through 2009, stock assessment and fishery evaluation, 309 p. [Available from Pacific Fishery Management Council, 7700 NE Ambassador Place, Suite 101, Portland, OR, 97220.]
- Hare, S. R., and R. C. Francis.  
1995. Climate change and salmon production in the Northeast Pacific Ocean. *Can. Spec. Publ. Fish. Aquat. Sci.* 121:357–372.
- Hare, S. R., N. J. Mantua, and R. C. Francis.  
1999. Inverse production regimes: Alaskan and West Coast salmon. *Fisheries* 24:6–14.
- Hilborn, R., I. J. Stewart, T. A. Branch, and O. P. Jensen.  
*In press.* Defining trade-offs between conservation of species diversity, profitability and food security in the California Current bottom trawl fishery. *Conserv. Biol.*
- Hollowed, A. B., S. R. Hare, and W. S. Wooster.  
2001. Pacific Basin climate variability patterns of Northeast Pacific marine fish production. *Prog. Oceanogr.* 49:257–282.
- Hsieh, C.-h., C. S. Rens, R. P. Hewitt, and G. Sugihara.  
2008. Spatial analysis shows that fishing enhances the climatic sensitivity of marine fishes. *Can. J. Fish. Aquat. Sci.* 65:947–961.
- Laidig, T. E., J. R. Chess, and D. F. Howard.  
2007. Relationship between abundance of juvenile rockfishes (*Sebastes* spp.) and environmental variables documented off northern California and potential mechanisms for the covariation. *Fish. Bull.* 105:39–48.
- Keller, A. A., B. H. Horness, E. L. Fruh, V. H. Simon, V. J. Tuttle, K. L. Bosley, J. C. Buchanan, D. J. Kamikawa, and J. R. Wallace.  
2008. The 2005 U.S. West Coast bottom trawl survey of groundfish resources off Washington, Oregon, and California: Estimates of distribution, abundance, and length composition. NOAA Tech. Memo. NMFS-NWFSC-93, 136 p.
- Keller, A. A., V. Simon, F. Chan, W. W. Wakefield, M. E. Clarke, J. A. Barth, D. Kamikawa, and E. L. Fruh.  
2010. Demersal fish and invertebrate biomass in relation to an offshore hypoxic zone along the U.S. West Coast. *Fish. Oceanogr.* 19:76–87.
- Lenarz, W. H., D. VenTresca, W. M. Graham, F. B. Schwing, and F. Chavez.  
1995. Exploration of El Niño events and associated biological population dynamics off central California. *CalCOFI Rep.* 36:106–119.
- Levins, P. S., E. E. Holmes, K. R. Piner, and C. Harvey.  
2006. Shifts in a Pacific Ocean fish assemblage: the potential influence of exploitation. *Conserv. Biol.* 20:1181–1190.
- Mantua, N. J., S. R. Hare, Y. Zhang, J. M. Wallace, and R. C. Francis.  
1997. A Pacific interdecadal climate oscillation with impacts on salmon production. *Bull. Am. Meteorol. Soc.* 78:1069–1079.
- Magill, S. H., and M. D. J. Sayer.  
2002. Seasonal and interannual variation in fish assemblages of northern temperate rocky subtidal habitats. *J. Fish Biol.* 61:1198–1216.
- Methot, R. D.  
2011. User manual for stock synthesis, 165 p. Model version 3.21d, May 12, 2011. NOAA-NWFSC, Seattle, WA.
- Mueter, F. J., and M. A. Litzow.  
2008. Sea ice retreat alters the biogeography of the Bering Sea continental shelf. *Ecol. Appl.* 18:309–320. NMFS (National Marine Fisheries Service).
2009. Our living oceans. Report on the status of U.S. living marine resources, 6th ed. NOAA Tech. Memo. NMFS-F/SPO-80, 369 p.
- Norton, J. G., S. F. Herrick, and J. E. Mason.  
2008. Fisheries abundance cycles in ecosystem and economic management of California fish and invertebrate resources. *In* The future of fisheries sciences in North America (R. J. Beamish, and B. J. Rothschild, eds.), p. 227–244. Fish Fish. Series, vol. 31. Springer, New York.
- Peres-Neto, P. R.  
1999. How many statistical tests are too many? The problem of conducting multiple ecological inferences revisited. *Mar. Ecol. Prog. Ser.* 176:303–306.
- PFMC (Pacific Fishery Management Council).  
2008a. Pacific coast groundfish fishery stock assessment and fishery evaluation, vol. 1, 221 p. [Available from Pacific Fishery Management Council, 7700 NE Ambassador Place, Suite 101, Portland, OR, 97220.]  
2008b. Pacific coast groundfish fishery management plan for the California, Oregon, and Washington groundfish fishery as amended through amendment 19, 155 p. [Available from Pacific Fishery Management Council, 7700 NE Ambassador Place, Suite 101, Portland, OR, 97220.]
- Sakamoto, Y., M. Ishiguro, and G. Kitagawa.  
1986. Akaike information criterion statistics, 290 p. D. Reidel Publ. Co., Tokyo.
- Schirripa, M. J.  
2007. Status of the sablefish resource off the Continental U.S. Pacific coast in 2007. *In* Pacific Coast groundfish fishery stock assessment and fishery evaluation, 104 p. [Available from Pacific Fishery Management Council, 7700 NE Ambassador Place, Suite 101, Portland, OR, 97220.]
- Schwing, F. B., W. T. Peterson, N. Cyr, and K. E. Osgood.  
2009. Future research requirements for understanding the effects of climate variability on fisheries and their management. *In* The future of fisheries sciences in North America (R. J. Beamish, and B. J. Rothschild, eds.), p. 621–636. Fish Fish. Series, vol. 31. Springer, New York.
- Smith, P. E., and H. G. Moser.  
2003. Long-term trends and variability in the larvae of Pacific sardine and associated fish species of the California Current region. *Deep-Sea Res.* 50:2519–2536.
- Stauffer, G.  
2004. NOAA protocols for groundfish bottom trawl sur-

- veys of the nation's fishery resources. NOAA Tech. Memo. NMFS-F/SPO-65, 204 p.
- Steingrund, P., and E. Gaard.  
2005. Relationship between phytoplankton production and cod production on the Faroe Shelf. *ICES J. Mar. Sci.* 62:163–172.
- Stewart, I. J.  
2007. Status of the U.S. canary rockfish resource in 2007. *In* Pacific Coast groundfish fishery stock assessment and fishery evaluation, 362 p. [Available from Pacific Fishery Management Council, 7700 NE Ambassador Place, Suite 101, Portland, OR, 97220.]
- Stewart, I. J., R. E. Forrest, C. Grandin, O. S. Hamel, A. C. Hicks, S. J. D. Martell, and I. G. Taylor.  
2011. Status of the Pacific hake (whiting) stock in U.S. and Canadian waters in 2011. *In* Pacific Coast groundfish fishery stock assessment and fishery evaluation, 206 p. [Available from Pacific Fishery Management Council, 7700 NE Ambassador Place, Suite 101, Portland, OR, 97220.]
- Sugimoto, T., and K. Tadokoro.  
1997. Interannual–interdecadal variations in zooplankton biomass, chlorophyll concentration, and physical environment in the subarctic Pacific and Bering Sea. *Fish. Oceanogr.* 6:74–93.
- Swain, D. P., G. A. Nielsen, A. F. Sinclair, and G. A. Chouinard.  
1994. Changes in catchability of Atlantic cod (*Gadus morhua*) to an otter-trawl fishery and research survey in the southern Gulf of St. Lawrence. *ICES J. Mar. Sci.* 51:493–504.
- Tolimieri, N.  
2007. Patterns of species richness, species density, and evenness in groundfish assemblages on the continental slope of the U.S. Pacific coast. *Environ. Biol. Fish.* 78:241–256.
- Tolimieri, N., and P. S. Levin.  
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.
- Trenkel, V. M., and J. Cotter.  
2009. Choosing survey time series for populations as part of an ecosystem approach to fishery management. *Aquat. Living Resour.* 22:121–126.
- Worm, B., R. Hilborn, J. K. Baum, T. A. Branch, J. S. Collie, C. Costello, M. J. Fogarty, E. A. Fulton, J. A. Hutchings, S. Jennings, O. P. Jensen, H. K. Lotze, P. M. Mace, T. R. McClanahan, C. Minto, S. R. Palumbi, D. Ricard, A. A. Rosenberg, R. Watson, and D. Zeller.  
2009. Rebuilding global fisheries. *Science* 325:578–585.
- Zheng, J., and G. H. Kruse.  
2006. Recruitment variation of eastern Bering Sea crabs: climate-forcing or top-down effects? *Prog. Oceanogr.* 68:184–204.