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Distribution of population-based indicators across multiple taxa to assess the status of Gulf of Alaska and Bering Sea groundfish communities

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Mueter, F. J., and Megrey, B. A. 2005. Distribution of population-based indicators across multiple taxa to assess the status of Gulf of Alaska and Bering Sea groundfish communities. − ICES Journal of Marine Science, 62: 344−352.

Ecosystem-based approaches to fisheries management require researchers and managers to take into account effects of fishing on other components of the ecosystem, including non-commercial species. Currently, stock assessments in the Northeast Pacific are limited to the most important commercial species, little being known about the status of non-commercial species. Nevertheless, standardized bottom-trawl surveys conducted in the eastern Bering Sea (EBS) and Gulf of Alaska (GoA), although primarily designed to assess commercial species, provide valuable information on the abundance, distribution, and mean weight of numerous taxa. Using a novel statistical approach and survey data for the years 1993−2003, we examined trends in catch per unit effort (cpue), frequency of occurrence, and mean weight of individuals for each taxon. Time trends were computed as the slope of a linear regression of each indicator on year, and were summarized separately for the eastern and western GoA and for the EBS. Within each system, trends were further compared between commercial and non-commercial taxa. Simulations were used to obtain reference distributions for the expected distribution of slopes across many dependent populations. Observed distributions of trends were compared with simulated distributions, suggesting that more taxa than expected showed a decreasing trend in cpue in the EBS, but not in the GoA. These trends likely resulted from low groundfish productivity in the EBS during the 1990s. At the same time, the frequency of occurrence of significantly more taxa than expected increased in the EBS and, to a lesser extent, in the western GoA. Increases in frequency of occurrence were much more common among non-commercial, invertebrate taxa, and may be a response to reductions in trawl fishing effort during the 1990s.

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Introduction

With the increasing awareness of the effects of fishing on non-commercial species, on habitats, and on other ecosystem components, scientists and policy makers increasingly advocate ecosystem-based approaches to fishery management to guard against unwanted changes in the ecosystem attributable to fishing (Gislason *et al.*, 2000). Such an approach requires the development of quantitative ecosystem indicators and associated reference points. Many indicators have been proposed and, in some cases, evaluated on the basis of objective criteria (Rochet and Trenkel, 2003). Biotic indicators of ecosystem change include population-based, community-level, and system-level indicators. Population-based indicators are relatively easy to measure and understand, often respond in known ways to fishing, are sensitive to changes, and are broadly applicable across systems (Brodziak and Link, 2002; Rochet and Trenkel, 2003).

Although population-based indicators are generally evaluated for commercially harvested stocks, such indicators are rarely examined for non-target species or species

groups. When assessing the impacts of fishing or environmental changes on a community or ecosystem, it is important to monitor trends in both commercial and non-commercial species. Fishing affects not only harvested species, but also many non-target species. For example, reductions in target species may allow competitors to increase in abundance (Fogarty and Murawski, 1998), bycatch and discarding results in mortality of non-target species (Alverson *et al.*, 1994), trawling impacts crush or injure many invertebrate species (Bergman and van Santbrink, 2000), and fishing may lead to increased abundance of scavengers and other opportunistic species in disturbed areas (Kaiser and de Groot, 2000). Therefore, any assessment of fishing impacts should include indicators for non-target species.

Our goal was to develop a broadly applicable approach to assess trends in Alaskan groundfish communities, based on simple indicators and their distribution across many populations, including both commercial and non-commercial species. In many coastal areas such as the continental shelves of the Gulf of Alaska (GoA) and eastern Bering Sea (EBS), comprehensive trawl surveys are routinely conducted to estimate the abundance of demersal fish. Using survey data from these regions, our specific objectives were to: (i) assess simple indicators of trends in catch per unit effort (cpue), frequency of occurrence, and mean individual weight across many interdependent populations; (ii) define reference points for the expected number of positive or negative trends; (iii) define reference distributions based on the expected frequency distribution of trends across multiple taxa; and (iv) compare observed trends in the groundfish communities with these reference points and distributions.

Methods

Data sources

All fish and invertebrate data used were obtained from the National Marine Fisheries Service trawl survey database. All surveys included in the analysis (GoA: 1993, 1996, 1999, 2001, 2003; EBS: annual surveys 1993−2003) used chartered fishing vessels, standardized sampling gear, and consistent (GoA: stratified random; EBS: systematic; Figure 1) sampling designs. Surveys prior to 1993 were excluded to avoid potential biases resulting from gear changes and from uncertainties in identification of certain taxonomic groups (primarily invertebrates). In the EBS, survey stations were generally located on the shelf to a depth of 200 m, while the GoA survey includes stations along the slope to a depth of 500 m. Details of sampling design, data collection, and sample processing are provided in Martin (1997) for the GoA, and in Wakabayashi *et al.* (1985) for the EBS. We included only hauls whose performance was classified as satisfactory in the database.

Catch data were aggregated into 79 fish and invertebrate taxa in the EBS, 91 taxa in the western GoA, and 88 taxa in the eastern GoA. All species consistently identified to species level were kept separate, while the remaining taxa were combined by genus, family, or higher taxon, as appropriate. If a taxon was present at <1% of stations in a single year, it was excluded. Epipelagic species such as salmon that were presumably captured during the setting or
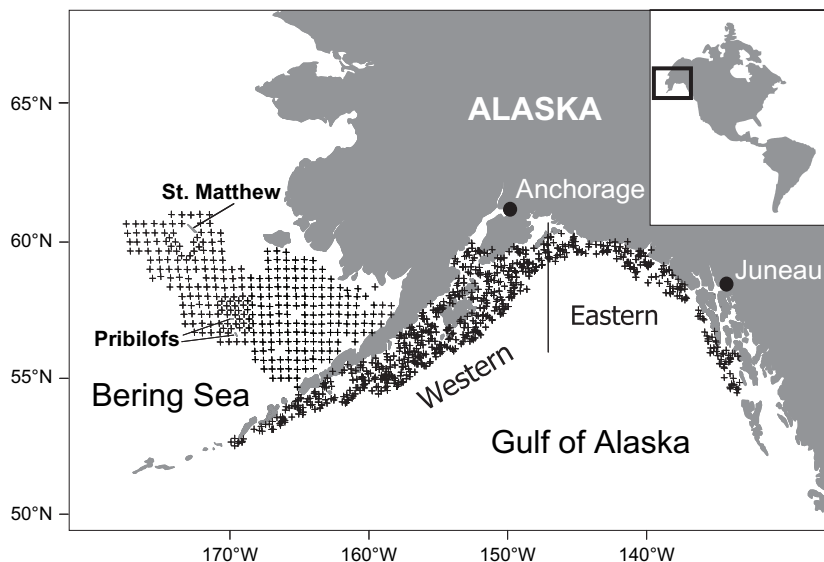

Figure 1. Map of 306 haul locations sampled during all bottom-trawl surveys, 1993−2003, in the eastern Bering Sea (systematic sampling grid), and 717 haul locations sampled in the Gulf of Alaska (stratified random sampling design; analysed separately for the eastern and western parts) during 1999.

retrieval of the net were also excluded. Small forage fish like capelin (*Mallotus villosus*), as well as several semi-demersal species, were included. Although not effectively sampled by a bottom trawl, the surveys do provide a relative index of abundance for such species.

Data analyses

We estimated trends in mean survey cpue, frequency of occurrence (FO), and mean individual weight of each taxon over time for the period 1993–2003 on the basis of 11 annual surveys in the EBS, five surveys in the western GoA, and four in the eastern GoA. A standardized cpue (kg km^{-2}) for each taxon and haul was obtained by dividing the measured or estimated weight of each taxon by a "swept-area" estimate, based on measured tow distance and width of the net opening. These estimates were combined into a mean cpue across all hauls by region. In the GoA, cpue was averaged first by stratum, then the area-weighted mean across all sampling strata was computed by region. A distinction was made between the eastern and western GoA because of pronounced differences in community composition (Mueter and Norcross, 2002), and because the eastern GoA was not sampled in 2001. To obtain consistent indices of abundance for the EBS, a mean cpue was computed across 306 stations that were sampled consistently during all surveys. Because the density of stations in two shallow areas (Pribilofs, St Matthew Island; Figure 1) was twice as high as elsewhere, cpue from those stations received half as much weight as the cpue from regular stations in computing the mean.

Because estimates of cpue are often influenced strongly by the presence of one or more exceptionally large catches, the FO provides a potentially more robust index of abundance. This index reflects the probability of capturing a given taxon in an "average" haul, and was estimated from the proportion of hauls within each sampling region containing a given taxon. Average FO by year, taxon, and region was calculated as a weighted mean, equivalent to the computation of mean cpue. This is consistent with sampling theory if the presence of a taxon is considered an attribute of each unit area measured by sampling a systematic or random subset of the total population of such units (Thompson, 1992). This assumes that each unit area (area swept) is constant across hauls, because the probability of capture varies with area swept. Although the duration of hauls was constant for all surveys, fluctuations in towing speed cause differences in area swept that may bias results. To assess potential biases, we examined patterns in area swept across space and time. To account explicitly for variations in area swept, alternative estimates of mean FO could be constructed by modelling the presence/absence of each taxon as a function of sampling year, spatial location, trawl depth, area swept, and other relevant covariates.

Mean individual weights (W) by region were only calculated for fish taxa, because the number of individuals

caught was generally not recorded for invertebrates. To compute W, the average numerical cpue (numbers km^{-2}) was calculated for each taxon, year, and region, equivalent to the computation of mean cpue by weight, then the latter was divided by the former.

To examine trends in mean cpue, FO, and W over time for the EBS, we estimated the slope of (1) a simple linear regression, and (2) a linear regression with first-order autocorrelated errors based on generalized least-squares regression on year t (1993–2003) by taxon (i) and region for each of the indices (x):

$$x_{i,t} = \alpha + \beta t + \epsilon_{i,t}$$

where (1) $\epsilon_{i,t} \sim N(0, \sigma_\epsilon^2)$, and (2) $\epsilon_{i,t} = \phi \epsilon_{i,t-1} + \nu_{i,t}$, and $\nu_{i,t} \sim N(0, \sigma_\nu^2)$. Prior to estimating trends, cpue values were fourth-root transformed, and FO (proportions) were arc-sine transformed, to obtain variables that were approximately normally distributed. To allow comparisons of estimated trends across taxa on a common scale, each (transformed) variable x was standardized to have a mean of zero and a standard deviation of one. If the estimated autoregressive coefficient was significant at the 90% level, we used slopes from method (2), otherwise from method (1). The limited number of surveys available for the western GoA (5 years) and the eastern GoA (4 years) precluded the estimation of an autoregressive coefficient, so only method (1) was applied for those areas. Good agreement between the slopes of both methods in the EBS suggests that the estimation of slopes was robust to the presence of autocorrelation in the time-series.

The observed slopes for a given taxon may differ from zero because of natural population fluctuations or measurement errors, and the difference can be tested for significance using standard regression techniques. However, when multiple tests are performed on many different taxa, the overall significance level is difficult to evaluate because time trends in different taxa are not independent. Therefore, rather than testing individual slopes, we examined the distribution of trends (slopes) across all taxa in the community. The expected distribution of slopes is determined by the length and correlation structure of the underlying time-series. An exploratory analysis suggested that time-series of fourth-root transformed cpue, arc-sine transformed FO, and W were distributed like multivariate normal series with or without first-order autocorrelation. The expected distribution of linear trends in such random multivariate time-series can be obtained readily through simulation (Appendix; Figure 2). The simulated distributions provide a natural null hypothesis (H$_0$) for a "balanced" community, in which random trends in a given taxon are balanced by concomitant changes in other (positively or negatively) correlated taxa. The actual frequency distribution of slopes estimated from survey data may differ from that expected in a balanced community in at least two important ways. First, the proportion of slopes larger than
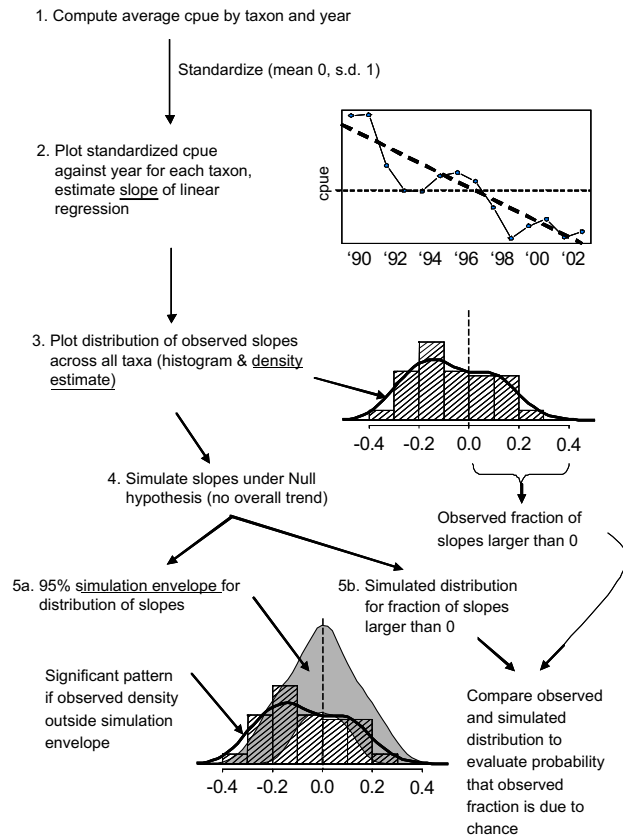
Figure 2. Schematic of data analysis and randomization tests to evaluate the frequency distribution of linear time trends in population characteristics.

zero (i.e. the proportion of taxa that have increased) may differ from the expected value under H_0 (typically 50%, i.e. slopes are centred on zero). Second, slopes may be more or less dispersed than expected under H_0. We defined reference points and reference distributions for a balanced community, and tested the observed distribution of trends for deviations from H_0 using randomization tests.

Randomization tests were based on the simulated distribution of slopes under the H_0 of no overall trend (Figure 2). First, a data set of N series with the same length, first-order autoregressive parameters, and correlation structure as the N observed series was generated randomly (see Appendix). Second, the slopes for each of the N simulated series were estimated as described for the observed data. These steps were repeated R times, and all $R \times N$ simulated slopes were tabulated. To evaluate the observed proportion of taxa with increasing trends, the distribution of the proportion of positive slopes for each of $R = 2000$ simulated data sets was compared with the observed proportion (Figure 2). Using the 2.5th and 97.5th percentiles as reference points, we concluded that the observed proportion of positive slopes was significantly

smaller or larger than expected if it was outside these limits of the simulated proportions.

To evaluate the full frequency distribution of observed linear trends across taxa, an estimate of the smoothed distribution (probability density function, pdf) of observed slopes was compared with the estimated pdf of the simulated slopes (Figure 2). Non-parametric estimates of these pdfs were obtained using a Gaussian kernel estimator whose bandwidth was chosen by cross-validation, as implemented in S-Plus (Venables and Ripley, 1999). Density was evaluated at 50 equally spaced points between -0.5 and 0.5, which covered the full range of all observed slopes. We then constructed pointwise simulation envelopes, based on $R = 2000$ simulated data sets that contained the central 95% of the simulated distributions at each point (Figure 2), to serve as reference for a balanced community. We concluded that the observed linear trends differed significantly from those expected under H_0 if the density distribution of observed slopes fell outside the simulation envelope. Repeated randomization tests with simulated data sets were conducted to estimate the probability that these simulation envelopes encompass the

Table 1. Number of taxa with increasing and decreasing ($\#+/\#-$) cpue, frequency of occurrence (FO), and average individual weight (W) in the eastern (GoA-e) and western Gulf of Alaska (GoA-w), and in the eastern Bering Sea (EBS), for all taxa combined, and for commercial and non-commercial taxa separately. Values of p are given for randomization tests of H_0 as to whether the proportion of taxa with increasing trends is equal to the proportion expected in a balanced community ($\sim 50\%$), and significant skewness (s) for the distribution of trends across taxa (n.s.: not significant; $+/-$: skewed towards positive/negative slopes; cf. Figure 3).

Parameter		All taxa			Commercial taxa			Non-commercial taxa		
		$\#+/\#-$	p	s	$\#+/\#-$	p	s	$\#+/\#-$	p	s
cpue	GoA-e	43/45	0.72	n.s.	19/15	0.45	n.s.	24/30	0.41	n.s.
	GoA-w	57/34	0.22	n.s.	19/15	0.46	n.s.	38/19	0.21	n.s.
	EBS	26/53	0.03	−	6/15	0.13	−	20/38	0.05	−
FO	GoA-e	39/49	0.29	n.s.	12/22	0.32	n.s.	27/27	0.73	n.s.
	GoA-w	53/38	0.37	n.s.	13/21	0.42	n.s.	40/17	0.19	n.s.
	EBS	49/30	0.23	+	8/13	0.28	n.s.	41/17	0.10	+
W	GoA-e	20/31	0.23	n.s.	11/21	0.13	n.s.	9/10	0.72	n.s.
	GoA-w	27/33	0.53	n.s.	16/15	0.81	n.s.	11/18	0.21	n.s.
	EBS	22/20	0.73	n.s.	11/6	0.19	+	11/14	0.57	n.s.

observed distribution of slopes when the true distribution of indices under H_0 is known.

Results

The number of taxa in the EBS that showed a significant linear decrease in cpue between 1993 and 2003 (53 out of 79) was much larger than that expected in a balanced community with no overall trend (Table 1). This was confirmed by the density distributions of slopes for both commercial and non-commercial taxa, which were bimodal with a larger than expected number of taxa whose cpue decreased over time (Figure 3a). The distribution of slopes in the GoA did not differ from expectation, although it was strongly skewed towards positive slopes across non-commercial taxa in the western GoA (Figure 3a).

In contrast to decreasing trends in mean cpue, the FO of a large number of taxa in the EBS increased, such that the distribution of linear trends was significantly skewed towards positive slopes (Table 1; Figure 3b). This pattern was only marginally significant across 21 commercial species, but was pronounced for non-commercial taxa. Taxa with strongly increasing trends include many invertebrate groups (Figure 4). In addition, the FO of several fish taxa increased strongly. Neither the eastern nor the western GoA showed a pattern across taxa that significantly deviated from expectation at the 95% significance level, although there was a tendency for a majority of increasing trends for the non-commercial taxa in the western GoA, similar to the EBS and including many of the same taxa. There were no obvious trends in area swept over time or space that would lead to biases in FO and could account for the observed patterns.

The distribution of trends in W was not different from that expected under H_0 in most cases. However, several commercial taxa in the EBS, including several flatfish species, Pacific cod (*Gadus macrocephalus*), and walleye pollock (*Theragra chalcogramma*), increased in mean weight such that the frequency distribution was significantly skewed towards positive slopes (Table 1). This is consistent with a marginally significant increase in mean individual weight computed across the whole (surveyed) groundfish community over the same time period (slope = 10 g year^{-1}; p = 0.082). Trends in cpue and FO were positively and significantly correlated within all three regions, suggesting that an increase in biomass typically coincided with the spatial expansion of a species, as would be expected (Table 2). Nevertheless, in the EBS there were a large number of taxa whose cpue decreased although their FO increased over the same period (upper left quadrant in Figure 4). Trends in W were not strongly correlated with trends in either cpue or FO (Table 2).

Repeated tests with known data suggested that 95% simulation envelopes contained the estimated pdf of slopes from a given simulated set of time-series (drawn from a known multivariate normal with autocorrelation) approximately 93% of the time. This suggests that the 95% pointwise simulation envelopes correspond approximately to a 93% overall significance level for the distribution of slopes. Therefore, significant results in Table 1 imply significance at a 93% confidence level.

Discussion

Trends in cpue based on numerical abundance or biomass are routinely examined to test for significant trends in individual populations of interest. For example, Rochet and Trenkel (2003) suggest the use of linear trends in
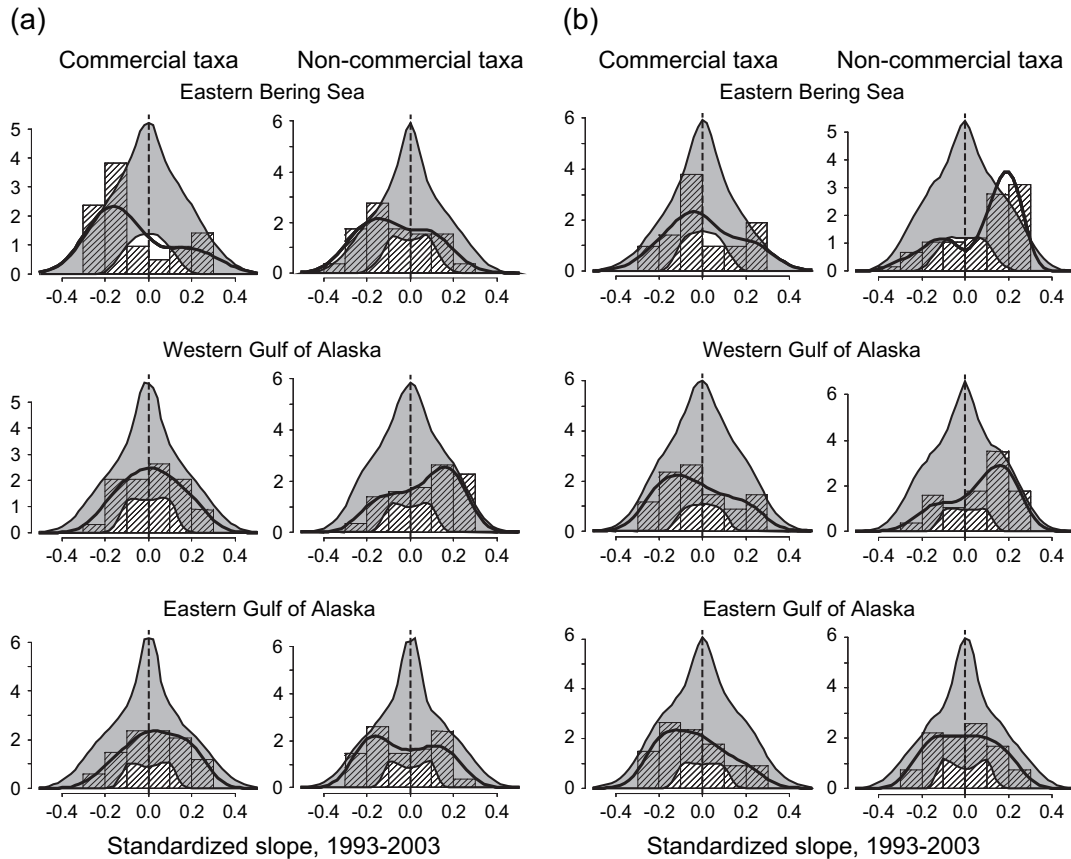
Figure 3. Histograms and estimated probability density functions (pdf; thick black line) of observed trends in (a) fourth-root transformed, standardized cpue, and (b) arc-sine transformed standardized frequency of occurrence (slopes from linear regressions on year, 1993−2003) for commercial and non-commercial taxa by region, in comparison with simulation envelopes encompassing 95% of the expected pdf under the null hypothesis of no overall trend.
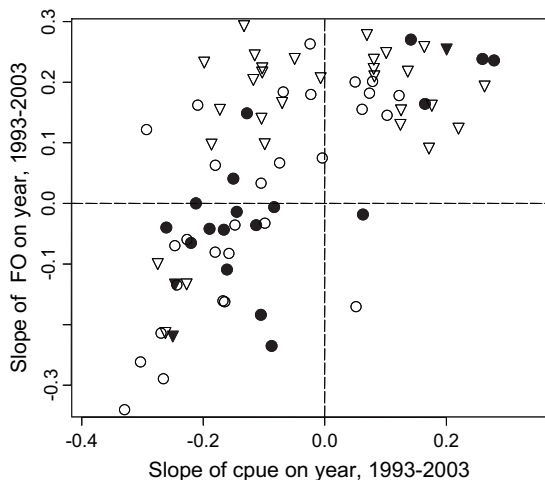

Figure 4. Scatterplot of linear trends in frequency of occurrence vs. linear trends in fourth-root transformed cpue for 79 taxa in the eastern Bering Sea (solid and open symbols: commercial and non-commercial taxa; circles: fish; triangles: invertebrates).

log-transformed numerical abundance (intrinsic population growth rate r; Quinn and Deriso, 1999) as an indicator, using $r = 0$ as a target reference point for stable populations. Our cpue index was based on biomass rather than numerical abundance, because trends in the latter are highly variable, resulting in a loss of power to detect significant trends (Trenkel and Rochet, 2003). Changes in the biomass of harvested populations are generally

Table 2. Correlation coefficients among linear time trends (slopes of regressions on year, 1993−2003; number of taxa in parenthesis) in fourth-root transformed cpue, arc-sine transformed frequency of occurrence (FO), and average individual weight (W) for taxa by region.

Parameter	cpue vs. FO	cpue vs. W	FO vs. W
EBS	0.66* (79)	0.09 (47)	−0.13 (47)
GoA-w	0.52* (91)	0.24 (61)	−0.11 (61)
GoA-e	0.46* (88)	0.03 (56)	−0.07 (56)

* Indicates p < 0.1.

monitored as part of annual stock assessments, whereas trends in non-target species have been examined less frequently (Heessen and Daan, 1996), and rarely trigger management actions. Most management systems are currently not designed to respond to changes in cpue of non-target species, because the effects of fishing on these species are poorly understood and difficult to distinguish from natural variability. Nevertheless, trends in non-target species may provide early indicators of fishing impacts on a community (Saila, 1993), and can be assessed easily on the basis of available survey data.

The results presented here suggest a significant over-representation of declining trends in cpue for both commercial and non-commercial species in the EBS between 1993 and 2003, but not in the GoA. Species that declined in the EBS included most commercially important flatfish species (except rex sole, *Glyptocephalus zachirus*, and starry flounder, *Platichthys stellatus*), Pacific cod, and tanner crab (*Chionoecetes* sp.). In contrast, the dominant commercial species in the EBS, walleye pollock, remained stable over the past decade. Declines across many harvested species appear consistent with an adverse effect of fishing on overall abundances, but several lines of evidence suggest other causes. First, exploitation rates are relatively low in both the GoA and EBS ($<10\%$), and have generally remained stable or decreased since the early 1990s (NPFMC, 2003a, b). Second, decreases in the abundance of several flatfish species in the region resulted from reduced juvenile survival during the 1990s, which is likely related to regional climate variability (Wilderbuer *et al.*, 2002). Third, because commercial and non-commercial species exhibited similar patterns (Figure 3a), it seems unlikely that the changes observed were caused primarily by exploitation.

To our knowledge, the frequency of occurrence of multiple taxa in a groundfish community as an indicator of ecosystem change has not been examined before. The expectation was that FO would be a more robust indicator of abundance than cpue, because it is based on presence–absence data and is therefore less sensitive to extreme values in the catch data. However, the FO index is sensitive to relatively small variations in area swept, particularly for rare species that have a low probability of capture. Therefore, we recommend using the index only if area swept is constant or if variability is small and free of spatial or temporal trends.

Strong increasing trends in FO, primarily of non-commercial species, were more common than expected in the EBS, and to a lesser extent also among non-commercial species in the western GoA, although the observed distribution of slopes was within the 95% simulation envelope (Figure 3b). Some taxa showing an increase in FO, such as polychaetes, shrimps, sea stars, and skates, represent opportunistic species that move into, or increase in abundance in, areas disturbed by fishing (Kaiser and de Groot, 2000). However, polychaetes are also important prey for flatfish and may have expanded in distribution or abundance as a result of the decreasing biomass trends in

several flatfish species. Moreover, other invertebrate taxa that apparently increased represent slow-growing species with limited motility (anemones, bryozoans, sea urchins) that are vulnerable to trawl fishing gear. Trawl fishing effort in both the EBS and GoA has been reduced substantially since the early 1990s (Boldt, 2003), potentially allowing vulnerable species to expand into areas where fishing disturbance has decreased.

Trends in individual weight have been examined in many communities, and may be averaged across individuals within a given species (Ricker, 1995) or across all species in a community (Trenkel and Rochet, 2003). Mean weight would be expected to decrease as a result of fishing, because fisheries typically harvest larger individuals of an exploited species, as well as larger species within a community. However, environmental or density-dependent effects on growth may change the mean weight of a species in the catch, regardless of fishing (Ricker, 1995). When averaging individual weight across all species in the community, such effects may be even more difficult to separate from fishing impacts. The approach presented here examines the full distribution of trends across all or across certain groups of species, so retaining species-specific information that can complement the analysis of aggregate indices such as average weight within the community. In spite of clear patterns in trends in cpue and FO in the EBS, and to a lesser extent in the western GoA, no such patterns were observed in W (weight). In particular, there was no evidence for a widespread decrease in mean individual weight of commercial species, consistent with previous results that show no evidence of "fishing down the foodweb" effects in these ecosystems (Boldt, 2003). On the contrary, the mean weight of many species in the Bering Sea, in particular flatfish species, increased over the time period examined, because of ageing populations resulting from poor recruitment throughout much of the 1990s (Wilderbuer *et al.*, 2002).

When examining trends in any index across multiple populations, univariate significance tests are not appropriate because multiple tests on correlated time-series are not independent. Multivariate methods can be employed to account for dependence among taxa (Saila, 1993; Mueter and Norcross, 2002), but may require restrictive assumptions, may not work with large number of species and short time-series, and are often difficult to interpret. The full distribution of trends across many populations provides a more holistic indicator of changes in the community than trends in selected populations, and is intuitively more appealing than multivariate methods. Furthermore, the distribution of trends in cpue, FO, or mean individual weight across taxa can help identify causes of observed changes, by examining the characteristics of taxa that show similar trends, or by examining trends separately for groups that are believed to respond in similar ways to fishing or environmental change. The power of our randomization tests to detect significant patterns is unknown and difficult to evaluate, because it depends on the number of taxa, the

number of surveys, variability in the time-series, and their correlation structure. It is possible that the small number of significant patterns in the GoA resulted in part from the small number of surveys conducted there.

The analysis here assumes that the residuals from regressions of cpue, FO, or W on survey year have constant variance over time. Variable sample sizes and true differences in variability among years may lead to non-constant residual variance. To account for this, index values for a given taxon, year, and region could be weighted by the inverse of their variance. For simplicity, and because we found no trend in residual variance over time, we ignored differences in variance among surveys.

The analysis illustrates a new and promising approach to examining trends over time across multiple species in a community, and adds to our understanding of recent changes in the EBS and GoA. Increasing trends in the FO of numerous non-commercial species are consistent with, and may be a response to, decreasing trawl fishing effort over the last decade. In contrast, decreasing trends in the cpue of numerous taxa in the EBS was unlikely a consequence of fishing, but may have been caused by much lower groundfish productivity in the 1990s than in the 1980s (Wilderbuer *et al.*, 2002). Similarly, increasing trends in average individual weight of long-lived (commercial) fish taxa in the EBS may reflect an increase in average age attributable to poor recruitment.

Acknowledgements

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Appendix. Randomization procedure

The observed data consisted of N multivariate series of length T years (x_{it} where $i = 1:N$ and $t = 1:T$, and the x_{it} are, for example, cpue estimates). After fitting various ARMA(p, q) models to the observed time-series, we

concluded that each series x_{it} could be reasonably approximated by a first-order autocorrelated process.

Hence, let ϕ_i be the first-order autoregressive coefficient of series i, such that $x_{it} = \phi_i x_{i,t-1} + \nu_{i,t}$, and the $\nu_{i,t} \sim N(0, \sigma_{\nu_i}^2)$ are random normal variables with variance $\sigma_{\nu_i}^2$. Let $V = var(\mathbf{x}_i)$ be the $N \times N$ covariance matrix of the observed data series $\mathbf{x}_i = [x_{i1}, x_{i2}, \dots, x_{iT}]$, with diagonal elements $var(\mathbf{x}_i) = \sigma_{x_i}^2$ and off-diagonal elements $var(\mathbf{x}_i, \mathbf{x}_j) = \sigma_{x_i x_j}^2$. It is easy to show that $\sigma_{x_i}^2 = \sigma_{\nu_i}^2 (1 - \phi_i^2)^{-1}$ and $\sigma_{x_i x_j}^2 = \sigma_{\nu_i \nu_j}^2 (1 - \phi_i \phi_j)$, where $\sigma_{\nu_i \nu_j}^2 = var(\nu_i, \nu_j)$. Therefore, the series $\nu_{i,t}$ follow a multivariate normal distribution that has covariance matrix Σ_ν, with diagonal elements $\sigma_{\nu_i}^2$ and off-diagonal elements $\sigma_{\nu_i \nu_j}^2$.

We simulated R series of length T ($\nu_{i,t}$) by randomly generating data from Σ_ν, based on a method using the Cholesky decomposition (Ripley, 1987). The $\nu_{i,t}$ were then used to construct simulated data series $\tilde{x}_{it}$ that had the same underlying autoregressive coefficient ϕ_i, and the same covariance structure V as the observed series x_{it}. The above assumes that V is the true underlying covariance matrix. However, V is only an estimate, so variability in the simulated series underestimates true variability in x_{it}. We added an additional step in the simulations to account for uncertainty in V. Specifically, for each iteration we simulated an initial set of series from V, computed a covariance matrix $\tilde{V}$ from the simulated series, then used $\tilde{V}$ instead of V to generate simulated data series $\tilde{x}_{it}$, as outlined above. Finally, we fitted linear regressions to each simulated series, and examined the distribution of simulated slopes (see text, Figure 2).