Original Article

Changes in the size structure of marine fish communities

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Marine ecosystems have been heavily impacted by fishing pressure, which can cause major changes in the structure of communities. Fishing directly removes biomass and causes secondary effects such as changing predatory and competitive interactions and altering energy pathways, all of which affect the functional groups and size distributions of marine ecosystems. We conducted a meta-analysis of eighteen trawl surveys from around the world to identify if there have been consistent changes in size-structure and life history groups across ecosystems. Declining biomass trends for larger fish and invertebrates were present in nine systems, all in the North Atlantic, while seven ecosystems did not exhibit consistent declining trends in larger organisms. Two systems had alternative patterns. Smaller taxa, across all ecosystems, had biomass trends with time that were typically flat or slightly increasing. Changes in the ratio of pelagic taxa to demersal taxa were variable across the surveys. Pelagic species were not uniformly increasing, but did show periods of increase in certain regions. In the western Atlantic, the pelagic-to-demersal ratio increased across a number of surveys in the 1990s and declined in the mid 2000s. The trawl survey data suggest there have been considerable structural changes over time and region, but the patterns are not consistent across all ecosystems.

Keywords: fishing effects, Pelagic-to-demersal ratio, L_{max}, size-structure, trawl survey data.

Introduction

The harvest of natural marine resources can have dramatic effects on species abundance and distribution (Jackson *et al.*, 2001; Ricard *et al.*, 2011; Engelhard *et al.*, 2014). Fishing directly removes biomass, leading to the decline of the targeted stocks, but can also have major impacts on the structure of marine ecosystems. Exploitation can cause changes in diversity (Halpern *et al.*, 2008), destruction of habitat (Collie *et al.*, 2000), removal of particular functional groups (Bellwood *et al.*, 2012), instability

(Anderson *et al.*, 2008), and changes in size-structure (Jennings *et al.*, 2002; Shin *et al.*, 2005).

Fishing often targets the largest, highest trophic level fish (Pauly *et al.*, 1998; Jennings *et al.*, 2002), which would result in declining trends for big fish over time (Christensen *et al.*, 2014). Many exploited ecosystems occur on continental shelves where the high trophic level species are often large-bodied demersals, such as gadoids and flatfish, and small pelagics are their prey. Harvesting larger fish may also reduce predation pressure on

lower trophic levels, leading to an increase in the biomass of smaller size classes (Shin *et al.*, 2005). For example, the abundance of large predators on the Scotian Shelf decreased with the expansion of the fishery while small pelagics increased, resulting in the reduction of the mean trophic level of the fish community (Frank *et al.*, 2005).

Fishing, however, also targets the abundant, valuable species, which could be small and/or at a lower trophic level (Sethi *et al.*, 2010). Targeting the abundant natural resource in an area would lead to a decline in particular species, but may not lead to changes in community biomass that are related to size or patterns in life history. Alternatively, ecosystems could be harvested across the entire food web resulting in the biomass trends of all the components of the ecosystem moving in the same direction (Branch *et al.*, 2010). With different levels of fishing pressure, the full cross-community exploitation (capturing and landing organisms across size, functional groups and trophic levels) could range from a balanced harvest in which organisms are exploited in relation to their productivity (Garcia *et al.*, 2012), to overfishing of the entire system. The fisheries in some African lakes have been suggested as following a balanced harvest model (Kolding and van Zwieten, 2014), while the fisheries in systems such as the Gulf of Thailand have been identified as over-exploited (Pauly and Cheungpagdee, 2003). In contrast, management regulations could limit the exploitation of different species reducing trends in biomass that might vary with size or life history group. We sought to examine marine ecosystems around the world that have experienced a range of exploitation intensities to determine if there was empirical evidence for size-selective or life-history specific structural changes that would be consistent with different patterns of fishing.

Many studies have examined fisheries landings as a proxy for ecosystem components (Pauly *et al.*, 1998; Pauly and Watson, 2005; Essington *et al.*, 2006); however, landings may not be a good proxy for fish biomass (Branch *et al.*, 2011; Hilborn and Branch, 2013). Following previous studies (Worm *et al.*, 2009; Shin *et al.*, 2010), we sought to examine empirical data from trawl surveys to track trends in biomass. Fishery-independent trawl surveys provide the most comprehensive information on changes in the abundance of natural marine resources (Hilborn and Walters, 1992). Trawl surveys are specifically designed to track variations in populations through long-term sampling of representative areas. Trawl surveys do not sample the entire food web, and seldom start prior to the onset of exploitation, but they do provide a relative index of abundance from a scientifically designed sampling program, unlike catches, that is available for large portions of the ecosystems (Gunderson, 1993). In recognition of some of the limitations of survey data, these analyses focused on trends in trawl survey biomass over time and not absolute changes in biomass.

Our goal was to examine exploited ecosystems around the world to determine if they exhibited similar changes in the structure of the ecosystem that would be consistent with hypothesized fishing patterns. If fishing was preferentially targeting and removing the high trophic level species in these marine systems (Christensen, 1996; Pauly *et al.*, 1998), one would expect a decline in the biomass of large-demersals and an increase, or at least, a lower magnitude decrease in small pelagics (Christensen *et al.*, 2014). Fishing across the entire community would likely result in the decline of the biomass in all size classes. Harvesting in relation to species value or abundance would likely manifest itself as a

decrease in biomass within a particular group, but the change in biomass would not trend with size or life history groups (demersal, pelagic) and would likely not be the same across all ecosystems. We examined the empirical trawl survey data to determine if the trends in biomass differed across maximum size and life history groups.

Methods

Two techniques were used to examine changes in biomass. Trends over time of organisms binned by their maximum lengths were tested with linear models and the pelagic and demersal groups of each trawl survey were examined for common trends across ecosystems with dynamic factor analysis (DFA) (Zuur *et al.*, 2003). DFA seeks to reduce numerous, non-stationary time series into the least number of common trends that represent the original data (Zuur *et al.*, 2003).

Survey data

Eighteen fishery-independent trawl surveys from around the world were examined. Each trawl survey had annual estimates of standardized biomass per unit of survey effort by taxa covering at least 18 years, with data for at least 11 of those years (Supplementary Table S1). Most of the surveys were much longer and the mean survey length was 34 years. For a detailed description of the data sets see Branch *et al.* (2010) and Bell *et al.* (2014). The standardized biomass per unit of survey effort is henceforth referred to simply as biomass, acknowledging that it is not the true biomass in the ecosystem. Trawl surveys capture a wide range of taxa, but do not provide a representative sample of all the taxa they have ever recorded. Some species are captured or recorded occasionally and their time series are too variable to detect trends. Persistence plots provided an objective way to remove taxa that were not well represented by the data (Genner *et al.*, 2004). For each taxon within each survey, the log of mean biomass over the length of the survey was plotted against the number of years the taxon was recorded. The inflection point from a third order polynomial fit to the data for each survey, provided the number of years that a taxon had to be recorded in the survey to be considered well represented. The well represented taxa typically accounted for over 98% of the biomass in a survey (Bell *et al.*, 2014). Raw biomass values from each survey were used because catchability values were not available for the majority of the taxa.

A species abundance in a trawl survey reflects both its abundance in the environment and its catchability in the gear. Trawl surveys, therefore, provide a relative index of abundance/biomass for taxa which allows their trends to be tracked through time. Though catchability can vary over time (Wilberg *et al.*, 2009), the use of standardized surveys attempts to control for the variability with the assumption that catchability varies about a mean and does not trend with time. Estimates of catchability would provide the actual scale of abundance/biomass for individual species. Without knowledge of the scale, specific quantities (e.g. total biomass, variance) cannot be compared across species or surveys, but the trends in biomass can be compared. The ability to measure both trend and scale is a challenge for all sampling gears.

When grouping biomass from different species caught in a trawl survey, the lack of catchability results in species being weighted by a combination of their presence in the environment and their selectivity to the gear, rather than just their true

Table 1. The L_{max} length bins.

ln(L_{max})	L_{max} (cm)
<3.5	<33
3.5–4	33–55
4–4.5	55–90
4.5–5	90–148
>5	>148

presence in the environment. The analyses conducted here were designed to examine changes in species size structure within the environment with the assumption that size is a major structuring component in marine ecosystems (Kerr and Dickie, 2001). External drivers would therefore, have an impact at the scale of a size bin. Although the contribution of each species within the size bin may not perfectly reflect its proportion in the environment, the assumption is that the trends in biomass of the size bin reflect what is truly happening in the environment.

Trends in survey biomass

For each survey, we estimated the time trend in the survey biomass for different size categories. The biomass data across all trawl surveys were divided into five logarithmic length bins (Table 1) based on the maximum length of each organism (L_{max}) from Fishbase (Froese and Pauly, 2014). The bins ranged from < 33 cm (natural log scale < 3.5) to >148 cm (natural log scale > 5.0). We used the L_{max} from Fishbase because size composition data were not available from all surveys. The first set of analyses fit linear models to each survey separately. A linear model was fit to the natural log of survey biomass by year with a length bin, categorical interaction term such that the biomass of each L_{max} length bin could have a separate intercept and slope (year cat (L_{max})). The slope of each length bin was the slope of the main effect plus the effect of the categorical length bin [slope = $\beta_1 + \beta_x$, where x = 2–5 representing the L_{max} length bins (Table 1)]. The confidence intervals were calculated from the combined standard errors for the main and interaction effect (SE = $\sqrt{\mathrm{var}\,(\beta_1) + \mathrm{var}(\beta_x) + 2 \cdot \mathrm{cov}(\beta_1, \beta_x)}$). The model was

$$\ln(\mathrm{Biomass}_{year,L_{max}}) = \beta_0 + \mathrm{cat}(L_{max}) + \beta_1 \cdot year + \beta_x \cdot year \\ \cdot cat(L_{max}) + \epsilon_t \quad (1)$$

Because the biomass was recorded over time, autocorrelation of the residuals (ϵ) was incorporated into the error structure of the model as a lag-one autoregressive term.

$$\epsilon_t = \phi\epsilon_{t-1} + v_t \quad \text{where} \quad v_t \sim \mathrm{NID}(0, \sigma^2) \quad \text{and} \quad |\phi| < 1 \quad (2)$$

The residuals (ϵ_t) in year t are equal to the residuals in year $t - 1$, times the autoregressive parameter (ϕ) plus a normally distributed error term (v_t). The term v_t is assumed to be normally independently distributed. The autocorrelation decays if the absolute value of ϕ < one.

To determine if there was a single overall trend in each L_{max} size bin across all surveys a second analysis was conducted. Trends in biomass by L_{max} size bins across surveys were assessed with a mixed-effects model (Pinheiro and Bates, 2004). Mixed-effects models allow the estimation of a single, overall slope and

intercept across surveys (the fixed effects) while accounting for the within survey-correlation structure. The slope and intercept of each L_{max} length class within each survey (the random effects) are normally distributed deviations from the overall slope and intercept. The same linear model was fit to the biomass data as above, but with slope and intercept random effects across the 18 surveys. A lag-one autoregressive parameter was also included in the error structure to account for autocorrelation in the residuals.

Different fishing strategies could lead to different impacts on the size-structure of the community. The same pressures could be exerted across all sized fish (non-selective fishing) or the pressure could be targeting only the high-valued resource. The expectation would be that either, the different L_{max} length classes all have the same slope and the interaction effect would not be significant or if the different L_{max} length classes have different slopes, the slopes would be randomly distributed around zero without a trend by length. If fishing is targeting the larger species, the expectation would be that the slopes would orient by L_{max} size bins, smaller fish would have positive slopes (or less negative slopes), while larger fish would have negative slopes.

Generalized additive models (GAMs) were used to determine if there had been changes in the trends in biomass of the different L_{max} length bins over time. GAMs are extensions of linear models in which the dependent variable is modelled as a linear combination of smooth functions of the independent variables. The log of biomass was modelled as a smoothed function of year with the interaction of the categorical L_{max} length classes. The models were run in the R package mgcv (Wood, 2006).

$$\ln(\mathrm{Biomass}_{L_{max}}) = f[year \cdot \mathrm{cat}(L_{max})] + \mathrm{cat}(L_{max}) + \epsilon \quad (3)$$

A lag-one autoregressive term to account for autocorrelation in the residuals was also included in the GAMs.

The community level fishing pressure index (FPI) (Bell et al., 2014) was included in the GAM plots to characterize the exploitation history in each survey area. The FPI is a mean exploitation rate for an area that is based on the available stock assessments in that area from the RAM database (Ricard et al., 2011). Within each area, the biomass of a species with an assessment was divided by its biomass reference point and then divided by the exploitation level at MSY to get a normalized exploitation level over all the species. These harvest ratios were then combined to produce the mean, community level FPI. It directly incorporates productivity because the reference points include the population growth rate. To compare across survey locations, the index was standardized by the harvest level that would produce maximum sustainable yield. The FPI for each survey area was averaged over five year time blocks and divided into one of three fishing pressure categories: high fishing pressure (FPI > 1.15); low fishing pressure (FPI < 0.85); and fishing pressure that would result in a mean, community level maximum sustainable yield (0.85 ≥ FPI ≤ 1.15).

Dynamic factor analysis

We investigated if there were common patterns over time in the pelagic-to-demersal ratio across surveys with DFA. DFA is a technique that distills multiple times series into common underlying state processes or trends within a state-space model. The technique is particularly suited to analysing large numbers of

relatively short time series, as most fisheries time series are (Zuur *et al.*, 2003).

Shifts in the pelagic-demersal ration have been reported in several ecosystems (de Leiva Moreno *et al.*, 2000). DFA was used to test the extent to which these patterns are shared among fish communities in different ecosystems. DFA is a flexible, empirical method that can identify a single common trend, or several separate trends shared by fewer ecosystems. Ecosystems can share temporal trends if they have common exploitation histories and/or climatic regimes that favour one life history over another (pelagic or demersal) (Frank *et al.*, 2016). For clarification, all the surveys were bottom trawls and catch demersal species better than pelagic species.

DFA fits a user defined number of state processes represented as random walks to multiple observed time series. The random walks are the common trends. The DFA model incorporates both process error and measurement error components.

$$x_{t+1} = x_t + w_t, \ \ \text{where} \ \ w_t \sim \text{MVN}(0, Q) \quad (4)$$

The x's are the common trends among the different time series with multivariate normal (MVN) process error. The Q matrix is set to the identity matrix. The observed time series (the pelagic-to-demersal ratio from each survey in the analysis) (y's) are a linear combination of the user defined number of trends (x's) and the parameter Z, defined as a matrix. The measurement error is MVN.

$$y_t = Zx_t + v_t, \ \ \text{where} \ \ v_t \sim \text{MVN}(0, R) \quad (5)$$

The matrix Z represents the contribution of each common trend to the original observed time series for each survey and is termed the factor loadings. Surveys with large, positive factor loadings (Z values) closely followed particular trends (positively covaried) and surveys with large, negative Z values strongly, negatively covaried with the common trends. The Z matrix can be analysed to determine whether a survey is represented by a particular trend and whether it loads positively or negatively for that trend.

Taxa in each trawl survey were defined as pelagic or demersal based on their listing in Fishbase (Froese and Pauly, 2014). Species that live near the bottom and are harvested with bottom trawl nets, but may feed in the water column (Benthopelagic) such as walleye pollock and hoki were defined as demersals. Within each survey the biomass was summed over all species considered pelagic and all species considered demersal. The summed biomass was then divided by each other to give the pelagic-to-demersal ratio. There were no weighting factors applied so individual taxa were implicitly weighted by their abundance in the survey. The pelagic-to-demersal ratios were normalized by subtracting the mean and dividing by the standard deviation, such that all surveys within the DFA had the same weight and equally impacted the determination of the common trends. The time series were restricted to the period 1970–2007 when there was the highest concentration of overlapping survey data. Two of the eighteen surveys did not contain data on pelagic species and were not included in the analysis (St. Pierre Bank and the Irish Sea).

Multiple DFAs were conducted with two variance-covariance structures and the number of trends ranging from one to six. In the simplest variance-covariance structure, the variance was constrained to be the same for all trends and there were no off-diagonal terms (diagonal and equal). The second variance-covariance structure had different variance estimates for the different common trends, but did not have off-diagonal terms (diagonal and unequal). Due to the number of relatively short time series, the model would not converge when the variance-covariance matrix had unconstrained diagonal and off-diagonal terms. The best model fit was selected based on the corrected Akaike Information Criterion (AICc) (Bolker, 2008), where L is the model Likelihood, k is the number of estimated parameters and n is the number of samples.

$$\text{AICc} = -2L + 2k + \frac{2k(k+1)}{n-k-1} \quad (6)$$

Models with AICc values less than two units apart are equivalent, while models that are four or more units apart are different (Bolker, 2008). To be conservative, if the AICc value of the best fitting models were separated by fewer than three units, the model with the least number of trends and the simplest covariance structure was selected.

Results

Survey data

The 18 fishery independent trawl surveys were located around the world (Figure 1). The surveys were in the Atlantic and Pacific and the Northern and Southern Hemispheres, but were largely clustered around North America.

Trends in survey biomass

The linear models for the different fishery-independent trawl surveys produced good model fits (Supplementary Figure S1) and exhibited three general patterns (Figure 2 and Supplementary Table S2). Seven of the eighteen surveys, particularly those in the North Atlantic, showed a decline in slope with increasing $\ln(L_{\max})$ length bins indicating decreasing trends for large-bodied, demersals. The seven exhibited significant negative slopes for the larger $L_{\max}$ length bins and positive or non-significant slopes for the smaller $L_{\max}$ length bins. The eastern Berring Sea survey had the opposite pattern with negative biomass trends for the smaller $L_{\max}$ length bins and positive trends for the larger size classes. Eight surveys, including South Africa, the mid-Atlantic and Aleutian Islands displayed relatively flat trends across $L_{\max}$ length groups. The slopes of these surveys did not vary with the $L_{\max}$ length classes and the estimates were generally non-significant or had one significant length class. None of the trends for the Southern Gulf of St Lawrence were significant. The results are consistent with fishing down top predators in seven regions, do not support the hypothesis in eight regions and three regions had variable biomass trends by $L_{\max}$ length class that did not fit a recognizable pattern.

The mixed-effects model was fit with a diagonal and unequal variance-covariance matrix to ensure numerical stability. A diagonal and unequal variance-covariance matrix assumes independent random effects across surveys. We tested this assumption and found the random effects were independent ($r \leq 0.85$), with only two pairs of an 18×18 matrix with a correlation coefficient > 0.6. The overall model fit well (Supplementary Figure S2).

The overall population level estimates (fixed effects) of the intercept indicated the general level of biomass on the natural log
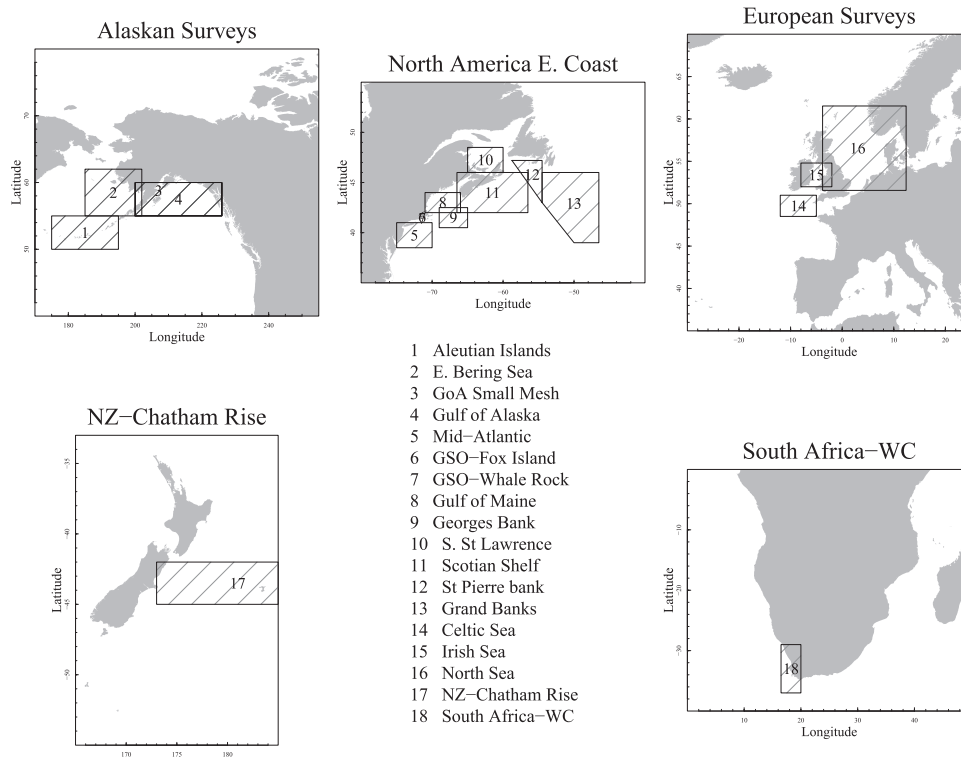
Figure 1. The approximate location of each fishery independent trawl survey (modified from Bell *et al.,* 2014).

scale in each L_{max} size class (Figure 3). The majority of the biomass sampled by the trawl surveys was in the four largest L_{max} size classes ($33 - >148$ cm) (Supplementary Table S3). In general, the overall slopes of the different L_{max} size classes were not significantly different from zero. The two smallest L_{max} size classes had increasing slopes with only the < 33 cm group having a significant positive value. The 54–90 cm L_{max} size exhibited no trend over time with the slope basically at zero. The 90–148 cm and >148 cm L_{max} size classes had declining slopes; however, they were not significantly different from zero. The spread of the random effects was relatively balanced (Figure 4).

The GAMs produced good model fits (Supplementary Figure S3) and captured the change in biomass of the different L_{max} length classes over time (Figure 5). The surveys generally followed a spectrum between two end members. At one end of the spectrum, often in the Atlantic basin over the time period of the data, surveys displayed evidence of a sequential change in the fish community. As exemplified by the Grand Banks and the Mid Atlantic Bight, the larger fish generally had negative trends in biomass in the early part of the time series while the smaller fish had positive trends. As time progressed, the biomass of some of the smaller L_{max} length classes switched and started to decline.

In the middle of the spectrum the trends in each L_{max} length class are relatively flat or non-significant such as in the Gulf of Alaska and the Scotian Shelf. At the opposite end of the spectrum are surveys like the Eastern Bering Sea and Gulf of Alaska Small Mesh in the Alaskan systems. In these ecosystems, smaller fish generally had negative trends in biomass, while the biomass of larger fish was increasing. The 18 trawl surveys displayed a range of results that varied between these two end members and generally agreed with the generalized least squares linear models in the previous section.

The community level FPI varied across the different survey areas (Bell *et al.,* 2014) (Figure 5). Along the east coast of Canada and the United States, the FPI indicated a high level of exploitation for much of the time series in most ecosystems, which then dropped in the 1990s. The mean community fishing pressure for each of the European systems was at the level that would produce a mean, community level maximum sustainable yield, though particular species were heavily targeted. The Alaskan systems, over the period of the survey time series, had low community level harvest rates and the FPI for the Chatham Rise and the West Coast of South Africa also indicated low community level exploitation rates.

Dynamic factor analysis
The trends in pelagic and demersal biomass varied for the different surveys (Supplementary Figure S4) and model selection determined that the DFA with two common trends resulted in the most parsimonious model of the pelagic-to-demersal ratio across all the ecosystems (Figure 6 and Supplementary Table S4). Trend one was relatively flat in the early years, exhibiting an increase (an increase in pelagics and/or a decline in demersals) in the mid-1990s and a subsequent decline in the ratio at the end of the time-series (Figure 6). Trend two was also relatively flat or decreasing for the first 15 years and then increased through the rest of the time series. Each survey was modelled as a combination of both trends one and two, the Z matrix, but more surveys had higher magnitude loadings on trend one. The pelagic-to-demersal ratio for a number of surveys in the North Atlantic more closely followed trend one, though the Celtic Sea had the opposite pattern (Figure 6 and Supplementary Figure S5). The Alaskan surveys loaded both positively and negatively on trend one without a
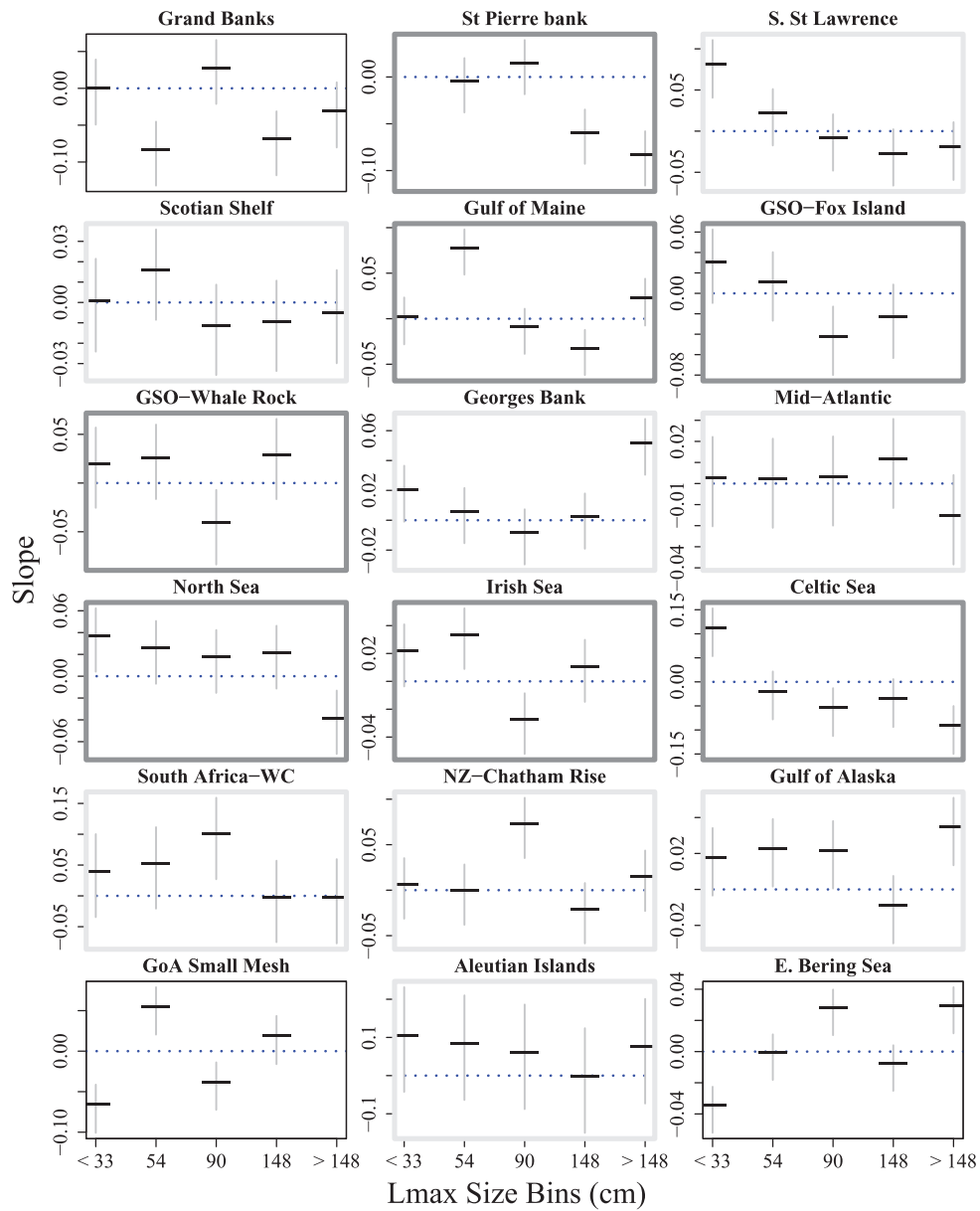
Figure 2. The slope of each $\ln(L_{max})$ length bin for the fishery independent trawl surveys. The dark grey outline designates surveys in which biomass trends declined with size. The light grey outline designates surveys in which biomass trends did not vary with size. The thin black outline designates surveys classified as other. Slopes are significant if the 95% CIs do not cross zero.
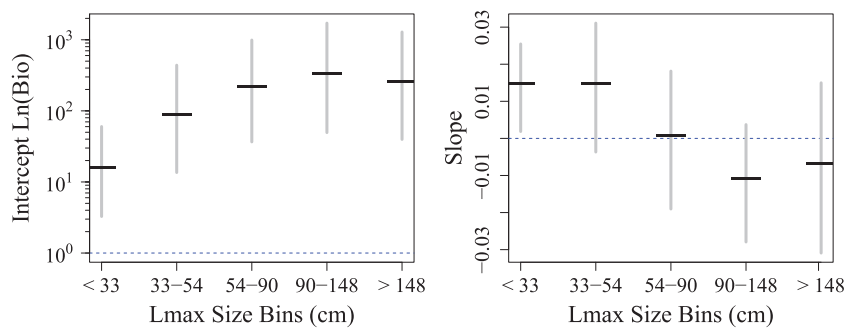
Figure 3. The overall intercept and slope of each L_{max} length bin across all surveys from the mixed-effects model with 95% CIs.
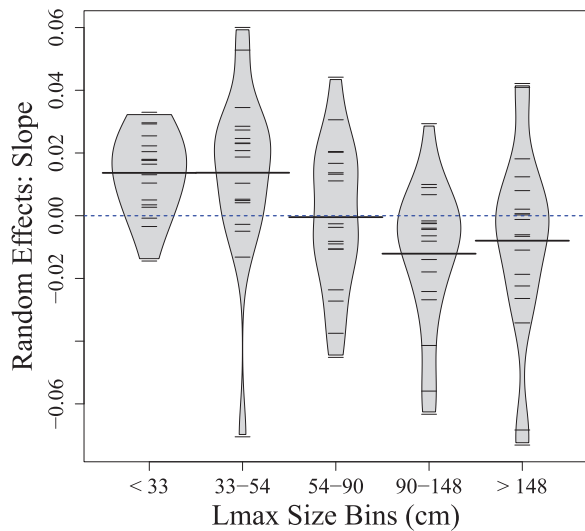
Figure 4. A bean plot of the random effects of slope across all L_{max} size classes and surveys. The width indicates the kernel density and the lines indicate the value of the random effect for each survey.

specific pattern. The Eastern Bering Sea survey had a relatively flat pelagic-to-demersal ratio resulting in a small loading (Supplementary Figure S5). Surveys loading negatively for trend two, such as the Celtic Sea and Mid Atlantic Bight, indicate a decline in the pelagic-to-demersal ratio in those areas (Supplementary Figure S5).

The changes in the pelagic-to-demersal ratio indicate that for a number of ecosystems there have been major changes in the biomass of the two life history groups over time. In some areas, such as the Southern Gulf of St Lawrence and the Scotian Shelf, the surveys indicate increases in pelagics and declines in demersals, while in areas such as Georges Bank, the demersals have increased while pelagics have decreased in the most recent time period (Supplementary Figure S4). Overall, however, the pelagic-to-demersal ratio has changed over the time period recorded for many areas, reflecting the changes in the abundance of the two life history groups, but has not displayed a single consistent pattern across the ecosystems.

Discussion

Similar to previous studies (Bundy et al. 2010; Shin et al., 2010), empirical data from fishery-independent trawl surveys indicate that many ecosystems have exhibited substantial structural changes over the period recorded in the data. The communities have changed with regard to both size-structure and life history groups, but did not exhibit a single, common pattern across all surveys. Some trawl surveys exhibited declining trends for large fish and positive trends for the small fish, while others showed the reverse pattern.

Seven of the surveys, all in the North Atlantic, exhibited changes in biomass that could be considered consistent with the concept of fishing down the marine food web (Christensen, 1996; Pauly et al., 1998). The size-based biomass trends, in areas such as St Pierre Bank and the Celtic Sea, support previous studies implicating the removal of large bodied predators as a major driver impacting the structure of the ecosystems (Myers et al., 1997; Pinnegar et al., 2002). The survey areas had high fishing pressure, at least in the early part of their time series (Bell et al. 2014), had

significant negative trends in biomass for large fish and positive or non-significant trends in small fish. The FPI did not indicate high fishing pressure in the European systems, however, there were high harvest rates on some of the large bodied species that could account for the trends in biomass (Jennings et al., 2002; Pinnegar et al., 2002). Positive trends in small fish could result from a release in predation or enhanced productivity along pelagic energetic pathways (Carscadden et al., 2001; Oviatt, 2004).

The full concept of fishing down the food web, however, implies that once the top predators are removed, commercial effort will target smaller and smaller fish, leading to a continued decline in the mean trophic level of the system (Christensen, 1996; Pauly et al., 1998). With the GAMs, the sequential depletion of L_{max} size-classes over time was also suggested in some surveys. On both the Grand Banks and the Southern Gulf of St. Lawrence, larger fish exhibited negative slopes in the early part of the time series when the fishing pressure was high, followed by declines in smaller size classes as time progressed. Fishing pressure was high throughout the time-series for the Grand Banks, which stops in 1995 when the survey changed gears, but exploitation did decline in the Southern Gulf of St Lawrence after the cod collapse (Myers et al., 1997). The larger fish did not recover with the reduction in fishing pressure and it has been suggested that the Southern Gulf of St Lawrence switched to an alternative stable state dominated by small pelagics and marine mammals (Savenkoff et al., 2007). Declining biomass trends did not progress through to the smallest size class in the Southern Gulf of St Lawrence, but because of the progressive expansion of significant declining biomass trends over time, we include the Grand Banks and the Southern Gulf of St Lawrence in the group of ecosystems that could be in accordance with the concept of fishing down the food web, increasing the number in that group to nine. The biomass trends in the GAMs also suggest that management regulations can slow or even reverse the declines in larger fish. After regulations were imposed by the United States in the mid 1990s (NOAA, 1996), a number of the biomass trends in the larger size classes on Georges Bank reversed and began increasing.

The common trends for the pelagic-to-demersal ratio were generally positive suggesting structural changes with a higher proportion of pelagic biomass due to declining demersals, increasing pelagics or both. A number of the surveys, however, loaded negatively on the common trends indicating that the ratio was declining for that particular ecosystem and the actual drivers might not be exploitation. In the Gulf of Alaska small mesh survey and the Scotian shelf, the pelagics and demersals were inversely related with one going up as the other was going down. Both were related to fundamental changes in the structure of the ecosystem, but the changes in the small mesh survey have been linked to the reorganization of the Gulf of Alaska after a switch in the Pacific Decadal Oscillation (Hare and Mantua, 2000). In contrast, the changes on the Scotian Shelf were attributed to fishing the large, high trophic level fish (Frank et al., 2005).

The declining trends of the large bodied predators in areas of the North Atlantic bring together a number of factors driving fishing effort. The large demersals, the gadoids and flatfish, were abundant, had high value, and had limited management restrictions (Fogarty and Murawski, 1998; Pinnegar et al., 2002; Lilly et al., 2008). Large-scale fishing effort is often directed where these factors combine and it is quite possible that in these ecosystems, led to a major reduction of biomass at the top of the food chain. Alternatively, a high valued, abundant species like abalone
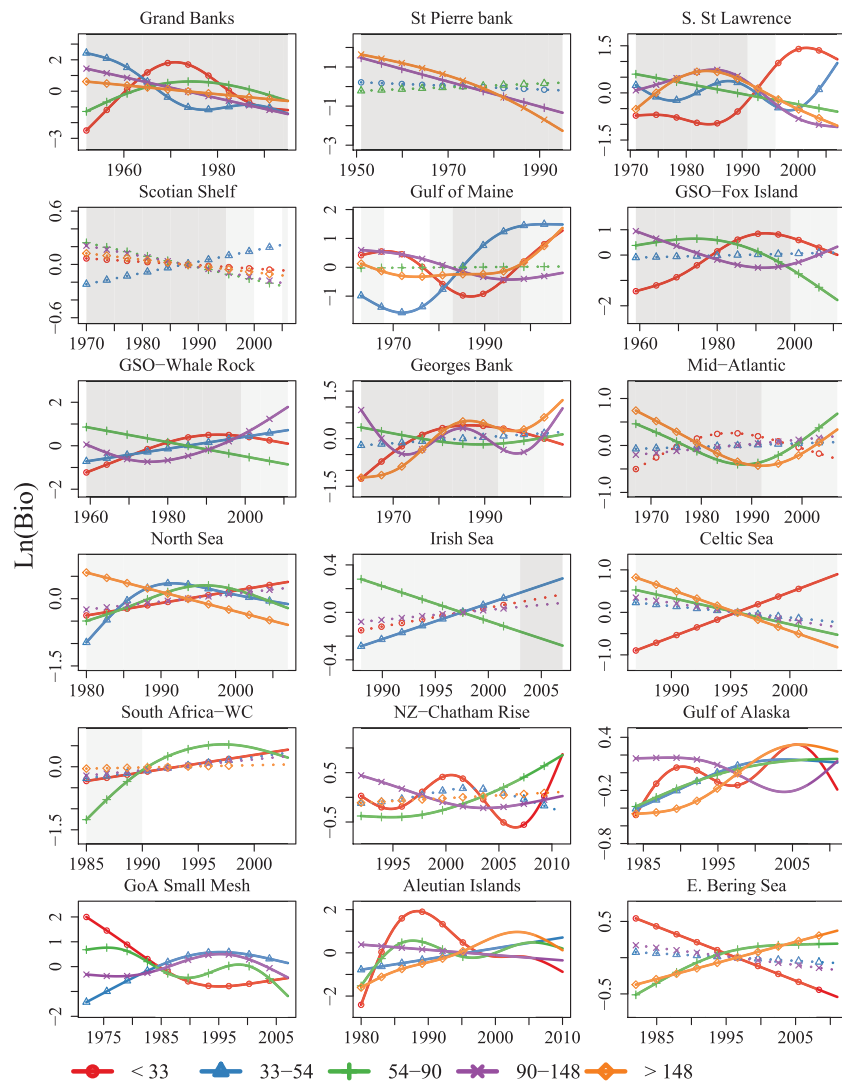
Figure 5. The smoothed function of ln(biomass) with time by each L_{max} length class over all the fishery-independent surveys. Biomass trends with solid lines were significant (p-value $\leq$ 0.05) while dotted lines were not significant. The background color represents the community level FPI from Bell *et al.* (2014). Dark grey is high FPI, light grey is medium FPI, and white is low FPI.

would also be heavily targeted (Davis *et al.*, 1996), but its decline would not lead to a pattern consistent with fishing down the food web. The reduction of an easily accessible, valuable, low trophic-level filter-feeder would be more consistent with the idea of fishing for profit (Sethi *et al.*, 2010) or an example of how exploitation often targets across the entire food web. Some of the earliest species to collapse in the Northwest Atlantic due to intensive exploitation were the filter-feeding oyster and the planktivorous right whale (Perry *et al.*, 1999; Kirby, 2004). Both were high valued, abundant, and had limited if any management restrictions. In a number of locations, historic records suggest that fishing effort initially targeted abundant, accessible species in the nearshore such as anadromous fish and shellfish. Once these nearshore species were reduced, effort expanded away from population centers and into deeper water where organisms were often larger (Perry *et al.*, 1999; Oviatt *et al.*, 2003; Kirby, 2004).

Simulations with Ecopath-Ecosim models from 25 ecosystems around the world showed that when exploitation targeted the most available taxa or harvested across the entire community

there was not a drop in the mean ecosystem trophic level (Branch *et al.*, 2010). The biomass of the system declined due to overfishing, but the structural changes in the community did not resemble the concept of fishing down the food web. Although a number of trawl survey data sets in the North Atlantic exhibit declines in large predators that suggest fishing down the food web, major declines in biomass can occur in any ecosystem, and will occur, in whatever part of the food web has high value, high availability, and limited management regulations.

Outside of the North Atlantic, the biomass trends were generally similar across different L_{max} length classes and did not vary with size. In seven ecosystems, there was no evidence for declines in the biomass of larger fish and the biomass trends across all size classes were relatively flat. Although there has been severe exploitation in the past in various ecosystems, over the time span examined, many of the fisheries represented by the trawl surveys have been regulated (Batstone and Sharp, 1999; NPFMC, 2016). Particular species may be overfished, but the mean, community level fishing pressure does not indicate community level over
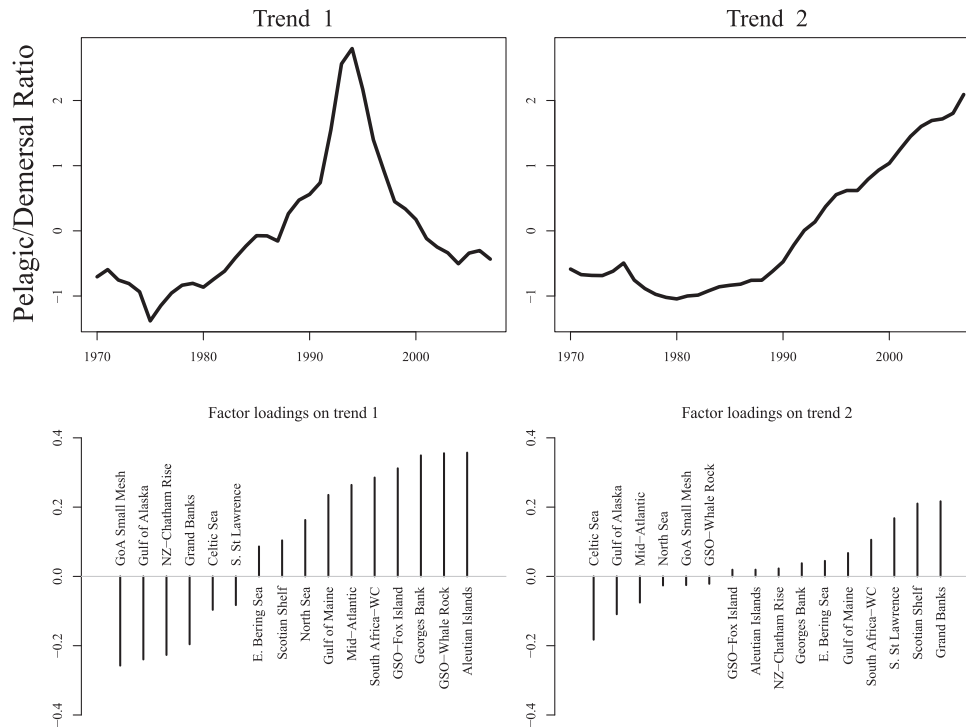
Figure 6. The two common trends and loadings for each trawl survey on the trends from the DFA.

exploitation for areas such as Alaska and New Zealand (Bell et al., 2014). The areas are active fishing grounds, but management constrains the overall fishing pressure and based on the data, limits the decline of the larger size classes. The result is similar trends in the biomass of different L_{max} length bins. While fishing has certainly altered the ecosystem, fishing mortality is not of a magnitude that it swamps the variation in the natural mortality and productivity of the species. This is evidenced by changes in biomass driven by environmental factors such as the Pacific Decadal Oscillation in the Alaskan ecosystems (Hare and Mantua, 2000). The structural changes in the community are likely driven by a combination of the environment and exploitation as regulated by management (Worm et al., 2009; Link et al., 2010; Fu et al., 2012).

Along the east coast of North America, where there has been heavy fishing pressure, regulations have been imposed in the last 10–20 years (NOAA, 1996), which have enabled the recovery of many parts of the ecosystem. The Gulf of Maine, Georges Bank, and Mid Atlantic Bight trawl surveys all exhibited declines followed by a similar recovery pattern. Not all the individual species are above their biomass reference points (NMFS, 2015), but as a group, the data indicates that large demersals are increasing. The goal of management is to regulate fishing pressure to ensure that stocks are not driven to depletion and to limit mortality on overfished stocks to promote recovery. By regulating exploitation, fisheries managers attempt to put bounds on the anthropogenic drivers of changes in ecosystem structure.

The environment is a major driver in marine ecosystems, affecting species distributions and shaping bottom up processes (Ware and Thomson, 2005; Friedland et al., 2012) which can manifest themselves as regime shifts (Gedalof and Smith, 2001). As species distributions change they could alter the size-structure of a given area, particularly if certain-sized organisms were more

likely to shift than others (Perry et al., 2005; Nye et al., 2009). Species which mature quickly and often have small maximum sizes may be able to respond to environmental changes more quickly and rapidly change abundance (Johannesen et al., 2012). Regime shifts can cause major changes in the species composition of the community that can have large impacts on the size-structure of the ecosystem. The environment could therefore have major impacts on the mean size of the community. The analyses presented here attempted to specifically examine the range of L_{max} length bins to get a better understanding of which size classes were driving biomass trends and may be impacted by the environment. Based on the biomass trends, only two areas exhibited patterns that were consistent with bottom up, environmental drivers (Gulf of Alaska Smallmesh survey and E. Bering Sea survey). It is likely that in all the ecosystems, fishing pressure combines with environmental drivers to regulate biomass trends, however, in heavily exploited systems fishing is often the dominant driver (Link et al., 2010).

Within the trawl survey data available, there have been large changes in fish biomass with regard to size and life history. Small fish and pelagic fish generally had positive trends or no trends, while larger fish exhibited both increasing and decreasing patterns. Since historic times, pre-dating the onset of the trawl survey data, there have been declines in large demersals in many areas (Rose, 2004; Bundy et al., 2010). However, trawl survey data suggest that while there have been major structural changes in ecosystems, there is not a single, universal pattern among them all. The models suggest declines that could be considered consistent with the concept of fishing down the food web in some ecosystems that have been heavily exploited. In other ecosystems, trends in size-structure were not apparent, either because the exploitation rate was low, the size-structure was altered prior to the start of the fishery-independent trawl survey (e.g. North Sea)

(Collie *et al.*, 2013), or environmental factors were major drivers. Although there are some relatively consistent patterns in exploited communities such as the decline in the mean size of individuals within a species (Jennings *et al.*, 2002); the structural changes in any particular ecosystem due to exploitation will reflect the abundance and value of the species present, the oceanography at that location and the past and present economic and political conditions of the area.

Supplementary data
Supplementary material is available at the *ICESJMS* online version of the article.

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