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Size-selective fishing drives species composition in the Celtic Sea

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Fishing alters community size structure by selectively removing larger individual fish and by changing the relative abundance of different-sized species. To assess the relative importance of individual- and species-level effects, two indices of fish community structure were compared, the relative abundance of large fish individuals (large fish indicator, LFI) and the relative abundance of large fish species (large species indicator, LSI). The two indices were strongly correlated for empirical data from the Celtic Sea and for data from simulated model communities, suggesting that much of the variability in the LFI is caused by shifts in the relative abundance of species (LSI). This correlation is explained by the observation that most of the biomass of a given species is spread over few length classes, a range spanning the factor 2 of individual length, such that most species contributed predominantly to either the small or the large component of the LFI. The results suggest that the effects of size-selective fishing in the Celtic Sea are mediated mainly through changes in community composition.

Keywords: ecological quality objective, ecosystem approach to fisheries management, fish community, large fish indicator, large species indicator, size structure.

Introduction

Does fishing alter marine community size structure mainly by selectively removing larger individual fish or by changing the relative abundances of species of different size? This question was investigated by contrasting a species-based with an individual-based index of fish community size structure for Celtic Sea survey data and for two model fish communities. The answer has implications for the ecosystem approach to fisheries management, because it indicates the extent of both biodiversity and trophic-structure responses to selective fishing pressure, highlighted by the Pauly *et al.* (1998) phrase "fishing down marine foodwebs". If community size structure is changed mainly by fishing through the warping of intraspecific size structures, then the expected effects are likely to be transitory and superficial: transitory because the small individuals of each species only have to grow to replace their larger conspecifics lost through fishing mortality (see, though, van Kooten *et al.*, 2005); superficial because community species composition at large remains unchanged. Conversely, if fishing alters size structure mainly through changing the biomass abundance of species, then species evenness and eventually composition will be affected, and long-term, possibly irreversible, community-scale effects can arise as Myers and Worm

(2003) observed. As marine communities exhibit strong correlations between body size and trophic level (Cohen *et al.*, 1993; Jennings *et al.*, 2001, 2007), changes in the size structure of fished communities may be used to indicate fisheries-induced strain in foodwebs (Rochet and Trenkel, 2003). Many size-based indicators (SBIs) have been proposed to quantify the effects of fishing on marine foodwebs, and they have been compared in several studies (e.g. Shin *et al.*, 2005). Blanchard *et al.* (2010) showed how time-series of community-level indicators, including SBIs, reveal strong effects of selective fishing, but no study has so far measured the relative importance of individual-level effects compared with species-level effects. Here, we contrast the effects of size-selective fishing as seen through the large fish indicator (LFI; Cury and Christensen, 2005; Greenstreet *et al.*, 2011) with the effects seen through the large species indicator (LSI; Shin *et al.*, 2010).

The LFI describes the community-aggregated proportion of fish biomass contributed by large individuals (as sampled by a specific survey protocol), where individuals are classified as large or small according to a chosen body-length threshold h. The LFI has been selected to support the fish community Ecological Quality Objective for the North Sea (OSPAR, 2006; Heslenfeld

and Enserink, 2008), and it was listed by the European Commission (EC, 2010) as an indicator of good environmental status in the marine foodweb. Detailed studies by ICES (2007a) concluded that the LFI with h set to 40 cm gives best management utility for the North Sea, and Shephard et al. (2011a) found that applying similar criteria for the Celtic Sea gave a value of $h = 50$ cm. Clearly, as well as registering a change in large fish abundance, the LFI will decline if the abundance of small individuals increases. This can be a consequence of predation and competitive release resulting from fishing on large-bodied fish predators (Daan et al., 2005; Greenstreet et al., 2011). The LFI is sensitive to both changes in intraspecific size structure and changes in the abundance of species of different size. To isolate the latter effect, the analogous LSI was considered by Shin et al. (2010), although it was discarded in favour of the proportion of predatory fish, to avoid setting a species size-threshold (Shin et al., 2010). The LSI is defined as the biomass proportion of large species in a community (as sampled by a specific survey protocol), where size is measured in terms of maximum length L_{max}, and species are classified as large or small according to a chosen threshold value g, which can be chosen in relation to h or independently.

Comparing LFI with LSI in the Celtic Sea demersal fish community and subsequently in two model fish communities, the extent to which changes measured by the LFI result from changes in species abundance are assessed. We then investigate the conditions necessary for the LFI to be similar to the LSI. This process provides new insight into the functioning of the LFI and also clarifies the mechanism by which (size-selective) fishing changes community structure.

Material and methods
Empirical analysis
The study used data from the recently discontinued first quarter (Q1; March/April) UK West Coast Ground Fish Survey (WCGFS), a survey operated by Cefas UK using a Portuguese high headline trawl with a 20-mm codend liner. Data for the period 1986–2004 were used, with reasonably consistent sampling effort and spatial coverage. The data consisted of the number of fish caught by species and length category per trawl sample of given duration (min) and swept area (wingspread × distance towed) in each ICES rectangle sampled. Data were standardized by deleting all hauls <25 min and >35 min in duration, giving standard tows of ~30 min. The survey did not sample all stations/rectangles in all years, so rectangles sampled in less than half of all the years were excluded to minimize the potential bias associated with spatial heterogeneity in fish community composition (Shephard et al., 2011b). Catch numbers at length (L) were converted to weight (W) at length using weight-at-length relationships ($W = \alpha L^{\beta}$), where the parameters α and β were obtained by direct analysis (main commercial species) or from FishBase (www.fishbase.org). Catch weight at length of each species and length class in each trawl sample were then converted to density (kg km^{-2}) by dividing by the trawl swept area.

Shift in size-dominance
By interpreting the protocol of Greenstreet et al. (2011), an optimal value for the LFI threshold h has been derived for the Celtic Sea (Shephard et al., 2011a). The resulting LFI time-series (1986–2004) based on this large fish threshold of $h = 50$ cm is

used here. This LFI index shows a notable decline over the observed time-series, indicating a shift from a large- to a small-fish dominated system. If the LFI expresses primarily changes in the abundance of species of different size, then the trends in annual biomass of small and large individuals that underlie the LFI should be well reproduced by trends in the annual biomass of small and large species. Correlations between standardized biomass (kg km^{-2}) time-series for large individuals vs. species and small individuals vs. species (summed across all individuals and species, respectively, in the community) were calculated. Trends in each of the four biomass series were then assessed using generalized least-squares (gls) models fitted by maximum likelihood and including an autoregressive moving average (ARMA) variance structure. The ARMA parameters p (the number of autoregressive parameters) and q (the number of moving-average parameters) were changed by iteration in the model to minimize temporal autocorrelation in the residuals (Zuur et al., 2009), with the best model being selected using Akaike's information criterion (AIC). Autocorrelation function plots were used to check that temporal autocorrelation in residuals was removed.

Empirical indices
The hypothesis that the LFI primarily detects changes in the abundance of species of different size should be rejected if it is not possible to construct an LSI that closely tracks the existing Celtic Sea LFI. Rejection specifically on ecological grounds requires an LSI threshold calculated to maximize correlation between the two indices, so that decorrelation cannot be attributed to the threshold value. Therefore, we used the same WCGFS biomass data (1986–2004) to derive an LSI series in which the threshold value g was tuned to maximize the correlation with the LFI. In addition, as for the LFI, the smoothness of the time-series was evaluated for management benefit by calculating the correlation of LSI between successive years and the correlation of LSI with year (Shephard et al., 2011a). As an additional consistency check, these three correlations were computed also using the value of g that maximized the correlation of LSI between successive years.

In a management context, indicators such as the LFI are defined based on the data produced by a specified survey, so technically not subject to measurement uncertainty. However, when interpreting and comparing such indices, understanding how much they are affected by chance events during survey collection is important. When computing indicator values, potential variability was therefore estimated using bootstrapping. Specifically, 10^4 hypothetical alternative survey datasets were constructed by sampling for each survey year randomly with replacement among all hauls of that year, until the actual number of hauls in that year's survey had been sampled. These resampled datasets were then used to estimate confidence intervals and other statistics related to indicator values.

Intraspecific length distributions
The relationship between the LFI and the LSI depends on the intraspecific distribution of biomass over individual lengths. If, hypothetically, all individuals belonging to a species had the same length, then the LFI and the LSI would be equal for equal thresholds h and g. In reality, intraspecific lengths differ as a result of growth and phenotypic variability. In this case, the LFI and the LSI will consistently attain similar values when (i) the biomass of small species is contributed mainly by individuals

shorter than the large fish threshold h, and (ii) the biomass of large species pertains mainly to individuals longer than h. These two conditions are more likely to hold if the distributions of biomass over length are narrow and stable for each species, so that they are less likely to straddle h. Therefore, cumulative distributions of biomass over individual log-transformed length were computed and characterized for all species in the WCGFS data, for each year in the period 1986–2004 in which more than one individual was sampled. Biomass-weighted means and standard deviations of log-length were then derived.

To quantify the combined effect of the widths of the intraspecific length distributions and the variability of the length distributions across years on the LFI, the following exact relationship between the LFI and the LSI was derived:

$$\text{LFI} - \text{LSI} = (\text{proportion of large fish among small species}) \times (1 - \text{LSI}) - (\text{proportion of small fish among large species}) \times \text{LSI}. \tag{1}$$

This mathematical relationship can easily be verified by expressing all its components in terms of the four types of relevant contributions to biomass: small/large individuals from small/large species. If the proportion of large fish among small species and the proportion of small fish among large species are small, then the LFI and the LSI do not differ much. To determine whether this was the case, time-series of these proportions were computed for the period 1986–2004.

Modelling

To clarify the ecological mechanisms underlying the results of the empirical analysis, we then used two different but complementary community models. The first was able to represent thousands of species, and the second could represent detailed intraspecific size-structure dynamics. The first, the population-dynamical matching model (PDMM) of Rossberg *et al.* (2008), was used to determine whether the observed relations between the LFI and the LSI relied on ecological mechanisms specific to the Celtic Sea fish community or on more general mechanisms that could be shared with other fish communities. The second, the fish community size-resolved model (FCSRM) of Hartvig *et al.* (2011), was used to understand the observed intraspecific size structures and their responses to size-selective fishing, using generic model assumptions.

The population-dynamical matching model
This is a multispecies dynamic model that describes changes in species population biomasses in terms of coupled ordinary differential equations, one for each species, incorporating effects attributable to competition, growth, predation, and losses by metabolism and natural death. Model species are either producers or consumers, distinguished by different growth terms in the equations (Rossberg *et al.*, 2008). Each model species has a set of traits, including the maturation body mass M_{mat}, that together determine the rates of the modelled ecological processes and hence the foodweb.

An iterative assembly algorithm was used to determine the trait values of all species. This algorithm starts with a model community with a few species, then repeatedly generates new species by randomly modifying the traits of extant species (so creating phylogenetic structure; Bersier and Kehrli, 2008) and adding new species

with positive invasion fitness to the community. After each set of invasions, species that go extinct are removed. This method of gradually building up a foodweb resolves the marine foodweb modelling problem first described by Andersen and Ursin (1977): without sufficiently strong non-trophic intraspecific competition, empirically parametrized foodweb models with many species tend to be dynamically unstable (Andersen and Ursin, 1977; Loeuille and Loreau, 2005; Andersen and Pedersen, 2010; Hartvig *et al.*, 2011). The PDMM assembly algorithm produces stable communities with inter- and intraspecific competition between consumers resulting only from trophic mechanisms that are well understood, namely resource- and consumer-mediated competition.

The PDMM was parametrized for a generic temperate shelf community in the Northeast Atlantic [Rossberg *et al.* (2008) for a detailed description of parameters]. Specifically, parameters representing the minimum and maximum possible species maturation body masses M_{mat} were defined using data from the Northeast Atlantic (Boudreau and Dickie, 1992; Duplisea, 1998; Froese and Pauly, 2010). Also, the area of the model system was set equal to that for the Celtic Sea (ICES, 1977); however, model dynamics are largely invariant to the area, such that the model area could take other values corresponding to other areas in the Northeast Atlantic. In addition, the parameter representing the maximum gross primary production of a single producer species was derived from data for Northeast Atlantic systems from the Sea Around Us Project (2010). The preferred predator–prey body-mass ratio (which implies a preferred M_{mat} ratio at the population level) was chosen based on data from the North Sea (Jennings *et al.*, 2002). The model also has a parameter determining the volumes of trait spaces available to model species. The larger these volumes, the greater the number of available niches, and hence the more species that can coexist. This parameter was chosen to give a model fish species richness that fell within the range found for demersal fish communities in the Northeast Atlantic, i.e. 102–225 (WCGFS; Froese and Pauly, 2010). Growth and loss rates for model species follow allometric scaling laws derived using data for plankton, invertebrates, and fish (Niklas and Enquist, 2001; Brown *et al.*, 2004; Savage *et al.*, 2004); the gross conversion efficiency for consumers is derived as the average of the efficiencies for herbivores and carnivores (Hendriks, 2007). With this parametrization, a model shelf community was generated with model species encompassing the body mass range from phytoplankton to large fish. A more detailed description and motivation of model parametrization will be published elsewhere. A model species is taken to be a fish species if it has $M_{\text{mat}} > 10^{-3.66}$ kg, which is the lowest M_{mat} for all fish species from the Celtic Sea (Froese and Pauly, 2010). Of the 7826 species in the model community, 208 are fish, compared with some 191 demersal fish species in the Celtic Sea (Froese and Pauly, 2010).

An LFI series for the modelled community was computed using the empirical intraspecific size distributions from the WCGFS data. The model LFI was calculated as follows: first, M_{mat} values for each model fish species were converted to a corresponding L_{max} using the empirical equation $\log_{10}(L_{\text{max}}) = 0.308 \times \log_{10}(M_{\text{mat}}) + 1.82$ ($r^2 = 0.640$) derived from 91 species in the WCGFS (Figure 1a). Then, for each model fish species with $L_{\text{max}} > 50$ cm, we estimated the proportion α of the total species biomass above $h = 50$ cm, using the empirically derived equation (from 38 species in the WCGFS), i.e. $\alpha = (L_{\text{max}} - 50 \text{ cm})^{1.39} / [(L_{\text{max}} - 50 \text{ cm})^{1.39} + (67.9 \text{ cm} - 50 \text{ cm})^{1.39}]$, with $R^2 = 0.477$ (where R^2 is the generalized coefficient of determination;
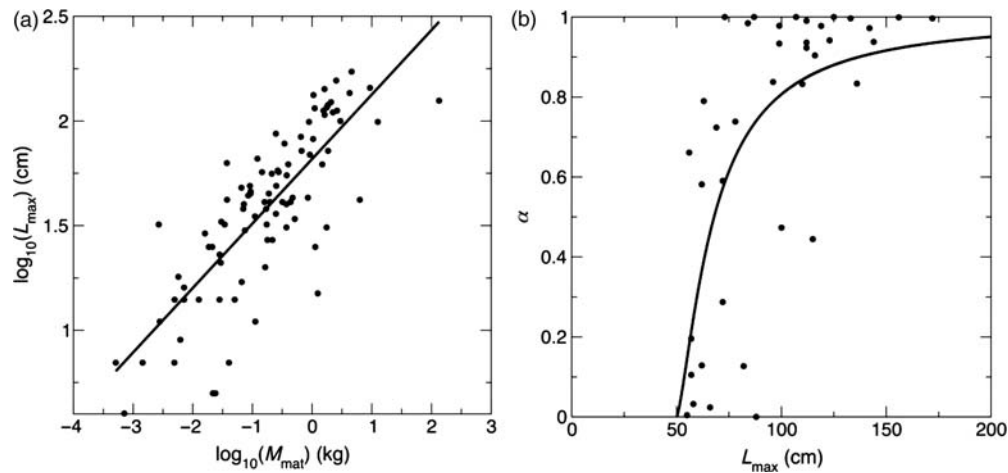
Figure 1. (a) The relationship between maximum length L_{max} of a fish species and the maturation body mass M_{mat}, on log scales. Points are derived from data for 91 fish species in the WCGFS. The solid line is a linear regression through the 91 datapoints, given by $\log_{10}(L_{max}) = 0.308 \times \log_{10}(M_{mat}) + 1.82$. (b) The relationship between L_{max} and the proportion α of the total species biomass attributable to large fish (with length $L > h = 50$ cm). Points are derived from data for 38 fish species from the WCGFS; for each species, α is estimated as the biomass-weighted average of the proportions of biomass attributable to large fish for each year in the period 1986–2004. The solid line is a non-linear regression through the 38 datapoints, given by $\alpha = (L_{max} - 50 \text{ cm})^{1.39}/[(L_{max} - 50 \text{ cm})^{1.39} + (17.9 \text{ cm})^{1.39}]$ ($R^2 = 0.477$). By definition, $\alpha = 0$ for $L_{max} \leq 50$ cm.

Figure 1b). The LSI for the PDMM community was computed using the same L_{max} threshold of $g = 85$ cm used in the analysis of empirical data reported below, and using the regression line of $\log_{10}(L_{max})$ against $\log_{10}(M_{mat})$ to classify model species as large or small.

To compare model dynamics in response to fishing with the Celtic Sea data, the model LFI, based on empirical size distributions, was calculated for the model community under a fishing regime corresponding to the Celtic Sea. Fishing pressure is measured in terms of the harvesting rate H, which we define as the rate at which a population's total biomass decreases as a consequence of removals by fishing. Comparing 142 H-values of eight assessed species in the Celtic Sea with the corresponding F-values (ICES, 2006, 2007b, 2008, 2009, 2010), the median F/H ratio was 1.21 (range 0.797–3.23). The pristine model community had an initial LFI of 0.708, higher than the empirical LFI of 0.454 for 1986. Exploitation before 1986 was modelled by harvesting all model fish species with a harvesting rate $H = 0.08$ year^{-1} for 200 years, after which the model LFI reached an equilibrium value of 0.440. Other values of H were tested, increasing from 0 year^{-1} in increments of 0.01 year^{-1}, but $H = 0.08$ year^{-1} gave the equilibrium model LFI closest to 0.454. For subsequent years (1986–2004), harvesting rates in the PDMM were modelled based on time-series of empirical catch and total-stock biomass estimates from the Celtic Sea (ICES, 2006, 2007b, 2008, 2009, 2010). For each of the years 1993–2001, an average H-value was calculated as the biomass-weighted average H for eight main fish stocks (anglerfish, blue whiting, cod, haddock, hake, megrim, monkfish, and whiting). For each of the years 1986–1992, an average H-value was calculated for the eight main fish species except for haddock, for which catch and abundance data were missing because assessments did not start until 1993. Similarly, for each of the years 2002–2004, an average H-value was calculated for the eight main fish species except for blue whiting, for which total-stock biomass estimates were missing. All eight species have stock areas that extend beyond the region

sampled by the WCGFS, although cod, whiting, and haddock stock areas were well covered by the survey. For each species, H was calculated by computing (catch)/(total-stock biomass) and converting it into a rate. Fishing was applied to all model fish species because the fishing mortality of non-target species can be substantial (Piet *et al.*, 2009). In any year, the same (average) H was applied to each model fish species, because a regression between $\log_{10}$(species-specific H) and $\log_{10}(M_{mat})$ for each of the years 1986–2004 always gave a very low correlation ($r^2 < 0.18$).

The fish community size-resolved model
The FCSRM (Hartvig *et al.*, 2011) extends the size-spectrum theory of Andersen and Beyer (2006) and represents a general temperate marine community of fish. Life-history parameters and trophic interactions between individuals are determined by individual body size and motivated by the observed strong size-dependence of life-history traits (Peters, 1983) and trophic level (Jennings *et al.*, 2001, 2007) on body size. A model community consists of several maturation size classes of fish, with each size class representing all species with maturation sizes in the range $[M_{mat}; M_{mat} + \Delta M_{mat}]$. In all, 21 maturation size classes with centres evenly spaced on a logarithmic body-mass scale from 25 mg to 25 kg were distinguished, corresponding to maturation lengths between 1.36 and 136 cm. For each maturation size class, size-structured population dynamics are described by a McKendrick–von Foerster partial differential equation (McKendrick, 1926; von Foerster, 1959). A coupled system of these equations accounts for the dynamic balance between growth and mortality throughout the community, which in turn determines community biomass dynamics. Equations governing relationships between feeding rate and growth rate, and reproductive output and mortality rate, follow Hartvig *et al.* (2011). Through these equations, the values of all rates emerge as properties of the organisms in their community context. The trophic role of individuals is determined by their body size (a predator–prey

size ratio window), independent of maturation size class. The smallest individuals feed on plankton, represented by a planktonic size spectrum, and larger individuals feed on smaller fish. The model is parametrized following Hartvig *et al.* (2011), using empirical values for temperate marine ecosystems. As the model is used here to develop generic expectations for intraspecific size structure in fished communities, it has not been validated specifically for the Celtic Sea.

Fishing mortality in this model refers to individual mortality, as is conventional. It was modelled using a length (L) dependent selectivity as characteristic for a trawlnet targeting large fish, given by $f(L) = (\exp(bL - a)/(1 + \exp(bL - a)))$ (Millar and Fryer, 1999). The length at 50% selectivity is then $L_{50} = a/b$, where a is the mesh size and $1/b$ is the selection factor (Millar and Fryer, 1999; Piet *et al.*, 2009). A mesh size of $a = 10$ cm was used to obtain an L_{50} of 30 cm with $b = 1/3$. This represents the average L_{50} for North Sea cod, haddock, sole, and whiting (Piet *et al.*, 2009) with typical gear. Fishing mortality F (year^{-1}) is given by the product of $f(L)$ and effort E. Body length (cm) was converted to body mass (g) using the simplified relationship mass = 0.01 (length)^3 of Peters (1983). Simulations compared the LFI and the LSI while varying fishing effort E from 0.1 to 1.5 year^{-1}. These simulations, too, used an LFI large fish threshold of $h = 50$ cm and an LSI large species threshold of $g = 85$ cm. Simulations with LSI thresholds of $g = 60, 65, 70, 75,$ and 80 cm were also performed. To compute the LSI from the model, these length thresholds were converted to M_{mat} values of 0.540, 0.687, 0.857, 1.05, 1.28, and 1.54 kg, respectively, using the same mass–length relationships as above and the approximation formula $M_{max} = 4 M_{mat}$ (Beverton, 1992).

Results
Empirical analysis
Shift in size-dominance
There were strong correlations between annual biomass of small individuals and biomass of small species ($r^2 = 0.979$) and between large individuals and large species ($r^2 = 0.955$),

suggesting that changes in community size structure were mediated at the species level. Two *gls* models fitted by maximum likelihood including a structure to account for temporal autocorrelation showed that both small fish trends (ARMA: $p = 3$, $q = 2$) were significantly positive (small species: $t = 7.13$, AIC = 259.26, $p < 0.001$; small individuals: $t = 7.65$, AIC = 259.67, $p < 0.001$), whereas both large fish trends (ARMA: $p = 1$, $q = 0$) were significantly negative (large species: $t = -4.69$, AIC = 233.7, $p < 0.001$; large individuals: $t = -4.86$, AIC = 231.80, $p < 0.001$; Figure 2). Autocorrelation function plots confirmed that there was no significant temporal autocorrelation in the residuals of these models. Standardized large fish species biomass declined from 401 kg km^{-2} in 1986 to 86 kg km^{-2} in 2004 (assuming that survey catchability was 1), whereas small fish species biomass increased from 483 to 611 kg km^{-2} over the same period. There was greater interannual variation in the small fish series (s.d. = 258 kg km^{-2}) than the large fish series (s.d. = 132 kg km^{-2}), presumably reflecting stronger (recruitment) sensitivity to environmental fluctuations or survey catchability.

Empirical indices
A large species L_{max} threshold g of 85 cm produced the Celtic Sea LSI time-series (1986–2004) that had the highest correlation with the corresponding LFI [$r = 0.94$, bootstrapping 95% confidence interval, *CI* (0.85, 0.990); we use r to denote Pearson's product-moment correlation throughout], with general trends and interannual fluctuations in the two series being remarkably similar (Figure 3). *CI*s for the indicator values obtained through bootstrapping suggest considerable measurement uncertainty, potentially accounting for much of their interannual variability (Figure 3). However, this measurement uncertainty is highly correlated between LFI and LSI (bootstrapping estimates this correlation to range from 0.48 in 1999 to 0.996 in 1987, with a median of 0.93). This result hints that the observed correlations between LFI and LSI largely reflect some feature of the underlying community that is robust to variability among samples. The
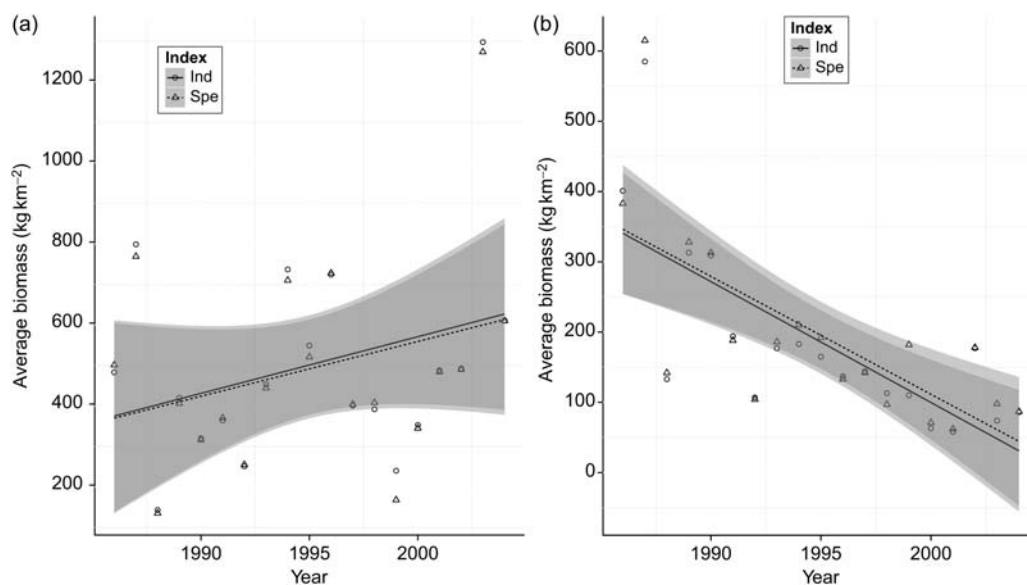

Figure 2. Trends in standardized annual biomass summed over each of (a) small and (b) large individuals and species in the WCGFS series. Individual (Ind) categories were based on an LFI size threshold of $h = 50$ cm, and species (Spe) categories were based on an LSI size threshold of $g = 85$ cm. Fitted lines are linear regressions for each index series, with 95% confidence bands.

absolute values of the two indicators were also similar, with an average absolute difference of just 0.026 (*CI* 0.018−0.041) across all years considered. Hence, the LSI with $g = 85$ cm seems to capture much of the variability in the LFI. The LSI series was relatively smooth, as expressed by a correlation of LSI between successive years of $r = 0.47$ (*CI* 0.11−0.74) and a correlation of LSI and year of $r = -0.75$ (*CI* −0.87 to −0.54), characteristics suggesting a reasonable signal-to-noise ratio in the indicator and good management utility. There was a marked difference in the indicators only for 1999, when two large hauls of spurdog (*Squalus acanthias*), a large species, elevated the LSI much more than the LFI. The (numerically) maximal year-to-year correlation for the LSI time-serie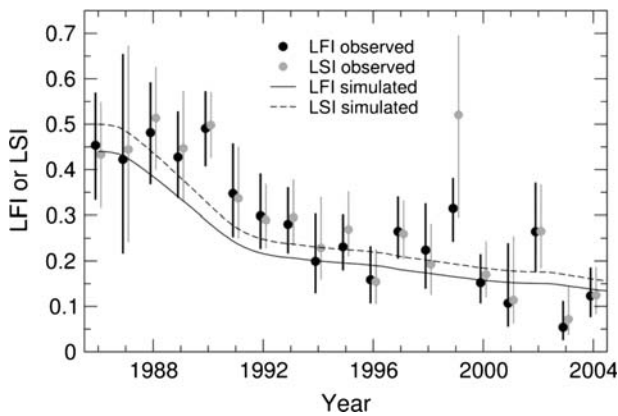s ($r = 0.51$) would have been reached with a somewhat larger threshold ($L_{max} = 110$ cm), at the cost of reducing the correlation with LFI to $r = 0.84$ and the LSI−year correlation to $r = -0.71$.

Intraspecific length distributions

Cumulative distributions of biomass over individual lengths are shown in Figure 4a for eight species sampled by the Celtic Sea WCGFS. Note that, up to shifts on the logarithmic size axis, the distributions are rather similar.

The empirical biomass distributions for each species are narrow compared with the body-length range covered by the survey, i.e. the range relevant for the LFI, in the following sense. The median biomass-weighted s.d. of $\log_{10}$ length across all species and all years in the period 1986−2004 was 0.0808 (Figure 4b). A range spanning 4 s.d. (by Chebyshev's inequality guaranteed to cover 75% of biomass) here corresponds to a factor $10^{0.323} = 2.1$. This value is small in relation to the size range 10−156 cm covered by the survey, which corresponds to a factor of $10^{1.19} = 15.65$. As a result, in a given year, only few species in the survey have length distributions that markedly straddled the individual-size threshold h.

The observed length distributions of small species such as blue whiting, megrim, and whiting only marginally cover the LFI length threshold of 50 cm (Figure 4a). They affect the LFI, therefore, only by changes in their population abundance. Similarly, large species such as cod or anglerfish contribute only minor proportions of their biomass to the small category; these species again affect the LFI mostly through their population biomasses. Species of intermediate size in the survey, such as haddock, hake, and monkfish, however, contribute to both size categories. The biomasses of these species therefore affect the LFI and the LSI in different ways. In particular, changes in their population structure can exert effects on the LFI that do not necessarily translate into corresponding changes in the LSI. The variability of length distributions in the survey data over the study period is therefore considered by
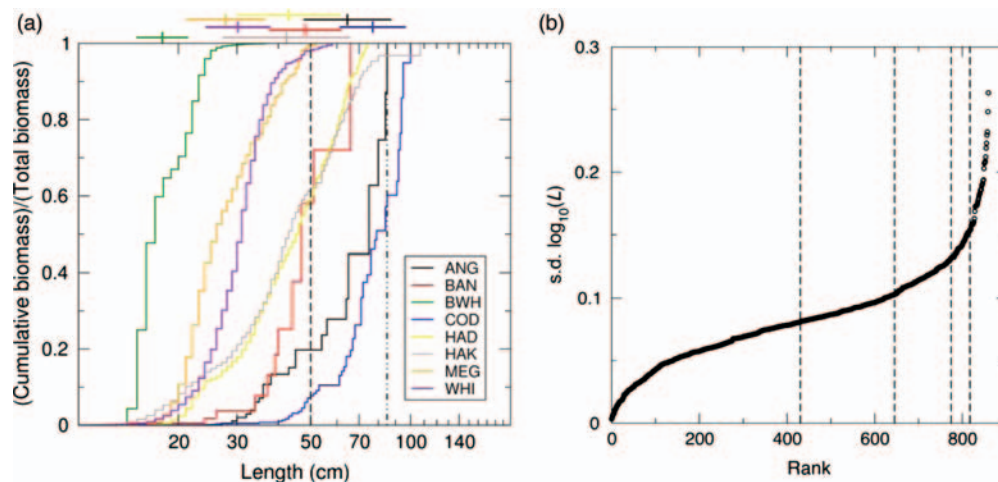

Figure 3. Time-series of the LFI (large fish threshold $h = 50$ cm) and the LSI (large species threshold $g = 85$ cm) for the Celtic Sea from WCGFS survey data (dots) with 95% *CI*s (bars). Also shown are corresponding simulation results using the PDMM (lines). The model LFI was calculated using regression lines derived from empirical WCGFS data (Figure 1).

Figure 4. (a) Cumulative distributions of population biomasses over individual lengths, for eight main species in the WCGFS in 1998. The threshold separating large and small individuals by definition of the LFI ($h = 50$ cm) is indicated by a dashed vertical line, and the threshold separating large and small species by definition of the LSI ($g = 85$ cm) by a semi-dashed vertical line. Blue whiting (BWH), megrim (MEG), haddock (HAD), and whiting (WHI) count as small species, whereas anglerfish (*L. piscatorius*; ANG), monkfish (*L. budegassa*; BAN), hake (HAK), and cod (COD) count as large species. Biomass-weighted mean logarithmic lengths and the corresponding s.d. values are indicated as horizontal lines. (b) The s.d. values of biomass-weighted $\log_{10}(L)$ for all species in the WCGFS and all years from 1986 to 2004 where more than one individual was sampled. The parameter s.d. $\log_{10}(L)$ is a measure for the width of an intraspecific length (L) distribution. In the graph, the s.d. $\log_{10}(L)$ values are ranked in order of increasing size, with the 50th (median), 75th, 90th, and 95th percentiles marked as vertical dotted lines.
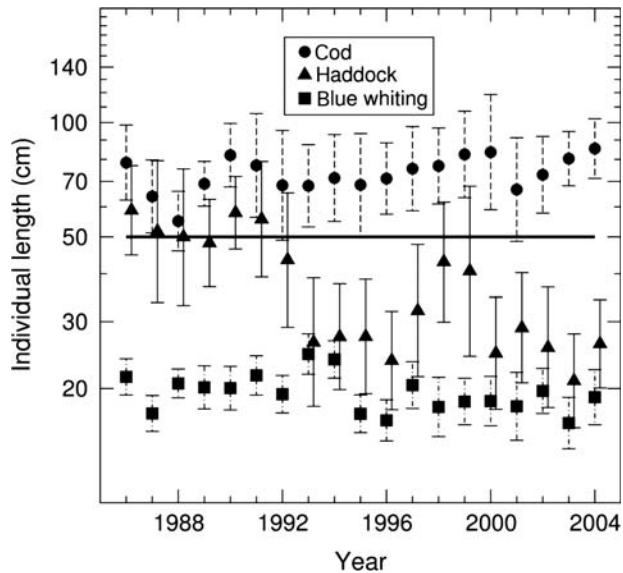
Figure 5. Time-series of means and s.d. (plotted as mean $\pm$ 0.5 s.d.) of biomass-weighted log-length, for selected species in the WCGFS. The horizontal line indicates the 50-cm length threshold separating small and large categories in the Celtic Sea LFI.

Table 1. The s.d. of biomass-weighted $\log_{10}$ length values for eight species in the WCGFS in 1998, calculated using raw survey data (Figure 4a) and survey data raised using each of three catchability curves (curve 1, cod; curve 2, haddock; curve 3, whiting) from Fraser *et al*. (2007).

Species	Raw	Curve 1	Curve 2	Curve 3
Anglerfish (*Lophius piscatorius*)	0.133	0.160	0.121	0.129
Monkfish (*Lophius budegassa*)	0.110	0.120	0.128	0.105
Blue whiting	0.078	0.084	0.054	0.088
Cod	0.100	0.119	0.099	0.100
Haddock	0.157	0.175	0.162	0.151
Hake	0.193	0.225	0.225	0.207
Megrim	0.120	0.147	0.155	0.143
Whiting	0.098	0.186	0.181	0.169

looking at temporal changes in mean biomass-weighted logarithmic length of individuals (Figure 5). For blue whiting and cod, there appears to be little systematic variation. For haddock, which is by our definition of the LSI a small species ($L_{max} = 82$ cm < 85 cm), there was a trend towards smaller lengths and a transition from a distribution dominated by large fish (length >50 cm) to a distribution mainly contributing to the small component of the LFI. Such trends in mean logarithmic length, seen also for a few other species, generally go along with pronounced changes in total abundance so that, over the periods when a population is abundant, the variation in its mean size is rather small.

The analyses of length distributions above were carried out directly on survey data, without correcting for variations in catchability with length. As such, the results are immediately relevant for interpreting indices such as LFI or LSI, which are defined in terms of survey data. Comparative studies find clear signals of length-dependent catchability in bottom-trawl surveys similar to that considered here (Korsbrekke and Nakken, 1999; Benoît and Swain, 2003), but absolute catchabilities are difficult to measure. Fraser *et al*. (2007) estimated catchability curves for several demersal species by comparing North Sea bottom-trawl survey data with
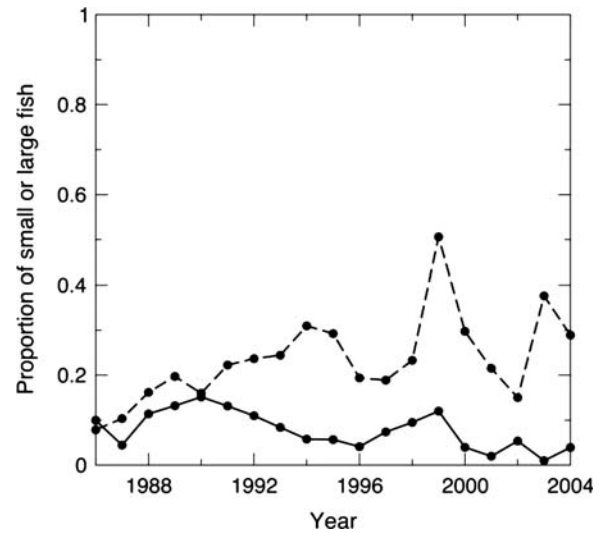

Figure 6. The proportion of the biomass of small fish species attributable to large fish (line) and the proportion of biomass of large fish species attributable to small fish (dashed line) for the period 1986–2004, for all species in the WCGFS.

VPA assessments. Those specific curves are unlikely to apply directly to the Celtic Sea WCGFS, but provide an opportunity to evaluate the effect on community length distributions of applying arbitrary but realistic catchability curves. The s.d. values of biomass-weighted logarithmic length (Table 1) were calculated for the eight species anglerfish (*Lophius piscatorius*), monkfish (*Lophius budegassa*), blue whiting, cod, haddock, hake, megrim, and whiting in the WCGFS in 1998, using raw survey data (Figure 4a) and survey data raised across all eight species using each of three catchability curves (cod, haddock, and whiting) from Fraser *et al*. (2007). The s.d. for given species changed little with catchability correction.

Evaluating the two contributions to the left side of Equation (1), we found that the proportion of large fish among small species was low (close to or below 0.10) throughout the period 1986–2004 (Figure 6). The proportion of small fish among large species increased over time, but remained, except 1999, below 0.40 (Figure 6). However, again excluding 1999, the proportion of small fish among large species was low (<0.20) when the LSI attained high values (>0.40). As a result, the second term on the right side of Equation (1) was generally small, with an average value of <0.07 and a maximum value of <0.09, excluding the 1999 value. Summarizing, the two contributions to the difference between the LFI and the LSI on the right side of Equation (1) were both relatively small and largely compensated each other (Figure 3). In passing, note that this approximate compensation is not just fortuitous. It follows from any situation in which (i) intraspecific distributions of biomass over logarithmic lengths are, up to a shift on the log-length axis, similar between species and approximately symmetrical (as in Figure 4a), and (ii) biomass is distributed approximately evenly along the logarithmic body-size axis, as suggested by Sheldon *et al*. (1972).

Modelling
Using simulations to compare time-series of the LFI and the LSI
The overall structure of the PDMM community used to simulate LFI and LSI dynamics is shown in Figure 7. Although this

community has a fish species richness, a range of fish body masses, and a range of fish trophic levels similar to the Celtic Sea community (Froese and Pauly, 2010), it differs from the Celtic Sea community in many details. In particular, as the model community was created though a stochastic assembly process, there are differences in the topologies of the underlying foodwebs. However, simulated exploitation of the PDMM community with empirical harvesting rates as input produced an LSI time-series for the period 1986–2004 that reasonably matched the empirical LSI
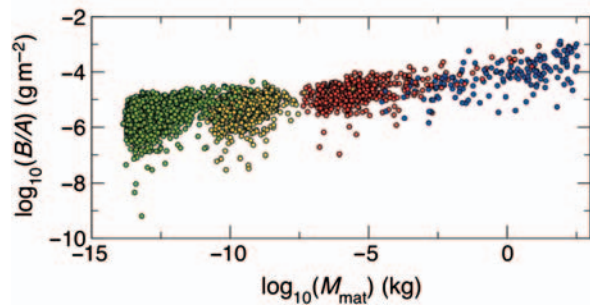

Figure 7. The model marine community assembled using the PDMM for the Celtic Sea simulation. The vertical axis gives the biomass density (biomass B divided by the total area A) on a log scale, and the horizontal axis gives the maturation body mass M_{mat} on a log scale. Each dot represents one species, colour-coded according to the nearest integer trophic level: green, yellow, red, and blue represent the trophic levels 1, 2, 3, and 4, respectively. The trophic level of all producer species was defined as 1, and the trophic level of a consumer species calculated as 1 plus the mean biomass-weighted trophic level of prey consumed. Model species with $M_{mat} > 10^{-3.66}$ kg are interpreted as fish, because $10^{-3.66}$ kg is the smallest M_{mat} found for Celtic Sea fish species in FishBase (Froese and Pauly, 2010).

values (Figure 3), with $R^2 = 0.474$ using all empirical values and $R^2 = 0.725$ if the outlier with the large spurdog catch in 1999 was not considered.

The LFI series for the PDMM community was computed using observed narrow intraspecific distributions of biomass over logarithmic length from the WCGFS (Figures 1b and 4a). The model LFI and LSI were similar, as for the empirical LFI and LSI. The average absolute difference between model LFI and LSI values at the start of each year was 0.0343. Model LFI and LSI were highly correlated ($r > 0.999$).

LFI and LSI series modelled using the FCSRM also showed similar values across all tested levels of fishing effort E. For each fishing regime and LSI threshold, the LFI and the LSI were similarly correlated over time and effort, so we present results for just the LSI threshold of 85 cm. A regression of LFI against LSI across values of E quantified their strong correlation ($r = 0.996$). Results of LFI against LSI for 19-year time-series with fishing effort ranging from $E = 0.1$ year^{-1} to $E = 1.5$ year^{-1} and using an 85-cm LSI threshold are shown in Figure 8a; these LFI and LSI values display high correlation for each E-value ($r > 0.943$). Figure 8b shows modelled cumulative biomass distributions over individual length for all maturation size classes in the FCSRM in the community equilibrium state attained with a fishing effort of $E = 1.5$ year^{-1}. Like the empirical distributions (Figure 4a), the model biomass distributions are narrow and largely consistent across species of different size. This result, independent of the survey data, supports the notion that the narrow empirical biomass distributions observed are a natural phenomenon and not a result of survey bias. Modelled mean biomass-weighted logarithmic lengths of individuals over time and the corresponding s.d. values are presented in Figure 9. With one exception, changes in the mean logarithmic length are within 1 s.d. of the original distribution.
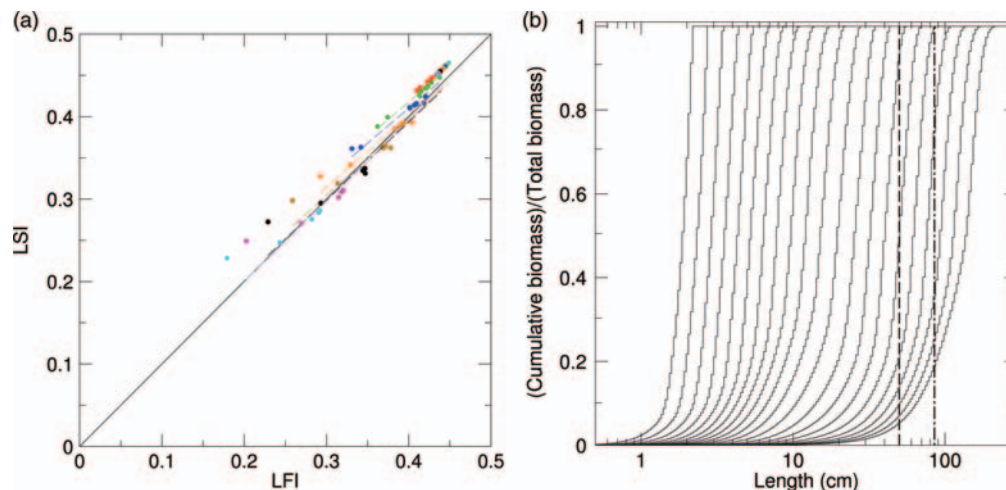

Figure 8. (a) Plot of LSI vs. LFI for eight simulations of the FCSRM for an LSI threshold of 85 cm. The red dots are annual LFI–LSI values for a fishing regime applied for 19 years, with trawlnet mortality resulting from fishing effort of $E = 0.1$ year^{-1} across all modelled fish species and years. The green, blue, orange, brown, black, magenta, and cyan dots are effort values of $E = 0.3, 0.5, 0.7, 0.9, 1.1, 1.3,$ and 1.5 year^{-1}, respectively. A regression line is drawn for each fishing regime (dashed coloured lines); each regression line gives a high correlation with $r > 0.943$. The solid black line corresponds to LFI = LSI. (b) Modelled cumulative distributions of population biomasses over individual lengths for the FCSRM in its equilibrium state for high fishing effort ($E = 1.5$ year^{-1}). The threshold separating large and small individuals by definition of the LFI ($h = 50$ cm) is shown by a dashed vertical line, and the threshold separating large and small species by definition of the LSI ($g = 85$ cm) by a semi-dashed vertical line. Each solid line represents one maturation size class, with size classes evenly spaced on a logarithmic body length from 1.36 to 136 cm.
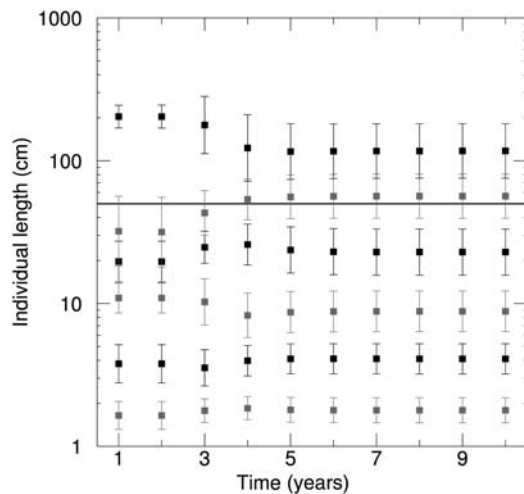
Figure 9. Modelled time-series of means and s.d. values of biomass-weighted log-length, for the FCSRM. Only every fourth maturation size class is shown for clarity. These are, in ascending order along the vertical axis, $M_{mat} = 0.025, 0.40, 6.3, 99.5, 1577$, and 25 000 g. The horizontal line indicates the large fish length threshold $h = 50$ cm separating small and large categories in the LFI. Time-series are shown from the commencement of fishing with effort $E = 1.5$ year^{-1}.

Discussion

The LFI characterizing the distribution of individual sizes was originally intended to show the direct effect of size-selective exploitation, i.e. the removal of large fish. However, it is also sensitive to changes in small fish biomass, such as those associated with predation release, and is now understood to integrate indirect trophic processes operating at multiyear scales (Daan *et al.*, 2005; Greenstreet *et al.*, 2011). The indicator also seems to respond to spatial heterogeneity in fishing effort (Shephard *et al.*, 2011b). Here, we compared empirical and modelled time-series of the LFI with corresponding series of the LSI characterizing the distribution of species sizes, and found that these indicators were highly correlated. This correlation suggests that fishing-induced change in the LFI can be explained by changes in the abundances of fish species of different size, at least for the Celtic Sea. Such changes in species abundances represent fundamental changes in community structure.

This investigation of the WCGFS data showed that, with an appropriate choice of large-species threshold *g*, the LFI and the LSI become highly correlated and attain numerically similar values. Even when choosing the large-species threshold *g* by regularity criteria independent of the LFI time-series, a good correlation between the two time-series is achieved. Following the empirical analysis, a close correlation and numerical agreement between the LFI and the LSI were also found when a fishing regime corresponding to that in the Celtic Sea was applied to a rather general model (PDMM) community. Commonalities between model and empirical communities were only at a macro-ecological level, suggesting that the relationship between the indicators may be a consequence of common and genuine ecological responses to fishing, not simply a particularity of the Celtic Sea. It would be useful to conduct empirical studies comparing the LFI and the LSI in other regions to confirm the generality of the relationship observed here.

Changes in the LFI might result readily from changes in species abundance if most of the biomass of small species was distributed below the LFI threshold, but most of the biomass of large species was above this threshold. In accordance with this scenario, the intraspecific size distributions from the WCGFS data were surprisingly narrow compared with the observed length range in the survey time-series, i.e. 10–156 cm. Notably, the s.d. of biomass distributions for eight species (Figure 4a) were quite robust to "correction" (Table 1) using three arbitrarily chosen catchability curves (Fraser *et al.*, 2007). There was also evidence that variations in mean logarithmic length over time were of similar magnitude. A mathematical analysis showed that this within- and across-year variability of the lengths of individuals belonging to a species leads to two contributions to the difference between the LFI and the LSI of opposite sign, which were both small (magnitude <0.1, except in 1999) and largely compensated each other. Except for these contributions, small species in the LSI consistently contribute most of their biomass to small fish in the LFI and vice versa for large species, so that the LFI and the LSI do not differ much. As both indices use the same denominator, differences in the attribution of individuals in species of intermediate size (spanning the threshold) are in essence the sole source of difference between the two indices.

A generic size-structured community model (FCSRM), in which intraspecific size distributions emerge from ecological and demographic constraints, reproduced the observations from survey data that these distributions were narrow compared with the surveyed size range and varied little over time (Figures 8b and 9). This corresponds to the result for the survey data (even when corrected for catchability) and for the PDMM. In each case, the narrowness of these distributions and the robustness of their shapes to fishing pressure lead to near numerical equivalence of the LFI and the LSI in that model.

Ecological implications

At the start of this article, we asked whether fishing alters marine community size structure mainly by selectively removing larger individual fish, or by changing the relative abundances of species of different size. The results of the analysis show that in the Celtic Sea, it is predominantly the latter. As the LFI and the LSI were very close over a range of conditions, the LFI may be used and interpreted as an indicator of community change caused by fishing (in the sense of changing the relative abundance of different species), rather than merely a measure of the excess mortality of large fish. This is a departure from its original purpose, but one that gives it more profound meaning. Taking the example from the Celtic Sea, the biomass of large species declined significantly over 19 years of exploitation while there was a significant increase in the biomass of small fish species. The decline in large fish species was consistent throughout the survey period, perhaps reflecting sustained exploitation. In contrast, the increase in small fish species abundance was highly variable, reflecting the greater sensitivity of those populations to short-term environmental and recruitment variability. These observations suggest that in the Celtic Sea, size-selective species removal by fishing imposed significant change in community structure/composition.

The direct link between the LSI and the populations of species is informative when focusing attention on long-term changes in community structure. Local extinction or substantial depletion of most large species may require long recovery times. Experience in heavily exploited demersal fish communities such
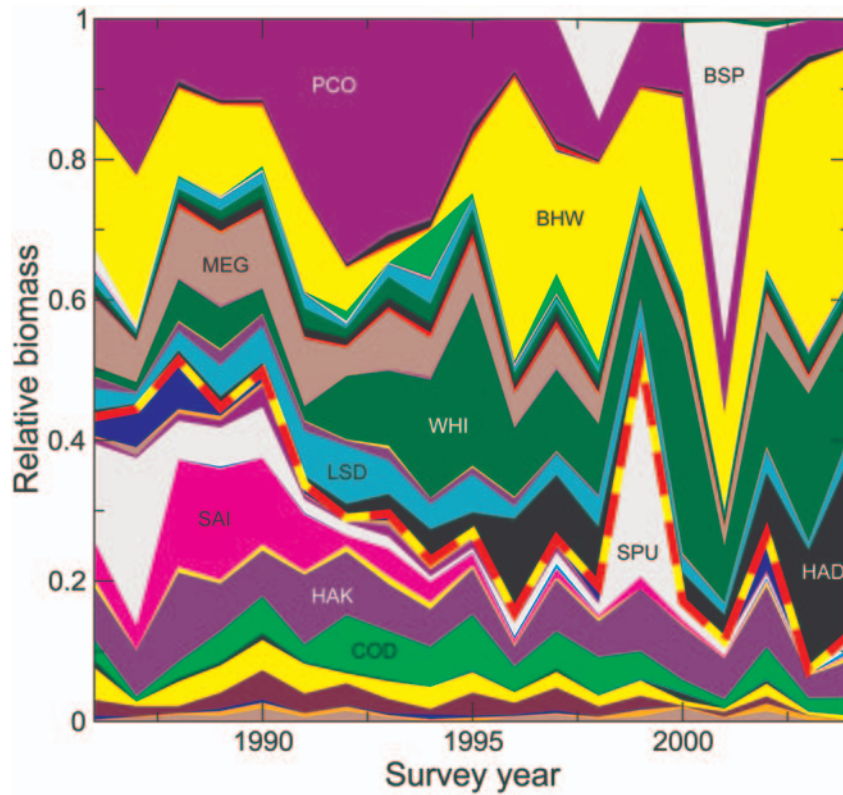
Figure 10. Decomposition of the WCGFS LSI into the contributions of each species. Species are sorted by asymptotic size. The alternating yellow–red line separates the large species component of the LSI (characterized by $L_{max} > g = 85$ cm), below the line, from the small-species component above it. For the major components of the Celtic Sea community, species are identified by three-letter codes (Irish Marine Institute): blue whiting (BHW), splendid alfonsino (BSP), cod (COD), haddock (HAD), hake (HAK), small-spotted catshark (LSD), megrim (MEG), poor cod (PCO), saithe (SAI), and spurdog (SPU).

as that on the Eastern Scotian Shelf suggests a multidecadal process (Hutchings, 2000; Choi *et al.*, 2004; Hutchings and Reynolds, 2004). In this context, perhaps current evidence of recovery in the North Sea LFI (Greenstreet *et al.*, 2011) is driven by recovery of the intraspecific size structure of species of intermediate size (e.g. haddock) spanning the index threshold. Once these intermediate species regain their natural size structure, LFI recovery may stall until larger species recover, revealed through the LSI.

The LFI and LSI: complementary indicators
Conventional survey data provide information about trends in population abundance and the size structure of catchable fish species (Cotter *et al.*, 2009), from which both the LFI and the LSI can be estimated, although both indices may require interpretation before being applied to new systems. The definition of the LSI involves the concept of the size of a species, specified by its maximum length L_{max}. In some borderline cases, different approaches to determining L_{max} might assign a species either to the large or to the small category, or change the size ranking among species. This uncertainty might be undesirable in management. For the LFI, species of intermediate size (i.e. spanning the index threshold) are partially apportioned to small and large categories. In effect, the LSI's sharp distinction between large and small species is smoothed by the LFI, with a set of empirical smoothing kernels each being the sampled population structure of a species entering the sample. In principle, other types of

smoothing kernel could be used to regularize the LSI (e.g. a fixed hypothetical population structure). The LFI can be considered as empirical smoothing of the LSI, which may be more appropriate where the management question specifically focuses on community size structure. On the other hand, because the LSI is explicitly species-based, changes in it are attributable to changes in particular populations (for instance the large catch of migratory spurdogs in 1999). Direct insights into the composition of a particular LSI time-series are offered by graphs that decompose total fish biomass into the proportional contributions of each species, ordered by species size, and separating small and large components (Figure 10). This representation shows the values the LSI would attain if the size threshold was chosen to lie above or below that of any given species. For example, we see at a glance that if haddock (HAD, $L_{max} = 82$ cm) had been included among the large species, the LSI would have slightly reversed its trend from 2001 to 2004. The graph also shows that the decline in small poor cod (PCO, $L_{max} = 30$ cm) considerably mitigates the decline in the LSI over the study period. If a somewhat larger mesh size had been used in surveys, poor cod could have been excluded, emphasizing the negative trend not only in the LSI, but also in the LFI. However, the graph also shows that, despite this dependence on parametrization of the LSI, any choice of threshold length would have resulted in either an LSI time-series without a clear trend or an overall decline over the 19-year study period. For the LFI, such analyses are possible too, but are generally less transparent.

The ecosystem approach to fisheries management sets substantial new demands for the monitoring of community change in response to fishing practice. Limited resources strongly favour the use of existing survey data, and these often provide long time-series. The LFI offers a flexible means of monitoring the effect of fisheries management on the size structure of communities. What the LSI and our analysis of this metric have added is insight into the underlying species-specific responses of the community to management. Previous studies have shown that fishing-induced changes in community species composition may demand longer recovery times than changes in intraspecific size structure. In light of this, we found that fishing in the Celtic Sea modifies community size structure mainly through changes in the population sizes of species. Such a phenomenon may extend to other areas; this is suggested by the modelling analysis, but further empirical studies in other areas are required to confirm this.

Acknowledgements

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