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Modelling recovery of Celtic Sea demersal fish community size-structure

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ABSTRACT

The Large Fish Indicator (LFI) is a size-based indicator of fish community state. The indicator describes the proportion by biomass of a fish community represented by fish larger than some size threshold. From an observed peak value of 0.49 in 1990, the Celtic Sea LFI declined until about 2000 and then fluctuated around 0.10 throughout the 2000s. This decline in the LFI reflected a period of diminishing 'large' fish biomass, probably related to high levels of size selective fishing. During the study period, fishing mortality was maintained at consistently high values. Average biomass of 'small' fish fluctuated across the whole time series, showing a weak positive trend in recent years. Inter-annual variation in the LFI was increasingly driven by fluctuation in small fish biomass as large fish biomass declined. Simulations using a size-based ecosystem model suggested that recovery in Celtic Sea fish community size-structure (LFI) could demand at least 20% reductions in fishing pressure and occur on decadal timescales.

1. Introduction

The Large Fish Indicator (LFI) is a univariate indicator of demersal fish community 'state' (Cury and Christensen, 2005; Greenstreet et al., 2011). This indicator describes the proportion (by weight) of the fish community that is larger than some pre-defined length threshold, i.e., ('large' fish biomass)/(total fish biomass). Thus, the LFI expresses a well-understood direct effect of fishing – loss of large individuals and large species that results in curtailment of community size-structure (e.g., Haedrich and Barnes, 1997; Shin et al., 2005; Shephard et al., 2012). However, the metric also integrates a longer-term indirect effect of fishing, i.e., increasing biomass of small fish contingent on reduced predation pressure associated with removal of large piscivores (Greenstreet et al., 2011; Shephard et al., 2011). The LFI has been adopted by OSPAR as a 'fish community' indicator (Heslenfeld and Enserink, 2008) and identified in the European Union's Marine Strategy Framework Directive (MSFD) as a 'food web' indicator.

The current study calculates LFI for two temporally overlapping fisheries surveys to describe the 'state' of the Celtic Sea demersal fish community from 1986 until 2011. This builds on the work of Shephard et al. (2011) whose single-survey LFI time series concluded in 2004. The Celtic Sea is an excellent location for such an analysis since good fisheries survey programmes were already established quite early in the fisheries development phase (Pinnegar et al., 2002). This means that data are available to calculate values of ecosystem indicators for the period before long-term intensive exploitation of the fish community, and also up to the present when many of the commercial species in the region are 'seriously depleted' (ICES, 2010a,b). In order to interpret observed trends in the LFI and to make useful management predictions, both empirical and modeling analyses are presented. Changes in the empirical indicator (1986–2011) are considered in relation to changes in 'large' and 'small' fish biomass and in fishing mortality. A size-based community model is then used to evaluate fishing scenarios that might move this heavily exploited fish community towards the MSFD target of 'Good Environmental Status' (GES) by 2020.

2. Methods

2.1. Empirical analyses

Fisheries-independent survey data and fishing mortality estimates from stock assessment models were used. Two survey time series were analysed:– the (no longer active) first quarter (Q1) UK West Coast Ground Fish Survey (WCGFS) and the fourth quarter

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(Q4) Irish Ground Fish Survey (IGFS). Both surveys were designed in accordance with the standard International Bottom Trawl Survey (IBTS) protocol and cover overlapping areas of the Celtic Sea (ICES area VIIg). The UK Centre for Environment, Fisheries and Aquaculture Science (Cefas) operated the WCGFS using a Portuguese high headline trawl with a 20 mm codend liner. This survey took place in March each year, with effort varying around $n = 30–60$ hauls per year in the study area. The first 2 years of the WCGFS had inadequate sampling effort and/or spatial coverage, and were thus excluded leaving valid survey data for 1986–2004. The Irish Marine Institute conducts the IGFS survey annually in October/November using a Grande Ouverture Verticale (GOV) trawl with a 20 mm codend liner. In a given year, trawl samples are collected at around $n = 60$ sites randomly selected from a pool of around $n = 100$ fixed sampling stations in the area. The IGFS commenced in 1997 using the RV Celtic Voyager but since 2003 has employed the RV Celtic Explorer. To avoid inconsistency introduced by changing survey vessel, we use IGFS data only from 2003 to 2011.

All fish in survey catches are identified to species. For the current study, catch numbers at length (L) were converted to weight (W) at length using weight–length relationships ($W = \alpha L^{\beta}$), where the α and β parameters were derived from survey data when available (only main commercial species are weighed in the survey) or from FishBase (http://www.fishbase.org). For the WCGFS, catch weight at length of each species and length class in each trawl sample was converted to a biomass density by dividing the observed catch by the area trawled, where area trawled is wingspread × distance towed. For the IGFS, catch weight at length of each species and length class was converted to a rate (biomass sampled per unit time) based on individual trawl duration. It should be noted that biomass of small fish is typically much greater in the Q4 IGFS than in the Q1 WCGFS, as the former survey encounters large numbers of small summer-recruited fish prior to winter mortality.

The established LFI protocol was followed (Greenstreet et al., 2011) to produce overlapping survey LFI series based on the same species complex and 'large' fish threshold (50 cm) as described by Shephard et al. (2011). ICES statistical rectangles sampled in fewer than half of all years of the WCGFS were excluded to minimise the potential for bias associated with variation in sampling effort or spatial variation in fish community composition. The IGFS has a much larger survey footprint than the Celtic Sea component of the WCGFS and in the two overlapping years (2003 and 2004) the two surveys only sampled around 10–14 ICES rectangles in common. The initial intent of the current paper was to use data from only the overlapping rectangles in order to produce a combined LFI based on the same underlying fish community. However, it was decided that this overlapping area was too small to be of management value and included too few data for robust analyses. As such, the same WCGFS data were used as in Shephard et al. (2011) and a partially overlapping, larger component of the IGFS data was selected to correspond. The selected IGFS area comprised all trawl samples located between longitude 5.00–9.00°W and latitude 50.00–52.00°N.

The observed maximum values of the WCGFS LFI (approximately 0.42–0.49 in the late 1980s) were taken to represent values for this metric during an earlier period in the Celtic Sea fisheries exploitation history when fish stocks were generally in better condition. These values may be considered to describe GES in this community. The LFI responds to changes in biomass of both 'large' and 'small' fish and it is important to understand the relative influence of these groups. Hence, mean annual biomass of each of large and small groups was plotted for the study period of each survey.

Fishing pressure in the Celtic Sea was considered in terms of the harvesting rate H, which we define as the rate at which a population's total biomass decreases because of removals by fishing. In the model community used below, entire populations (including

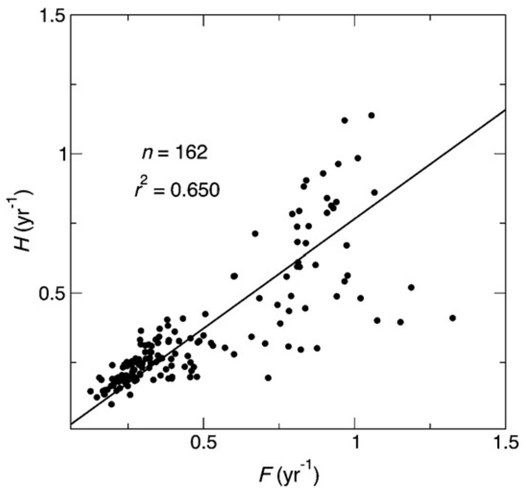

Fig. 1. Correlation between annual harvesting rates (H) and fishing mortality rate (F) for eight assessed fish species in the Celtic Sea, for the years 1986–2008. The slope of the regression line is 0.786.

all age groups) of fish species are modelled, so the use of H is more appropriate than F, because, unlike F, H gives the fishing mortality for the whole population. Use of H in the current paper for both empirical and modelling analyses allows a direct comparison. Harvesting rates were calculated from time series of empirically derived catch and total stock biomass estimates for the Celtic Sea (1986–2008) from ICES reports (ICES, 2006, 2007, 2008, 2009, 2010a). For each year over the period 1986–2008, a mean H value, $\bar{H}$, was calculated as the biomass-weighted mean H for eight main fish stocks assessed in the Celtic Sea [anglerfish, blue whiting, cod, haddock, hake, megrim, monkfish (*Lophius budegassa*) and whiting], although there were some missing years for anglerfish (2006–2008), blue whiting (2002–2004, 2007–2008), cod (2008), haddock (1986–1992), megrim (2006–2008) and monkfish (2006–2008) because of missing catch and/or total stock biomass data. For each species, for each year where data was available, H was calculated by computing the proportion (catch)/(total stock biomass) and converting this proportion into a rate in units of year^{-1}. This conversion was required because the model used below operates in continuous time. Annual harvesting rate (H) by species showed a close linear relationship with F (Fig. 1). The two observed LFI series were qualitatively interpreted in terms of temporal changes in large and small fish biomass and annual mean harvesting rate $\bar{H}$.

2.2. Modelling

The ecological mechanisms underlying changes in the LFI are complicated. Greenstreet et al. (2011) suggested that the slow response of the North Sea LFI to reductions in fishing pressure could be due to the time it takes to reverse increases in biomass of small fish individuals that have arisen from predation release. Mechanisms underlying this maintenance of increases in small fish individuals are uncertain, but could include depensation effects, whereby increases in small fish species result in increased predation and/or competition with the juveniles of larger species, thus preventing or delaying their growth into large individuals (Walters and Kitchell, 2001; Fauchald, 2010; Rossberg, 2012; Minto and Worm, 2012). Shephard et al. (2012) showed that changes in the Celtic Sea LFI during 1986–2004 were mainly due to changes in relative species abundances, rather than changes in intraspecific size-structures. The dominance of species composition in changing community size-structure implies that recovery of the LFI may depend on corresponding recovery of large species.

The ecological complexity inherent in LFI trends means that mechanistic modelling approaches are necessary when making management predictions for the LFI (Greenstreet et al., 2011; Shephard et al., 2011). For this study, we use the Population-Dynamical Matching Model (PDMM) of Rossberg et al. (2008). The PDMM constructs multispecies model communities through an iterative assembly algorithm, following Caldarelli et al. (1998), that starts with an empty community and then repeatedly adds species and simulates community dynamics with the new species, removing those that go extinct. Community dynamics are specified by a set of ordinary differential equations, one for the biomass of each species population. The equations describe for each species population the strength of competition for resources, consumption, growth, predation and non-predation losses. These processes together set energetic constraints on community dynamics, and the rates of these processes are determined by values of modelled species traits. The model distinguishes between consumers and (primary) producers. The growth of consumer populations depends on food availability, while producer growth is limited by intra- and interspecific competition amongst producers. Both producer and consumer species are assigned a maturation body mass (M_{mat}), so that model species are size-differentiated. Each new species added to an existing community has trait values that are random variations of the traits of a randomly chosen extant species (Rossberg et al., 2008); this leads to phylogenetic constraints, found to be an important determinant of food-web structure in real systems (Cattin et al., 2004; Bersier and Kehrli, 2008; Naisbit et al., 2012). The PDMM assembly algorithm is run until the targeted number of coexisting model species is reached.

The PDMM has been parameterised for a temperate shelf community in the Northeast Atlantic (see Shephard et al. (2012) for further details on the parameterisation methodology, including data sources used); and was used to construct a model shelf community with 208 fish species (Shephard et al., 2012), comparable to the number of demersal fish species in the Celtic Sea (approximately 191; Froese and Pauly, 2010). A model consumer species is taken to be a fish species if it has $M_{\mathrm{mat}} > 10^{-3.66}$ kg, the empirically derived lower threshold for fish species (Froese and Pauly, 2010; Shephard et al., 2012). In total, the resulting model community describes the biomasses and interactions of thousands of species over a large size range (range of M_{mat}), covering phytoplankton to large fish. Model community properties, such as distributions of species over trophic levels and sizes, broadly match empirical data (Shephard et al., 2012). At the community level, the model is thus expected to exhibit similar dynamics as the Celtic Sea community, motivating its use in this study.

Since the PDMM does not represent the intraspecific size-structure of species, the LFI for the model community had to be calculated using the procedure developed by Shephard et al. (2012). By this procedure, for each model fish species, a (fixed) proportion of the population biomass, α, was assumed to be due to large fish individuals. The assumption of fixed α is justified by the empirical analysis of Shephard et al. (2012), which showed that changes in the Celtic Sea LFI during 1986–2004 were largely due to changes in relative species abundances, not changes in intraspecific size-structures. The α values were calculated for model fish species based on the empirical relationship between α and M_{mat} (Shephard et al., 2012). Specifically, M_{mat} for each model fish species was first related to a corresponding maximum observed length (L_{max}), using the linear regression line $\log_{10}(L_{\mathrm{max}}) = (0.308)\log_{10}(M_{\mathrm{mat}}) + 1.82$ ($r^2 = 0.640$) for the 91 species from the WCGFS with sufficient available data. Values of L_{max} were derived from the WCGFS, and M_{mat} values were derived using length at sexual maturity (L_{mat}) values from FishBase (Froese and Pauly, 2010) and length–weight conversion parameters from the WCGFS (where possible) and FishBase (Froese and Pauly, 2010). Secondly, L_{max} for each model fish species was related to α using $\alpha = 0$ for $L_{\mathrm{max}} \leq 50$ cm (by definition) and the non-linear regression curve $\alpha = (L_{\mathrm{max}} - 50\,\mathrm{cm})^{1.39}/[(L_{\mathrm{max}} - 50\,\mathrm{cm})^{1.39} + (17.9\,\mathrm{cm})^{1.39}]$ (obtained using a non-linear least squares fit to all 102 species from the WCGFS, with generalised coefficient of determination $R^2 = 0.477$) for $L_{\mathrm{max}} > 50$. Assigning α values to all model fish species allowed straightforward calculation of the LFI using the formula $\mathrm{LFI} = \sum_i \alpha_i B_i / \sum_i B_i$, where α_i and B_i are α and the population biomass, respectively, for fish species i.

Fishing pressure in the model was measured in terms of the harvesting rate H (see above). The LFI for the unfished model community was 0.71, which is higher than the empirical value of 0.45 in 1986. Thus, as in Shephard et al. (2012), fishing was first applied to the community at a low constant rate of $H = 0.08\,\mathrm{year}^{-1}$ on all model fish species, reducing the model LFI to an equilibrium value (0.44) close to that observed in 1986. Then, for each year in 1986–2008, fishing was applied to each model fish species at a harvesting rate equal to the empirically derived annual mean harvesting rate $\bar{H}$ (see above). Fishing was applied to all model fish species because fishing mortality of non-target species can be substantial (Piet et al., 2009). From the end of the empirical harvesting rate data in 2008, trajectories in the LFI until 2100 were modelled using six possible exploitation scenarios: $\bar{H} = 0, 0.05, 0.1, 0.2, 0.3$ and $0.4\,\mathrm{year}^{-1}$. In comparison, the maximum observed Celtic Sea $\bar{H}$ during 1986–2008 is $0.35\,\mathrm{year}^{-1}$.

3. Results

From an observed peak value of 0.49 in 1990, the Celtic Sea LFI declined until about 2003 and then fluctuated around 0.1 throughout the 2000s (Fig. 2). The two LFI series showed similar values for the 2 years of overlap. Different annual values probably reflect sampling variation and also survey timing in relation to annual small fish recruitment cycles. The decline in the WCGFS LFI reflected a period of diminishing large fish biomass (Fig. 3a) that is likely explained by sustained high harvesting rates $\bar{H}$ throughout the time series (mean = 0.27; SD = 0.03). Average biomass of small fish in the WCGFS fluctuated quite widely across the study period (SD = 254 kg km^{-2}) but showed a positive trend inverse to the decline in large fish (Fig. 3a). In the IGFS, small fish biomass also fluctuated strongly (SD = 219 kg h^{-1}) with some positive trend (Fig. 3b).

The six modelled fishing scenarios yielded a considerable range in LFI trajectories (Fig. 4). For 1986–2004, the model LFI values at the start of each year give a good match to the WCGFS empirical LFI values, with $R^2 = 0.544$ ($n = 19$); this indicates a good model

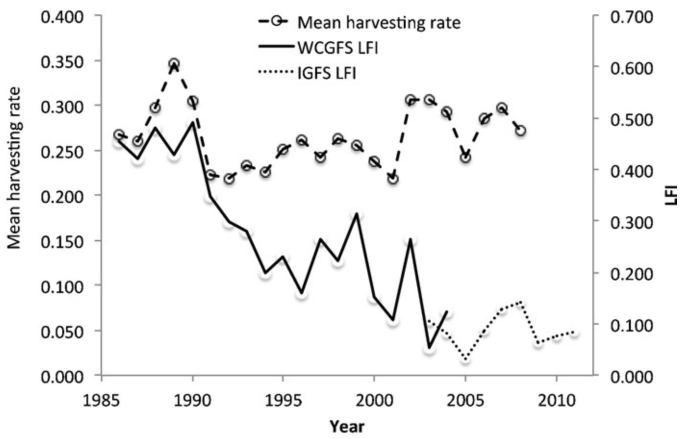

Fig. 2. Time series of annual mean harvesting rate $\bar{H}$ and the Large Fish Indicator (LFI) for the Celtic Sea. Two overlapping LFI series are shown: the UK West Coast Groundfish Survey (WCGFS) that concluded in 2004, and the ongoing Irish Groundfish Survey (IGFS).

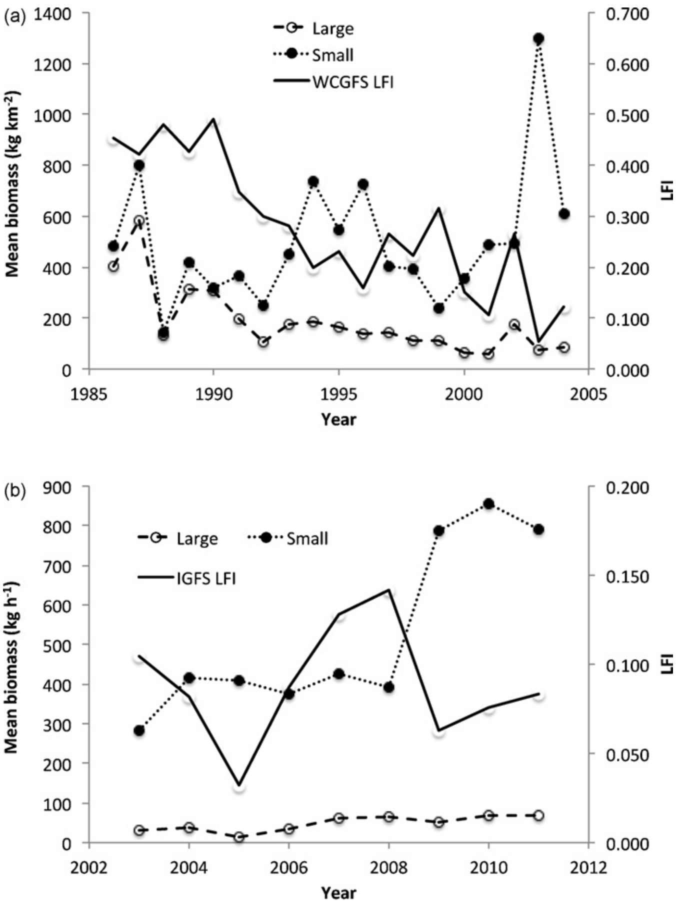

Fig. 3. Celtic Sea LFI series derived using (a) the WCGFS (1986–2004) and (b) the IGFS (2003–2011), with corresponding average annual biomass in each of 'Small' ($\leq$50 cm) and 'Large' (>50 cm) categories (note different *y*-axis biomass scales).

fit. After 2008, simulations suggested that a harvesting rate of $\bar{H} \leq 0.2$ year^{-1} would be required for the LFI to increase at all by 2020, while recovery to the observed 1986 LFI value of 0.45 would demand a rate of $\bar{H} \leq 0.1$ year^{-1}. The rates 0.2 year^{-1} and 0.1 year^{-1} are approximately 80% and 40% of the mean observed $\bar{H}$ in the Celtic Sea, respectively. Thus, the simulations suggest that maintaining fishing mortality at historical levels is unlikely to allow any increase in the LFI by 2020, or even 2100 (Fig. 4). Furthermore, they suggest that substantial reductions in fishing mortality are required for the LFI to recover to the observed 1986 level (Fig. 4).

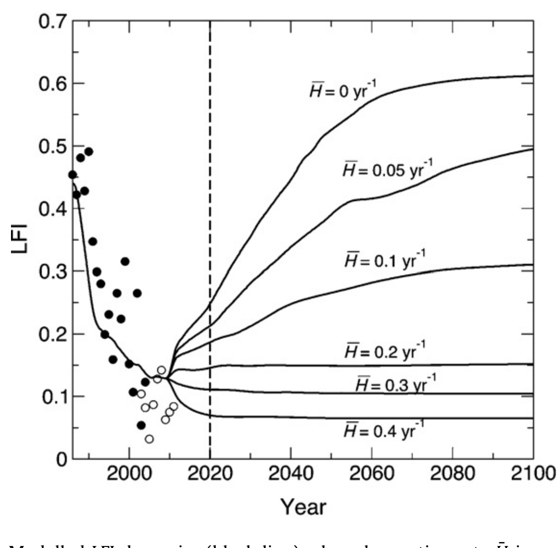

Fig. 4. Modelled LFI dynamics (black line) where harvesting rate $\bar{H}$ is applied to all fish species at values observed in the Celtic Sea for 1986–2008. From 2009, six candidate harvesting rates $\bar{H}$ are applied until 2100. A threshold of 50 cm is used for the LFI. The black filled and open circles are the empirical LFI values from the WCGFS and IGFS, respectively; the dashed vertical line marks the year 2020.

4. Discussion

Size-structure in the Celtic Sea demersal fish community was markedly curtailed between 1986 and 2003 (Blanchard et al., 2005). Using a widely recognised size-based indicator, we find that this trend continued at least until 2011. The decline in the WCGFS LFI appears to primarily reflect sustained direct removal of large fish by high rates of (size-selective) fishing. There was some impact on the WCGFS LFI trend of an increase in average biomass of small fish, but small fish had a stronger effect on inter-annual fluctuation in the indicator. In the IGFS, small fish biomass had a similar effect on annual LFI values, showing an inverse effect on the indicator. The dominance of large fish biomass in the WCGFS Celtic Sea LFI was also suggested by Shephard et al. (2011) and is in contrast to the North Sea metric, which is most strongly influenced by biomass of small fish (Greenstreet et al., 2011). Since small fish most strongly influence the IGFS and North Sea LFIs, which both refer to periods after sustained fisheries exploitation, it could be inferred that there is a shift in the primary determinant of size structure from large to small fish as the community becomes more perturbed. This is of interest as it implies that community dynamics in heavily fished systems are more influenced by (environmentally driven) shifts in small fish biomass.

Modelling results captured the rapid change in community size-structure seen in the empirical data. In addition, model predictions suggested that only exploitation below about 80% of the current rate will allow any recovery in the LFI by 2020, the target year of the EU MSFD for reaching 'Good Environmental Status'. Even in the optimistic case with exploitation below about 40% of the current rate, it would take at least several decades for the Celtic Sea LFI to return to reference values observed in the early part of the WCGFS LFI series. In practice, reductions in $\bar{H}$ of this scale are likely to have serious negative consequences for the fishing industry, and might fail to meet societal needs. Hence it is uncertain if the Celtic Sea fish community will soon achieve GES as defined by the current LFI. In view of these constraints, it is important to be clear about management objectives. If the overarching goal of the MSFD is 'sustainable exploitation', then it may be unnecessary to attempt a restoration of the fish community to a state close to the 'pristine' one. Managers could aim for some acceptable level of 'large' fish biomass and set exploitation levels correspondingly. The outcome would be only partial recovery of the LFI. However, as the management process develops further, it might become clear that full recovery of the LFI is demanded. Larger values of LFI might also allow higher fishing yields (a question not addressed here). Our analysis suggests that the Celtic Sea fish community is strongly perturbed, and only radical reductions in fishing mortality will support recovery to the state observed in the early 1980s. Fishing prior to this time might already have pushed community size-structure away from a pristine state. It is now critical to clarify the management priorities for Celtic Sea fisheries.

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