Fishing and environment drive spatial heterogeneity in Celtic Sea fish community size structure

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The Large Fish Indicator (LFI) is a univariate size-based indicator of fish community state that has been selected to support the OSPAR fish community Ecological Quality Objective (EcoQO). To operate this EcoQO, a survey-based LFI for each OSPAR region needs to be developed. However, fish communities in these regions are spatially heterogeneous, and there is evidence of within-region spatial variation in the LFI that could confound an overall indicator series. For Celtic Sea trawl-survey sites, spline correlograms indicate positive spatial autocorrelation at a similar range (≏40 km) for the LFI and for fishing effort (h year–1) from vessel monitoring systems. Statistical models reveal a strong negative effect on annual LFI by site of fishing effort within a radius of 40 km. There was a weak effect of fishing within 20 km and no effect at 10 km. LFI also varied significantly with substratum and with local fish community composition identified by a resemblance matrix derived from the survey data. Finally, there was a weak effect of survey year on LFI. Spatial stratification of LFI calculations may be necessary when developing size-based indicators for OSPAR or Marine Strategy Framework Directive regions.

Keywords: Ecological Quality Objective, ecosystem approach to fisheries management, Large Fish Indicator, marine protected areas, VMS.

Introduction

The Large Fish Indicator (LFI) is a univariate size-based indicator of fish community state (Greenstreet et al., 2011; Shephard et al., 2011). Following development in the North Sea, this metric has been selected to support the OSPAR fish community Ecological Quality Objective (EcoQO). The LFI describes the proportion (by weight) of the fish community that is larger than some length threshold, i.e. (biomass of fish > length threshold)/(total biomass of fish). Using archived fisheries-independent survey data, multidecadal LFI series have been developed for the North Sea and the Celtic Sea. The North Sea represents a single OSPAR region, and the LFI will act as a fish community indicator at that scale. In contrast, the Celtic Sea is part of a larger OSPAR region, so a broader-scale LFI series needs to be developed.

Applying indicators such as the LFI over large marine areas may be problematic because demersal fish communities are not typically spatially homogenous at such scales. The underlying ecologically mediated spatial structure has been identified as a problem for calculating fish biodiversity indicators from survey series (Greenstreet and Piet, 2008). In the North Sea, the structure and composition of the demersal fish community varies in space, but the pattern of variation is consistent over time (Daan et al., 1990; Fraser et al., 2008). Spatial structure reflects fish community links to habitat features that provide essential ecological functions, such as the provision of cover from predators, and suitable feeding habitat (Kaiser et al., 1999; Hinz et al., 2006; Dimech et al., 2008). Habitat type may also influence usage at different life-history stages for many fish, such that numerical prevalence in the community may vary strongly among habitats. Such ontogenetic changes in habitat use are well documented for plaice (Pleuronectes platessa; Gibson et al., 2002) and other groundfish species, including cod (Gadus morhua) and haddock (Melanogrammus aeglefinus; Methratta and Link, 2007).

Examination of spatial variation in the LFI across the North Sea revealed distinct patterns that were essentially consistent over time (ICES, 2010a), and consistent with spatial variation in the structure and composition of the fish and benthic communities determined using other univariate community descriptors (Fraser et al., 2008; Ehrich et al., 2009). Nonetheless, the recognized utility of the LFI as an ecosystem indicator is in its close response to shifts in fishing effort (Greenstreet et al., 2011; Shephard et al., 2011). Therefore, it seems possible that strong spatial gradients in fishing effort might impose an additional driver of local size structure, especially because the effort footprint can be quite stable over long periods (Hinz et al., 2003; Kaiser, 2005). This hypothesis is supported by meta-analyses suggesting that spatial management of fishing effort can enhance fish community descriptors such as size structure when the managed area is sufficiently large in relation to the ecological scale of the target community (Halpern, 2003; Micheli et al., 2004; Claudet et al., 2008; Lester et al., 2009). Understanding the spatial heterogeneity in fish community size structure and the possible confounding effects of local...
gradients in fishing effort is important if size-based indicator series are to be interpreted robustly at the scale of OSPAR regions. In addition, this information can inform possible future modifications in survey protocol that may be required to better deliver the ecosystem approach to fisheries management (EAFM). The current study investigated (i) the spatial resolution of regions of correlated LFI in the Celtic Sea, and (ii) the importance of ecological factors and fishing effort in driving local LFI values.

**Methods**

**Biological data**
The study was based on fisheries-independent data from the Irish Groundfish Survey (IGFS). The IGFS is a standardized bottom-trawl survey that extends to parts of the Celtic Sea (ICES Area VIIg; Figure 1c) and has been undertaken in the fourth quarter (Q4) of each year since 1997 (before 2003, the survey was carried out on a different vessel under the name Irish Sea/Celtic Sea Groundfish Survey). In a given year, survey samples (30 min hauls using a GOV trawl; ICES, 2010b) are conducted at sites selected randomly from a pool of fixed prime sampling stations. All fish captured are counted and measured (total length, to the nearest cm below) and individuals of the main commercial species are weighed (g). For each haul recorded in the IGFS series from 2006 to 2009 (the period of available high-resolution international fishing effort data), catch numbers at length ($L$) were converted to weight ($W$) at length using weight-at-length relationships ($W = aL^b$), where the $a$ and $b$ parameters were derived by direct analysis (main commercial species) or from FishBase (www.fishbase.org). Catch weight at length of each species and length class in each haul ($n = 103$) was then converted to density (kg km$^{-2}$) by dividing by the trawl footprint (swept-area). The LFI was calculated by dividing the biomass of fish exceeding the “large” size threshold of 50 cm (Shephard et al., 2011) by the total biomass of all demersal fish caught. The final dataset consisted of LFI values for some 25 sites (hauls) per year (103 hauls over 4 years), a total of 43 different prime stations. Variation in the LFI among sites was calculated as a range with CV.

Each prime sampling station was allocated to a substratum class (gravel, sand, or mud) using maps on the MESH (Mapping European Seabed Habitats) website (http://www.searchmesh.net/).

**Species composition regions**

To account for spatial variation in fish assemblage structure that might underlie the response of the LFI indicator with time, each of the samples was allocated to an assemblage category. Using this approach, we were able to refine further the subdivision of the fish community data beyond the simple substratum descriptor. To identify samples with similar species and abundance characteristics, species abundance data from the IGFS were root-transformed, and a resemblance matrix was generated using the Bray–Curtis index of similarity. A dendrogram was created (Figure 1a) using the group-average linkage clustering method, and a SIMPROF test was used to define clusters a posteriori that were significantly ($p < 0.05$) different (Clarke et al., 2008). This analysis was repeated for each year separately. The groupings (clusters) of sample sites identified using this approach were used to define a species composition (spcomp) region factor for the subsequent analyses. Clusters with only two sites (sites 152 and 153; Figure 1a) or single sites (sites 106 and 151; Figure 1a) that could not be allocated with certainty to a specific group were not considered to be indicative of a specific species composition region, and these sites were excluded. These groupings (clusters) were then related to their geospatial location (see Figure 1b for geographically plotted spcomp regions in 2008). Temporal stability in the footprint of each spcomp region was examined by

![Figure 1](https://academic.oup.com/icesjms/article-abstract/68/10/2106/610062)
calculating (i) the proportion of survey sites that were allocated by this analysis to the same spcomp region throughout the time-series, and (ii) the number and location of different spcomp regions occupied by each remaining “unstable” site.

Fishing effort data
International fishing effort was derived from vessel monitoring system (VMS) data for the Celtic Sea. The VMS transmits the position and speed of fishing vessels at least every 2 h. The VMS data from all EU fishing vessels >15 m inside the Irish EEZ were available for the period 2006–2009. All mobile gears were included, and speed criteria were applied to distinguish fishing activity from steaming and other non-fishing activity. Using records from on-board observers, Gerritsen and Lordan (2011) found that for otter bottom trawlers, vessel speeds between 1.5 and 4.5 knots correctly identified fishing activity in 88% of cases. Each VMS record where the vessels were deemed to be fishing was allocated an effort value equal to the interval between successive VMS records (generally 2 h). For each IGFS sampling station, the effort values used for analysis were (h year$^{-1}$) in successive circles of 10, 20, and 40 km radius (20 km circles in Figure 1c). Stelzenmüller et al. (2008) used a similar approach to show the distance from a marine protected area (MPA) at which a positive effect on the fish community was evident. International VMS data were only available for survey sites within the Irish Exclusive Economic Zone (EEZ). However, some circles extended outside this national boundary and/or onto land. In such cases, effort was corrected for the fishable area of each circle for which data were available by dividing recorded values by the proportion of each circle comprising sea within the EEZ (Figure 1c). This approach assumes homogenous fishing effort within and outside the Irish EEZ in boundary circles. Only circles for which ≥50% of the area was fishable and within the Irish EEZ were used, leaving 43 valid stations. Variation in fishing effort (h year$^{-1}$) among sites was calculated as a range with CV. Gridded charts of Celtic Sea fishing effort for each study year (2006–2009) were also produced. To develop these charts, each VMS record was allocated an effort value (h), the time since the previous VMS record. The data were then filtered for speeds between 1.5 and 4.5 knots to exclude non-fishing activity, then gridded at a resolution 0.03° longitude and 0.02° latitude. Effort values in each cell were standardized to the surface area of each cell (1.1 nautical miles$^2$).

Spatial structure in the LFI and in international fishing effort
A spline correlogram (Bjornstad and Falck, 2001) was used to model spatial autocorrelation in each LFI among sites and gridded fishing effort. Such spline correlograms graphically represent correlation in some variable at a range of lag distances from sampling sites and can reveal autocorrelation (non-independence) between sites. The distance at which autocorrelation is identified provides insight into the spatial resolution of structure, defined by among-site similarity in the variable of interest, in this case, the spatial structure in LFI of the Celtic Sea demersal fish community and in international fishing effort in the study area of the Celtic Sea. For the LFI, data were pooled over all years and sites. For fishing effort, 2009 data were used on a grid of 0.1° by 0.06°. Where cells inside the EEZ and not on land had NA values, these were replaced with zeroes.

Modelling the spatial fishing effect on fish community size structure
Statistical models were developed to explore environmental and fishing effects on size structure (LFI) by site and year. As fishing effort in successive circles was not independent, because larger circles contained smaller ones, a separate model was produced for each of the three circles (10, 20, and 40 km radius). Given that the LFI provides a proportion (a value bounded by 0 and 1), a binomial distribution was used. The response variable (large fish biomass weighted by total fish biomass) was pooled by site by year to produce a single annual proportion of large fish, i.e. LFI, for each survey site.

For each effort scale (circle), the full initial models related LFI by site to fixed effects of effort, substratum, species composition region (spcomp), and year, and the two-way interactions between all these explanatory variables. To account for the effect on LFI of unknown environmental variability associated with prime sampling sites, a random effect of sampling site was included. Generalized linear mixed models (glmm) were employed, using the glmmpQL package (Venables and Ripley, 2002) in the R statistical software (http://cran.r-project.org/).

Non-significant interactions and then main effects were sequentially removed at p > 0.025. This slightly conservative decision rule allowed for the approximate p-values produced by glmmpQL. Residual plots for each model were used to check for homogeneity of residuals. The model for each effort scale had the form

\[ Y_{ij} \sim \text{Bin}(1, p_{ij}) \]
\[ \text{logit}(p_{ij}) = \alpha + \beta_1 \text{effort}_{xkmij} + \beta_2 \text{year}_{ij} + \beta_3 \text{substratum}_{ij} + \beta_4 \text{spcomp}_{ij} + \beta_5 \text{years} \text{spcomp}_{ij} + \alpha_i + \text{residuals} \]

where $p_{ij}$ is the probability that fish $j$ from sampling station $i$ is large (>50 cm), effort$_{xkmij}$ the fishing effort (h year$^{-1}$) within xkm (10, 20, or 40 km), year$_{ij}$ the sample year (2006–2009), substratum$_i$ the habitat (gravel, sand, or mud), spcomp$_i$ the species composition region (inshore, midshore, offshore, or east), and $Y_{ij}$ is 1 if fish $j$ from sampling station $i$ is large and 0 otherwise. The random station effect $\alpha_i$ is assumed to be normally distributed with mean 0 and variance $\sigma^2_{\alpha}$. Because there was known spatial autocorrelation in Celtic Sea LFI values by survey site, a spline correlogram (see above) was used to assess whether there was spatial autocorrelation in the Pearson residuals of each of the two final models once any spatial autocorrelation explained by the explanatory variables had been accounted for.

Results
The footprint of species composition (spcomp) regions showed strong temporal stability, with 37 prime sampling stations (86%) being allocated via a similarity matrix to the same spcomp region throughout the 4 years. The remaining six stations shifted between a maximum of two geographically adjacent spcomp regions.

LFI values varied strongly among sampling sites: for 2006, 0.004–0.685, CV = 1.189; for 2007, 0.017–0.579, CV = 0.866; for 2008, 0.011–0.592, CV = 0.744; for 2009, 0.000–0.484, CV = 1.009. The spline correlogram of Celtic Sea LFI values by
site (Figure 2a) showed positive spatial autocorrelation in the LFI among sites ≤40 km apart, with no significant spatial correlation in LFI for sites farther apart. This result suggests that in the Celtic Sea, the demersal fish community is structured into somewhat independent subregions (as defined by correlated LFI) at a range of about 40 km.

Fishing effort (h year⁻¹) in the 40 km circles also varied markedly among sites: for 2006, 12 716–44 160, CV = 0.29; for 2007, 6226–60 631, CV = 0.39; for 2008, 9424–43 284, CV = 0.31; for 2009, 3444–45 065, CV = 0.41. Visual examination of annual gridded charts of fishing intensity in the study area (Figure 3) suggested temporal stability in the spatial distribution of effort, with areas of consistently higher and lower effort over time. The spline correlogram for gridded fishing effort data showed stronger positive spatial autocorrelation than for the LFI, but at a similar range (≈45 km; Figure 2b).

There was a strongly significant negative effect (p = 0.005) of fishing effort within a radius of 40 km on LFI by site, reflecting spatial autocorrelation in both effort and LFI at about that range, and marked spatial heterogeneity in each variable. The 40 km model also showed significantly interacting effects of spcomp, substratum, and year (Table 1). A correlogram of Pearson residuals from that model showed no spatial autocorrelation (Figure 4a), demonstrating that the explanatory variables included in the model fully accounted for spatial autocorrelation in LFI values among survey sites in the Celtic Sea. The distribution of residuals for the final model indicated homogeneity (Figure 5a).

There was no significant effect (p > 0.025) on LFI by site of fishing effort at either 10 or 20 km. This resulted in a common final model showing significantly interacting effects only of substratum and year. A correlogram of Pearson residuals from that model showed no spatial autocorrelation (Figure 4b), demonstrating that the explanatory variables included in the model accounted fully for the spatial autocorrelation in LFI values among survey sites in the Celtic Sea. However, the CI for that correlogram was wider than for the model including effort. The distribution of residuals for this final model showed a weak pattern (Figure 3b), possibly suggesting heterogeneity induced by the absence of effort as a fixed effect.

Whereas the glmmPQL technique (Venables and Ripley, 2002) handles proportional data (e.g. the LFI) well (Zuur et al., 2009), it does not estimate r² or the Akaike information criterion. Therefore, it is difficult to estimate how much of the variability in LFI is explained by effort vs. environmental variables. However, the random distribution of residuals and narrow CI in the spline correlogram suggest that the 40 km effort model robustly expresses the factors driving spatial heterogeneity in the Celtic Sea LFI. This is supported by plots of LFI against effort by spcomp region (Figure 6). For the model excluding fishing effort, the random effect of Prime Site had a variance σ² of 0.318 (95% CI for the site effect, naï = 0 ± 1.105). For the model including the effect of fishing within a 40 km radius, the random effect of Prime Site had a reduced variance (σ²) of 0.225 (95% CI for the site effect, naï = 0 ± 0.931). This variance associated with the random effect indicates minor to moderate between-site variation and suggests that it was important to account for the site effect on the LFI in the model.

Discussion
The LFI has been selected as the fish community EcoQO metric for OSPAR regions (Heslenfeld and Ensink, 2008; Greenstreet et al., 2011) and proposed as a GES indicator for the foodweb descriptor of the Marine Strategy Framework Directive (EC, 2010). However, it has been suggested that spatial structure in marine fish communities may confound indicator series calculated at such wide geographic scales (Greenstreet and Piet, 2008; ICES, 2010a). For the Celtic Sea, LFI values at IGFS sampling sites showed positive spatial autocorrelation up to about 40 km over the period 2006–2009, indicating regions of similar fish community size structure that remained stable at that temporal scale. Statistical modelling indicated that the observed LFI by site was related to substratum and to fish assemblage region (spcomp), a variable that integrates broader habitat factors such as depth, temperature, and benthic community (Fraser et al., 2008; Ehrich et al., 2009).

Such ecologically mediated spatial heterogeneity in the Celtic Sea LFI has implications for the operation of size-based community indicators. However, imposed on this underlying spatial structure in the fish community was marked heterogeneity in the distribution of fishing effort (Figure 3). Most of the effort in the Celtic Sea (2006–2009) was mixed-species otter trawls. There were some areas of high effort, in particular on the eastern edge, focused on distinct mud patches where Nephrops norvegicus is the main target species, but larger areas where the seabed...
is unsuitable for otter trawling and which received correspondingly little effort. The effort of vessels targeting gadoids was distributed throughout the remaining area. Effort was spatially autocorrelated at a similar scale to the LFI.

In addition to substratum and fish assemblage, fishing effort within 40 km was a strongly significant explanatory variable in our statistical model of the Celtic Sea LFI. The spatial relationship between effort and size structure could simply mean that fishers distribute effort in response to local patterns in the fish community that can be captured by the LFI. However, another reasonable interpretation is that fishing can induce fine-scale heterogeneity in demersal fish community size structure. Such a response would demand surprising fidelity of fish community components to given localities, because even moderate spatial mixing would probably blur local correlations between fishing and size structure. Spatial fidelity contrasts with the assumption that the exploited demersal fish community is essentially mobile, and may be explained by strong ontogenetic habitat association (Gibson et al., 2002; Hinz et al., 2006; Methratta and Link, 2007) and a weak realization of the ideal free distribution (e.g. in haddock; Hiddink et al., 2005).

In terms of implementing robust monitoring programmes for the LFI, spatial stratification of survey data may thus be necessary to account for possible confounding effects of fishing- and

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Table 1. Test statistics ($p$-values) for explanatory variables [fishing effort, demersal fish assemblage region (spcomp), substratum, and year] in a statistical model of LFI at IGFS survey sites in the Celtic Sea.

<table>
<thead>
<tr>
<th>Effort (km)</th>
<th>Effort</th>
<th>Spcomp</th>
<th>Substratum</th>
<th>Year</th>
<th>Effort–year interaction</th>
<th>Effort–substratum interaction</th>
<th>Effort–spcomp interaction</th>
<th>Year–substratum interaction</th>
<th>Year–spcomp interaction</th>
</tr>
</thead>
<tbody>
<tr>
<td>10</td>
<td>0.326</td>
<td>0.222</td>
<td><strong>0.005</strong></td>
<td>0.037</td>
<td>0.031</td>
<td>0.941</td>
<td>0.322</td>
<td><strong>0.004</strong></td>
<td>0.044</td>
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<tr>
<td>20</td>
<td>0.049</td>
<td>0.199</td>
<td><strong>0.005</strong></td>
<td>0.037</td>
<td>0.027</td>
<td>0.767</td>
<td>0.088</td>
<td><strong>0.004</strong></td>
<td>0.038</td>
</tr>
<tr>
<td>40</td>
<td><strong>0.005</strong></td>
<td>0.037</td>
<td>0.026</td>
<td><strong>0.023</strong></td>
<td>0.211</td>
<td>0.443</td>
<td>0.189</td>
<td><strong>0.006</strong></td>
<td><strong>0.017</strong></td>
</tr>
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$p$-values that are significant at $p < 0.025$ are shown emboldened.
environmentally induced heterogeneity in the indicator. This could consist of post-stratification of LFI calculations by effort regime (e.g. high/low), and by substratum and/or assemblage. Such stratification should allow for large-scale factors that could drive changes in community composition and spatial footprint; a changing climate is likely to shift defined fish assemblages north and/or allow the immigration of new species, which could alter community size structure and hence spcomp regions. However, it should be quite simple annually to redefine the spatial pattern of effort (from VMS) and of fish assemblage (spcomp) regions (see Methods), and to update the strata correspondingly. Indeed, the emergence of change in previously stable communities, and the rate of this change, could act as an additional management diagnostic.

In addition to implications for monitoring methodology, fine-scale spatial correlations between fishing effort and the LFI may indicate leverage for spatial management, e.g. MPAs in an EAFM. Meta-analyses suggest that MPAs can enhance descriptors such as size structure in exploited fish communities (Halpern, 2003; Micheli et al., 2004; Claudet et al., 2008; Lester et al., 2009). However, such studies typically emphasize communities strongly associated with discrete physical features such as reefs, where the spatial range of the community can be encompassed in a relatively small area. With some exceptions (see Apostolaki et al., 2002), more-mobile fish communities have been considered
unlikely to benefit from MPAs, because characteristics such as size structure are assumed to be mediated at broad spatial scales (Hilborn et al., 2004; Blyth-Skyrme et al., 2006). Protecting up to 80% of home ranges may be required to achieve a positive effect (Guénette et al., 2000; Le Quesne and Codling, 2009), so spatial management of mobile assemblages (Baskett et al., 2007) could demand large areas (Walters, 2000), with serious socio-economic implications (Klein et al., 2008).

In contrast to these assumptions, our results indicate that change in the Celtic Sea LFIs, a size-based indicator of fish community state, is related to fishing effort within a radius of just 40 km. This observation supports the suggestion from a recent meta-analysis that small, temperate marine reserves may have been beneficial globally (Lester et al., 2009), with potential to add resilience to exploited populations of mobile species (Guénette and Pitcher, 1999; Apostolaki et al., 2002). MPAs appear to be most effective as part of an integrated fishery management strategy (Gaines et al., 2010), in which “a profound understanding of the spatio-temporal dynamics of the fishing fleets involved is essential” (Stelzenmüller et al., 2008). Notably, displacement of fishing effort into previously minimally exploited areas can have a net negative ecological effect through extended damage to the benthos (Hiddink et al., 2006). In the Celtic Sea, a small region in the east has been closed for 2 months in spring of each year since 2005 (EU, 2009), without a substantial effect on the overall distribution of fishing effort (ICES, 2007). MPAs sited to answer ecological objectives such as achieving the fish community EcoQO, while considering implications for effort distribution may have a role in achieving good environmental status in the MSFD.

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References


