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Community management indicators can conflate divergent phenomena: two challenges and a decomposition-based solution

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Summary

- 1. Community indicators are used to assess the state of ecological communities and to guide management. They are usually calculated from monitoring data, often collected annually. Since any given community indicator provides a univariate summary of complex multivariate phenomena, different changes in the community may lead to the same response in the indicator. Sampling variation can also mask ecologically important trends.
- 2. This study addresses these challenges for community indicators, with a focus on the large fish indicator (LFI), internationally used to report status of marine fish communities. The LFI expresses 'large' fish biomass as a proportion of total fish biomass and is calculated from species—size—abundance data collected on trawl surveys. We develop new methods to decompose the contributions of species, sampling locations and season to trends over time in the LFI, and highlight consequences for assessment and management.
- 3. Our results showed that both species and locations made divergent contributions to overall trends in the LFI indicator, with contributions differing by several orders of magnitude and in sign. Only small proportions of species and locations drove overall LFI trends, and their contributions changed with season (spring and autumn surveys). To assess significance of component trends, a resampling method was developed. Our method can be generalized and applied to many other community indicators based on survey data.
- 4. Synthesis and applications. Our new method for decomposing community indicators and generating confidence intervals makes it possible to extract much more information on what drives a 'headline' indicator, providing a solution to challenges arising from multiple possible interpretations of changes in the indicator and from sampling variation. Analysis of the effects of indicator components on headline indicator values is recommended, because the results allow assessors and managers to identify and interpret how divergent factors (e.g. species, sampling locations and seasons) contribute to the headline indicator value.

Key-words: community indicators, ecosystem approach to management, fish community, fisheries management, large fish indicator, North Sea, resampling method, size-based indicators, trawl surveys

Introduction

Ecological indicators are indices of the state of an ecosystem and are widely used for environmental assessment, reporting and management support (Rice 2003).

Indicators typically provide information on the status and trends of ecosystem components and attributes, usually those which are sensitive to human and environmental impacts.

Ecological indicators are often used in marine systems to describe the effects of climate or fishing pressure on the composition or function of a marine community or part

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of that community (Shin et al. 2005, 2010). Indicators range from those that summarize responses of certain species to those describing changes in properties resulting from direct and indirect interactions of species. To provide reliable information on the effects of human and environmental pressures on communities, the response of the indicator should be sensitive and specific to the pressures (Fulton, Smith & Punt 2005; Rice & Rochet 2005; Rombouts et al. 2013). For example, an indicator of fishing effects on fish communities should respond to changes in fishing intensity rather than climate. In practice, community indicators have often been proposed and adopted more quickly than they have been evaluated, leading to the risk that changes in values are uninformative about community responses to pressure and leading to challenges to indicator legitimacy (e.g. Branch et al. 2010). Best practice would require testing the properties and performance of indicators before they are used to report changes in the state of the environment and guide management (e.g. Rice 2003; Jennings 2005; Rice & Rochet 2005).

Values of many community indicators are determined by the relative numbers or biomass of species and/or body size categories in the community. This poses a challenge to interpretation because the indicator provides a univariate summary of complex, multivariate, ecological phenomena. This summary is sought by indicator developers because it provides simplicity, but it also means that multiple and potentially different changes in community structure or function may result in the same overall change in an indicator value. We call this the challenge of multiple meanings. Recognizing this challenge, any 'headline' community indicator would ideally be used and interpreted in conjunction with a suite of component indicators that help to decompose the properties of the community accounting for changes in the 'headline' indicator. Unfortunately, community indicators are often used or reported in isolation (e.g. STRIVE 2013; ICES 2014), without explanatory decomposition. Decomposing an indicator is not the same as using many unrelated indicators because constituent indicators from decompositions are chosen to illuminate causes of changes in the 'headline' indicator.

Another challenge to interpretation of community indicators is that reported trends are often based on annual point estimates (Rice & Gislason 1996; Blanchard et al. 2005; Greenstreet et al. 2012a; ICES 2014). Such estimates may exhibit changes due to real trends, or due to statistical sampling variation, or variation in the timing and location of trawls (which is distinct from statistical sampling variation). We call this the challenge of sampling uncertainty. Commonly used marine data sets are taken from trawl surveys where compromise designs are adopted to fulfil multiple needs (e.g. ICES 2012). Formal statistical approaches for determining the effects of sampling variation, and whether changes and trends in fish community indicators are significant, are still not widely developed or

used. Properly assessing sampling variation has been a challenge because of the intrinsic complexity of sampling procedures.

Several size-based community indicators have been developed to evaluate changes in marine communities and food webs in response to fishing and environmental pressures (e.g. Shin et al. 2005). The large fish indicator (LFI) is one simple, widely recommended indicator that has been adopted to describe fish community responses to fishing. It is a ratio of the biomass of large fish to the biomass of small fish caught in survey trawls (Greenstreet et al. 2011; a precise definition is in 'Materials and methods'). The LFI is designed to show changes in the size structure of the community and thus provide more information than would be gleaned from the study of individual species. It is also assumed to be relatively robust to the changing dynamics of individual species (Greenstreet et al. 2011; Houle et al. 2012). The LFI is expressed as a ratio to reduce its sensitivity to changes in primary production as opposed to fishing, based on the assumption that a ratio is less influenced by system productivity than absolute biomass of small or large fishes (ICES 2014).

The LFI is unlikely to be immune to the challenges of multiple meanings and sampling uncertainty introduced above. These challenges may limit the value of the LFI for assessing status and trends. We assess the extent and consequences of these challenges for the LFI and show how a decomposition of the indicator by species, space and time informs interpretation of trends. Although differences in the contributions of individual species to the LFI are recognized (Greenstreet et al. 2012a; Shephard et al. 2012), a systematic method to determine how each species contributes has not previously been developed. Since the LFI is now being used or considered as an indicator of the state of biodiversity and food webs in the North Sea (Greenstreet et al. 2011), Celtic Sea (Shephard, Reid & Greenstreet 2011), North East Atlantic (Modica et al. 2014) and Mediterranean (Edelist, Golani & Spanier 2014), it is timely to assess its performance and the potential for improving interpretations of it. It is also relevant to consider the extent to which trends in region-wide estimates of the LFI are representative of trends across these regions as a whole, or whether they can be driven by local phenomena.

Given constraints on sampling resources, LFI time series are usually based on data from trawl surveys that are conducted just once each year. For the North Sea, the data usually used come from the Quarter 1 (Q1; first 3 months of the year) International Bottom Trawl Survey (IBTS; ICES 2012). The use of sampling data from discrete annual surveys means that seasonality effects cannot be addressed. For discrete annual surveys, the structure of the community in any defined time window may be influenced by seasonal changes in movement, migration and phenology. Data from the longer-running Q1 IBTS are usually used in preference to the shorter Quarter 3 (Q3)

time series. Proposed management targets for the North Sea LFI are also based on values calculated from Q1 data. Within either time series, changes in phenology may lead to changes in the LFI, especially as the North Sea is an open system, with fishes migrating in and out through the course of the year (Daan et al. 1990). Values of indicators calculated from Q1 and Q3 surveys may therefore reflect seasonal differences in the timing of the survey. Comparison between results using Q1 and Q3 data may provide insight into the extent of seasonal changes and their effects on values and trends in the LFI.

Here, we address the challenges of multiple meanings and sampling uncertainty in community indicators, with a focus on the factors driving changes in the LFI in the North Sea. We ask whether: (i) some species are more dominant than others in driving trends in the LFI, and whether different species contribute with different signs, as well as different magnitudes, to changes in the LFI, so that overall LFI trends are not representative of all species; (ii) LFI trends differ spatially across the North Sea, and whether different regions contribute differently to overall trends, so that overall trends are not representative of all areas; (iii) there are seasonal differences in LFI trends (Q1 vs. Q3), such that apparent trends may be confounded by phenological shifts; and (4) combined influences of the factors species, sampling location and season affect our responses to (i)-(iii). Our methods involve decomposing the LFI into constituent parts to address the challenge of multiple meanings and using a novel resampling-based statistical tool to address the challenge of sampling uncertainty. Combining these methods allows more information to be extracted from a 'headline' indicator to determine causes of change and to show which components of an indicator are contributing significantly to overall trends. Our decomposition-based method offers a solution to address the challenges of multiple meanings and sampling uncertainty and can straightforwardly be generalized to many other community indicators.

Materials and methods

LFI DECOMPOSITION

The LFI is defined for the North Sea as the proportion of biomass in a set of trawls comprising fish over a given length threshold, L, typically 40 cm. It is therefore a sum of the biomass of 'large' fish (defined as those over L in length) in each species, divided by the total biomass of fish in the trawls. If B is the total biomass of all fish in the trawls, and B_L is the total biomass of fish greater than L in length, then the LFI is as follows:

$$LFI_{L} = \frac{B_{L}}{B} = \frac{\sum_{i=1}^{n} B_{L,i}}{B} = \sum_{i=1}^{n} \frac{B_{L,i}}{B} = \sum_{i=1}^{n} LFI_{L,i},$$
 eqn 1

where n is the total number of species, $B_{L,i}$ is the large fish biomass for species i, and $LFI_{L,i}$ is the contribution of the ith species to the LFI. The total LFI is the sum of the species LFI contributions. Species with no large fish have a zero contribution, although they contribute biomass to the denominator, B.

If a trend in the LFI over any defined time period is computed using an ordinary linear regression of LFI against year, then the slope of the trend can be decomposed into the sum of slopes for each species: $S_{LFI} = \sum_{i=1}^{n} S_{LFI,i}$, where S_{LFI} is the slope of the regression of the LFI against year and $S_{LFI,i}$ is the slope of the regressions of the LFI_{L,i} against year (Fig. 1, see Appendix S1 in Supporting Information for a proof). The slope of the regression of the LFI against year is referred to throughout as the 'slope of the LFI', calculated over the time period selected.

The LFI, as well as the slope of the LFI, can be decomposed not only with respect to species, but with respect to any other factor or combination of factors (Appendix S1; i in equation 1 then indexes the values of the other factor or combination of factors). The slope of the LFI can therefore be decomposed by spatial location (we use 1° × 1° grid cells) or by spatial location and species simultaneously. The latter decomposition can be summed over grid cells, or over species, to recover the decompositions solely by species or solely by grid cell, respectively.

The summands in the decomposition of the LFI by grid cell are not equal to the LFI values that would be computed by considering grid cells in isolation. The summands LFI_{Li} in equation 1 have the quantity B in their denominators, which equals the total biomass of all fish caught in the complete set of trawls used. This use of a whole-sea denominator means that the LFI_{Li} values are contributions to the overall LFI and not LFI values of each grid cell i in isolation, a choice appropriate for our goals.

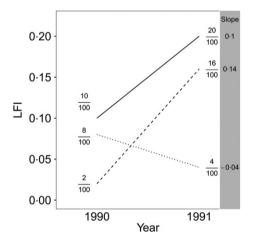


Fig. 1. Decomposition of a large fish indicator (LFI) slope in a simplified two-species, two-year example. The overall LFI slope (solid line) is decomposed into species 1 (dashed line) and species 2 (dotted line), with example values used to calculate the LFI (B_I/B) and LFI_i $(B_{I,i}/B)$ in each year shown. The overall LFI slope (solid line) is calculated as $S_{LFI} = ((0.2 - 0.1)/(1991 - 1990)) = 0.1$. The component slopes are calculated for species 1 (dashed line) as $S_{LFL,1} = ((0.16 - 0.02)/(1991 - 1990)) = 0.14$ and for species 2 (dotted line) as $S_{LFI,2} = ((0.04 - 0.08)/(1991 - 1990)) = -0.04$, which sum to the overall slope, 0.1. Large fish biomass does not necessarily have to decline in order for a species to have a negative LFI slope contribution: a species could have a negative contribution to the LFI slope even if B_L increases (for example, from 8 in 1990 to 16 in 1991) if there were a counteracting increase in B (for example, from 100 to 400, producing $S_{LFI,i} = -0.04$ in this

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DATA AND RESAMPLING METHOD

Data were taken from the North Sea Q1 and Q3 IBTS (ICES 2014). The IBTS is a spatially structured sampling survey across the North Sea, which records the number of fish caught by length category for each species in each haul (ICES 2012; Appendix S2). The time series used was for the years 1991-2013, during which data were available for both quarters. The data were cleaned to remove erroneous entries (Daan 2001; Fung et al. 2012; Appendix S4) and to include only grid cells sampled in both quarters. To ensure that spatial extent was comparable in each year and for Q1 and Q3, records for any grid cell missing two or more years' data, in either quarter, were excluded (Greenstreet et al. 2012b). Grid cells in the Kattegat and Skaggerat were also excluded, as is standard; those regions are heavily influenced by processes in the Baltic Sea. Remaining data were averaged over ICES rectangles (the spatial unit of stratification in the IBTS design: 0.5° latitude by 1° longitude) and then over 1° × 1° grid cells for our spatial analy-

For assessing significance of values and trends, we developed a resampling method specific to trawl catch data. We used the method to produce 'surrogate' (i.e. resampled) IBTS data sets (Appendices S2 and S3). Confidence intervals for statistics calculated from the IBTS data were computed by calculating the same statistic on the surrogate data sets and generating percentiles.

Results

SPECIES DECOMPOSITION OF THE LFI SLOPE

There was significant and very substantial heterogeneity in contributions of species to the overall slope of the LFI, indicating that trends in the LFI conflate divergent phenomena at the species level (Fig. 2). Species contributions differed substantially in magnitude and in sign, and this heterogeneity was significant based on our resamplingbased confidence intervals. For instance, some species made significant positive contributions to the overall slope, while others made significant negative contributions (Fig. 2). Positive contributions varied over 5.3 orders of magnitude. Negative contributions varied over 4.5 orders of magnitude. The largest positive contribution to the overall slope in Q1 (9.35 \times 10⁻⁴ year⁻¹) came from saithe Pollachius virens, and the largest-magnitude negative contribution $(-5.19 \times 10^{-4} \text{ year}^{-1})$, from cod *Gadus morhua*. In Q3, the largest positive contribution $8.52 \times 10^{-4} \text{ year}^{-1}$, from saithe, and the largest-magnitude negative contribution was $-1.20 \times 10^{-4} \text{ year}^{-1}$, from tope Galeorhinus galeus.

Very few species contributed a large proportion of the LFI slope, and the rest contributed very little (Figs 2 and S1). In Q1, the absolute LFI slope contributions of saithe and cod together were 50% of the sum of absolute slope contributions of all species (Fig. S1). To reach 95% of this sum, 16 species were needed. Thus, the LFI slope was dominated by the contributions of a few species, but was still somewhat influenced by the contributions from a

larger collection of species. In Q3, the absolute LFI slope contributions of saithe and cod together were 41% of the sum of absolute slope contributions of all species; to reach 95%, 16 species were again needed.

SPATIAL DECOMPOSITION OF THE LFI SLOPE

The contribution of grid cells to LFI slope varied strongly across the North Sea, both in magnitude and sign, indicating that trends in the LFI conflate divergent phenomena spatially (Fig. 3). There were more positive (red in Fig. 3) contributions in the north-west of the North Sea and in coastal areas, and more negative (blue in Fig. 3) contributions in the central North Sea. This pattern was also apparent when comparing the lower and upper confidence intervals for each grid cell, so the general pattern is unlikely to be driven by chance sampling variations. Both positive and negative contributions of cells varied by several orders of magnitude.

A few grid cells contributed a large proportion of LFI slope, with the rest contributing relatively little (Figs 3 and S2). A few grid cells towards the north of the North Sea and two close to the English Channel made a dominant contribution to the trend (Fig. S2), indicating that the overall trend for the North Sea is influenced primarily by changes in just a few areas.

SEASONAL COMPARISON OF LFI SLOPES

The overall LFI slope in Q1 was 1.22×10^{-3} year⁻¹ (CI 1.06×10^{-3} , 1.38×10^{-3}) and in Q3 was 3.06×10^{-3} year⁻¹ (CI 2.96×10^{-3} , 3.17×10^{-3}). Confidence intervals did not overlap between quarters; therefore, the Q3 slope was significantly more positive than the Q1 slope.

INTERACTIONS BETWEEN SEASON AND SPECIES

Contributions of species to the overall positive LFI slope in each quarter were similar across quarters for some species, but markedly different for others (Fig. 2, black lines). This indicated an interaction between the species decomposition of the LFI and season. The strongest species-level Q1 vs. Q3 differences were for cod, which was the largest-magnitude negative contributor to the LFI slope in Q1, but the second-largest positive contributor in Q3. The tope shark G. galeus and the Atlantic mackerel Scomber scombrus are additional examples: they were the two most negative contributors to the LFI slope in Q3, but were positive contributors in Q1. Species that contributed similarly and strongly to LFI slopes in both quarters included saithe P. virens (the largest positive contributor in both quarters) and haddock Melanogrammus aeglefinus (the fourth-largest positive contributor in both quarters). These contributions were mostly consistent with changes in large fish biomass (Appendix S5).

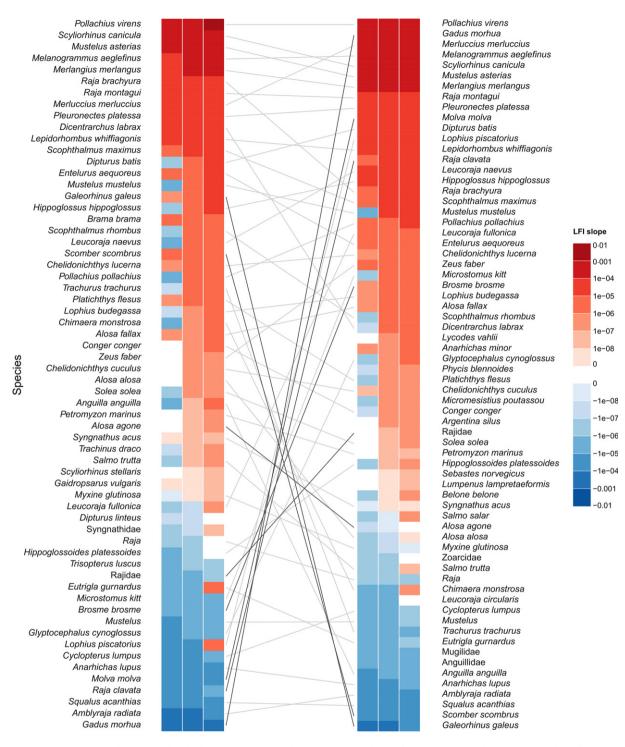


Fig. 2. Decomposition of the large fish indicator slope (S_{IFI}) by species. The block of three vertical colour scales on the left shows Q1 results, and the block on the right shows Q3 results. Within each block, central columns show point estimates of large fish indicator (LFI) contributions by species, left columns show lower 95% confidence interval bounds based on 1000 resampled data sets, and right columns show upper 95% confidence interval bounds. The colour ramp (right) is linked to a log scale for display purposes, with reds representing positive contributions to the overall LFI slope and blues negative contributions. Species were ordered by contribution from positive to negative, separately in each quarter. Lines join species for which individuals >40 cm were sampled in both quarters, to facilitate comparisons of whether species contributed similarly or differently to the LFI slope in the two quarters. Dark lines link species that have switched from either a significant negative to a significant positive contribution or vice versa.

INTERACTIONS BETWEEN SEASON AND SPACE

Contribution of grid cells to the overall LFI slope differed between seasons (Figs 3 and 4). There were more positive

contributions in the north-western North Sea, and more negative contributions in the centre, for both Q1 and Q3, but this spatial difference was more pronounced in Q3 (Fig. 3). Differences in LFI slope contributions between

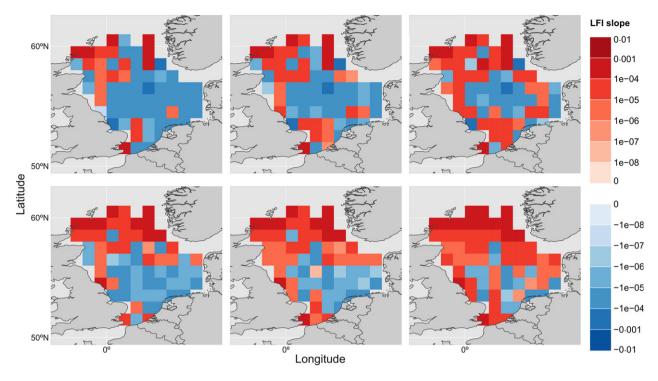


Fig. 3. Decomposition of the large fish indicator slope by $1^{\circ} \times 1^{\circ}$ grid cells. The first row of panels shows the decomposition for Q1 data, the second row for Q3 data. The middle column in each row is the point estimate, the left column is the lower 95% confidence interval bound based on 1000 resampled data sets, and the right column is the upper 95% confidence interval bound. Colours are based on a log scale (right) for display purposes, reds representing positive contributions to the overall slope and blues negative contributions.

quarters show that some grid cells in the south switched from a positive to a negative contribution between quarters, while some grid cells in the north did the opposite (Fig. 4). This spatial pattern of more positive contributions in the northern region in Q3 was significant for grid cells that had large contributions to the overall slope (dark red cells above 58° latitude in Figs 3 and 4).

The same grid cells made the largest contributions to the LFI slope in both Q1 and Q3, but for Q1, some of these contributions were positive and some were negative, whereas for Q3, they were all positive (Fig. S2; 0×60 , 3×60 , -3×59 , -2×59 , 3×59 , 3×58 , 4×58 , 1×51 , -1×54). The differences in these key grid cells between Q1 and Q3 accounted for the more positive overall LFI slope in Q3.

INTERACTIONS BETWEEN SPECIES AND SPACE

When the LFI slope was decomposed by species and grid cell, species did not contribute consistently over space (Figs S5 and S6), again showing that divergent phenomena can be conflated by LFI slopes. Very few species present in more than two grid cells contributed to the LFI slope with the same sign in all of those cells. There was also heterogeneity in the magnitude of the contribution across cells, within species. For example, grid cell 1×51 in the southern North Sea made a large positive contribution in Q1 that was driven largely by the biomass of large lesser spotted dogfish *Scyliorhinus canicula*, a species that

is distributed across the whole North Sea but was abundant in that one cell. It can also be seen that the northernmost cells that made a dominant contribution to the LFI slope (cells 3×60 , 0×60 , 3×59 , -2×59 , -3×59 ; see Figs 3, S5 and S6) are driven by saithe *P. virens*, or cod *G. morhua*, which were the dominant species in those cells in both quarters. Cod made the largest overall negative contribution to the LFI slope in Q1, but the contribution was not consistently negative across space; in two of the northernmost grid cells, its contribution was positive and it was the largest contributor to the overall positive slope (-2×59 , -3×59).

The decomposition of the LFI slope by species and grid cell enables examination of the spatial contribution of each of the abundant and commercially important species that were shown to be important contributors to overall trends (Fig. 2; P. virens saithe, G. morhua cod, M. aeglefinus haddock, M. merlangus whiting and M. merluccius hake). Maps of contributions to the LFI slope for these species (Figs 5, S7 and S8) showed that they contributed differently in different regions of the North Sea. Saithe and cod have previously been recognized as dominant contributors to the overall LFI, but the decomposition of their contributions by space across the North Sea varied between negative and positive. Saithe, although present only in the northern North Sea, showed a similar general tendency to that in the overall spatial decomposition in Q1, with positive contributions in the northernmost grid cells and more negative contributions elsewhere. Cod

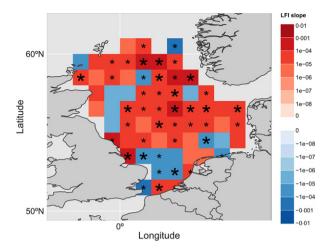


Fig. 4. Seasonal difference in the decomposition of the large fish indicator slope by 1° × 1° grid cell. Differences were calculated by subtracting the Q1 slope contribution for each grid cell (Fig. 3, top middle panel) from the Q3 slope contribution (Fig. 3, bottom middle panel) in the cell. Values are shown on a log scale for display purposes, red representing a positive difference in the contribution between seasons (a contribution that was larger in Q3 than in Q1) and blue a negative difference. Stars identify grid cells that showed a significant difference (based on 1000 surrogate data sets) between Q1 and Q3, and larger stars identify grid cells that also showed a change in the direction of contribution between seasons (red cells switched from negative in Q1 to positive in Q3, whereas blue cells switched from positive in Q1 to negative in Q3).

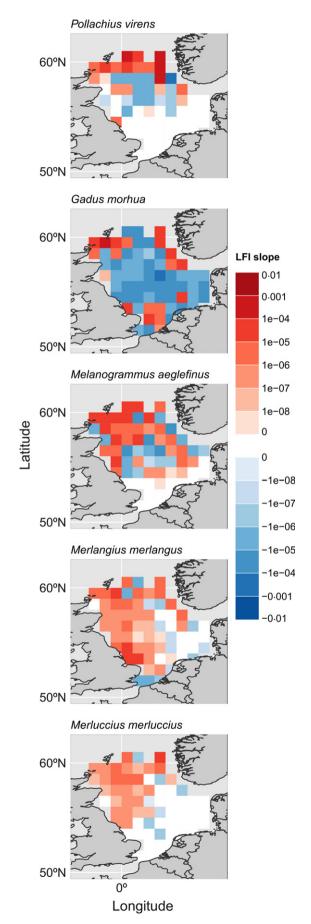
showed a negative tendency in the central North Sea in Q1, but not in Q3 (Fig. S8), and the contribution of cod was positive in more grid cells in Q3 than in Q1.

Our main findings that component LFI trends varied in magnitude and sign, and that the overall LFI trend is determined by a few species and areas, were both supported by alternative calculations using a combination of different measures of catch rates, fish length cut-offs and exclusion/non-exclusion of pelagic species (Appendix S6).

Discussion

The challenges of multiple meanings and sampling uncertainty both complicate the interpretation of the LFI when assessing status and trends. Our study confirmed this, showing that trends in the overall LFI slope conflate divergent phenomena. There was significant

Fig. 5. Contributions to the large fish indicator (LFI) slope, decomposed by 1° × 1° grid cell in Q1, for each of five species that are abundant and make a large contribution to the LFI slope (Pollachius virens saithe, Gadus morhua cod, Melanogrammus aeglefinus haddock, Merlangius merlangus whiting and Merluccius merluccius hake). Confidence intervals are shown in Fig. S7 and Q3 results in Fig. S8. Values are represented on a log scale for display purposes, red represents a positive contribution to the overall slope and blue a negative contribution. White cells represent a contribution of zero to the overall slope, where surveys were carried out but no large fish from that particular species were found.



substantial heterogeneity in species' and locations' contributions to the trend in the LFI; a few species and a few regions mostly control overall trends in the LFI. Our decomposition-based method provides a solution to the challenges and allows more information to be extracted from the 'headline' LFI indicator.

There are several management implications highlighted by our results, all related to the overall conclusion that interpreting trends in the LFI without considering component trends may provide limited insight into changes in fish communities. First, trends in the LFI can be misleading, as they are the aggregate of highly divergent components. When trends were decomposed into species and spatial components, both negative and positive contributions comprised the overall trend. The largest-magnitude contributions also showed heterogeneity in signs. Interpretation of the LFI without considering components has the potential to suggest, falsely, that the same processes drive overall LFI trends. This may lead to misguided assumptions about the state of the fish community and inappropriate management responses.

The second management implication is that the value of the LFI is mostly driven by only a few species, and thus, trends in the LFI will be disproportionately influenced by population fluctuations in these species. Our results quantify the contributions of species and confirm prior observations that LFI values and trends are most sensitive to a few abundant species (Greenstreet et al. 2012a; Speirs, Greenstreet & Heath 2016). Since most of the main species contributing to the LFI are already assessed in single-species stock assessments, the LFI may provide little additional information on the state of the North Sea that would not be obtained from the proportions of large fishes in assessed stocks. Interestingly, although saithe and cod were found to drive overall trends, their effects were opposing in Q1. When cod switched to a positive contribution in Q3, the annual rate of increase in the LFI was correspondingly greater. This may have reflected a changing spatial-seasonal distribution of cod. If so, an analogue of the LFI indicator based instead on stock assessments should not show this bias, as stock assessments seek to represent populations rather than portions of populations in the survey area at survey time.

The third management implication is dual: because few grid cells contribute inordinately to trends in the LFI, such trends may be very sensitive to the geographic region included in the analysis; and North Sea-wide trends could potentially be influenced by management actions affecting just a few grid cells. It has been noted before that inclusion of survey catches from just one ICES rectangle (a $1^{\circ} \times 0.5^{\circ}$ grid cell) could lead to a different interpretation of trends in the North Sea-wide LFI (Greenstreet *et al.* 2012a; Sundelof, Wennhage & Svedang 2013; the particular rectangles considered in those studies were omitted from our analysis). The rectangle studied in Sundelof, Wennhage & Svedang (2013) contained a productive and somewhat isolated cod subpopulation that contained

very high proportion of large individuals. While North Sea-wide trends in the LFI are typically reported (Defra 2014; Greenstreet et al. 2011; Fung et al. 2012), it may or may not be specified which grid cells are included in an analysis, making it more difficult to compare studies. Our decomposition by both species and space further demonstrated that changes in abundance of a relatively nonabundant species, the lesser spotted dogfish, in just one grid cell, contributed greatly to overall trends. The fact that fluctuations in catches in just one grid cell or rectangle can influence values of the LFI for the North Sea so strongly is a concern when the LFI is adopted as a state indicator for the region as a whole. Interpretation of the 'headline' LFI for the North Sea would be enhanced by information on spatially disaggregated trends (Shephard et al. 2011; Greenstreet, unpublished, in ICES 2014). Our methods provide the disaggregation tools.

Although the LFI is identified as a community indicator (ICES 2014), we showed that values of the LFI are mostly determined by a few species in a few areas, and this limits the LFI's usefulness for state assessment and management if our decomposition methods are not applied. To emphasize these points, Fig. 6 shows that multidecadal trends in large fish biomass in the North Sea in Q1 can be adequately described from data on only seven species (of 163) in only ten grid cells (of 67), a small minority of the total data collected during annual trawl surveys. If an indicator is dominated by small areas and a few species, then management efforts concentrated on those populations could greatly affect the indicator value and be misinterpreted as influencing conditions across the whole sea. These issues are only identified by our procedure for decomposing the LFI.

Trends in annually gathered data have the potential to conflate phenological changes with community abundance and compositional changes; our Q1 vs. Q3 comparisons were a rough attempt to assess the importance of this effect for management, and we found that it may well be important. For example, if a trawl survey is carried out at the same time each year and cod populations appear to decline in abundance over time, this could be because cod populations are declining, or because the presence of cod in that region is occurring later each year and being missed by the survey. By comparing Q1 and Q3, we hoped to capture some of the seasonal variation due to changes in phenology. If Q1 and Q3 data showed similar trends in the LFI, then the timing of the trawl surveys within seasons would not be likely to affect abundance estimates. Results showed that while the overall slope of the LFI was positive in both quarters, the LFI increased more rapidly in Q3, with species and spatial components differing significantly in magnitude and sign between quarters. These differences between quarters exceeded sampling variability, suggesting an influence of survey timing and therefore conflation of phenological and abundance trends.

Spatial contributions tended to be greater and more positive across both quarters in the northern areas of the

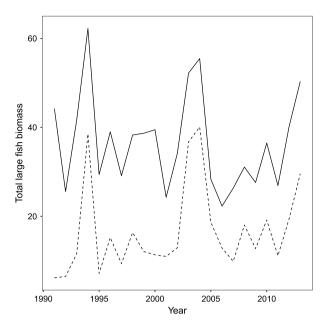


Fig. 6. Large fish biomass plotted against time (1991-2013) for all species in the whole North Sea (solid line) and a selection of species and grid cells (dashed line). Large fish biomass is the total biomass (based on catch per unit area) of fish above 40cm summed over all species and grid cells in each case. The species and grid cells in the selection represent the largest contributors to the large fish indicator (an absolute value of their slope greater than 1×10^{-4}). The species are Gadus morhua, Amblyraja radiata, Merlangius merlangus, Melanogrammus aeglefinus, Mustelus asterias, Scyliorhinus canicula and Pollachius virens. The grid cells are: 1×51 , 0×53 , 3×56 , 3×58 , 4×58 , -2×59 , -3×59 , $3 \times 59, 0 \times 60, 3 \times 60.$

North Sea, suggesting that populations with range centres outside the North Sea may be driving trends for the North Sea as a whole. Cod is one of the most significant contributors in both quarters, but switched from making a negative contribution in Q1 to a positive one in Q3, which corresponded with changes in large cod biomass (Appendix S5, Fig. S3). Reasons for this switch are unclear, but the contribution of cod had greater magnitude around the boundaries of the North Sea, especially in the north, which might suggest migration of large cod into the North Sea in Q3 from more northerly latitudes where cod are larger (Neuenfeldt et al. 2013). However, cod populations in the northern region of the North Sea have been shown to have limited movement and likely stay within the survey area (Neat et al. 2014) throughout the year. Results overall may thus suggest that a behavioural difference in cod populations in Northern subregions, leading to changes in catchability, may be the main reason for the faster recovery of the LFI in Q3.

Our results show the complexities of choosing a geographic region and season for assessment of fish community status. Even locations such as the North Sea that are partly bounded by land are strongly linked by currents and seasonal migrations of fauna to other regions (Daan et al. 1990). At any point in time, community composition will be determined by fauna resident in the North

Sea and by fauna that are present seasonally. This confounds the understanding of trends in species' abundance in surveys (Blanchard, Maxwell & Jennings 2007) and will have resulting effects on attempts to measure trends in community structure. Competition, predation and other interactions that structure the community will be transient and dynamic owing to seasonal movements. The apparent effects of North Sea fisheries on community composition will also vary in space and time, as fauna move in and out of the survey area. The methods we developed support assessment of the consequences of selecting different study regions and identifying species and locations that drive differences among regions.

Our results showing divergence of component LFI trends were based on linear regressions of the LFI against year. Fitted linear trends in the LFI would often not be principal tools for state assessment; rather, smoothed trends or annual values of the LFI compared to a reference point are more common (0.3 is a currently recommended reference point, Greenstreet et al. 2011). Our methods focussed on longer-term trends but could also straightforwardly be used to decompose the LFI and changes therein for time periods of 2 years or more, thus determining which species, sampling locations or other factors contribute to the LFI falling below or exceeding a reference point. However, short-term analyses would not capture dominant signals over time because changes on short time-scales are dominated by stochasticity rather than by consistent changes that may warrant management intervention (e.g. Engelhard et al. 2015).

There are plans to use the LFI for additional state reporting and to guide management decision-making, but our results show how the challenge of multiple meanings complicates the interpretation of trends. Simple indicators are useful because they reduce a complex food web into a single metric that can be tracked or compared to a set benchmark. But our results show it is more informative to also consider component parts of indicators, so as to understand the main drivers behind the 'headline' indicator and changes in it. Introducing such component indicators complicates interpretation for managers, but the added insight also reduces the risk of squandering resources and credibility because assessment and management efforts are less likely to be misguided. The greater complexity of interpreting a decomposition is unlikely to be as great as working with additional, unrelated indicators, because the elements of the decomposition are conceptually unified under the headline indicator. The solution offered by our decomposition-based method provides more information alongside the LFI, supporting more informed assessment and better management advice.

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Data accessibility

IBTS data can be downloaded from $\label{logistal} http://www.ices.dk/marine-data/data-portals/Pages/DATRAS.aspx.$

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

- Appendix S1. Proof of LFI slope decomposition.
- Appendix S2. Resampling method description.
- Appendix S3. Assumptions and limitations of the methods.
- Appendix S4. Cleaning of the IBTS data.
- Appendix S5. Decomposition of large fish biomass slopes.
- Appendix S6. Alternative analyses.
- **Fig. S1.** Ranked contributions to the slope of the LFI, decomposed by species.

Fig. S2. Decomposition of the LFI slope by grid cell with a linear colour scale.

Fig. S3. Decomposition of the total large fish biomass slope by species.

Fig. S4. Decomposition of the total large fish biomass slope by grid

Fig. S5. Decomposition of the LFI slope by both species and grid cell, Q1.

Fig. S6. Decomposition of the LFI slope by both species and grid cell, Q3.

Fig. S7. Decomposition of the LFI slope by grid cell for 5 species,

Fig. S8. Decomposition of the LFI slope by grid cell for 5 species, Q3.

Fig. S9. Yearly LFI values for Q1 IBTS data compared with previous reports.

Table S1. Example rows of IBTS data.

Table S2. Species list.