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Short Communication

Recent data suggest no further recovery in North Sea Large Fish Indicator

Tak Fung[1]*, Keith D. Farnsworth[1], David G. Reid[2], and Axel G. Rossberg[1]

[1]*School of Biological Sciences, Queen's University Belfast, 97 Lisburn Road, Belfast BT9 7BL, UK*
[2]*Fisheries Science Services, Marine Institute, Rinville, Oranmore, Co. Galway, Ireland*

**Corresponding Author. tel: +44 28 9097 2103; fax: +44 28 9097 5877; e-mail: tfung01@qub.ac.uk.*

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We detail the calculations of North Sea Large Fish Indicator values for 2009–2011, demonstrating an apparent stall in recovery. Therefore, recovery to the Marine Strategy Framework Directive's good environmental status of 0.3 by the 2020 deadline now looks less certain and may take longer than was expected using data from 2006 to 2008.

Keywords: community ecology, EAFM, LFI, MSFD, North Sea, OSPAR.

Introduction

The Large Fish Indicator (LFI) is a univariate metric characterizing the size spectrum of a fish community. It is defined as the biomass of fish above a length threshold ("large" fish) expressed as a proportion of the total fish biomass (Heslenfeld and Enserink, 2008; Greenstreet *et al.*, 2011; Shephard *et al.*, 2011). This means that the LFI captures decreases in large fish biomass caused by size-selective fishing (Pauly *et al.*, 1998; Shin *et al.*, 2005), as well as increases in small fish biomass caused by release from predation by large fish that have been fished (trophic cascades;, e.g. Frank *et al.*, 2005). Therefore, the LFI responds to both the direct and indirect effects of fishing (Greenstreet *et al.*, 2011; Shephard *et al.*, 2011).

The LFI has been adopted by OSPAR as an indicator for defining a fish community Ecological Quality Objective, under the Ecosystem Approach to Fisheries Management (Pikitch *et al.*, 2004; Heslenfeld and Enserink, 2008). It has also been listed as an indicator of "good environmental status" (GES) of foodwebs for the Marine Strategy Framework Directive (MSFD; Descriptor 4; European Commission, 2010). The MSFD requires member states to "take the necessary measures to achieve or maintain good environmental status in the marine environment by the year 2020 at the latest" (EU, 2008), so, if adopted, the recovery of the LFI to GES reference levels will become a statutory management goal.

Greenstreet *et al.* (2011) reviewed and summarized a decade of work by ICES that led to the selection and subsequent development of the LFI as a univariate metric for the state of demersal fish communities. Following the MSFD (EU, 2008), the LFI has been applied to several regions, including the North Sea (Greenstreet *et al.*, 2011), Celtic Sea (Shephard *et al.*, 2011), Baltic Sea (ICES, 2011b), and Grand Banks (ICES, 2011b). However, the operational development of this index is most advanced for the North Sea. Here, a large fish threshold of 40 cm was proposed for the demersal fish community, since it maximized the LFI sensitivity to fishing as opposed to environmentally driven recruitment variations (Greenstreet *et al.*, 2011). A reference level of 0.3 (using the 40-cm threshold) was proposed for the North Sea (Greenstreet *et al.*, 2011), where the LFI declined from 0.3 in 1983 to a low of 0.05 in 2001, followed by some recovery to 0.22 in 2008 (Greenstreet *et al.*, 2011). If this form of the LFI for the North Sea is adopted by MSFD member states with jurisdiction in the North Sea, fisheries management will have to ensure continued recovery to the GES reference level of 0.3 by 2020. Regular estimates of the North Sea LFI are therefore needed, but the last published was for 2008. Here, we report our calculations of the North Sea LFI for the years 2009–2011, displaying an apparent stall in recovery. We then present a discussion of the implications for fisheries management, including the consideration of the frequency with which it is useful to update the LFI.

Material and Methods

By definition (Greenstreet *et al.*, 2011), the North Sea LFI is based on data from the North Sea International Bottom Trawl Survey (IBTS) for the first quarter of each year. The IBTS covers the

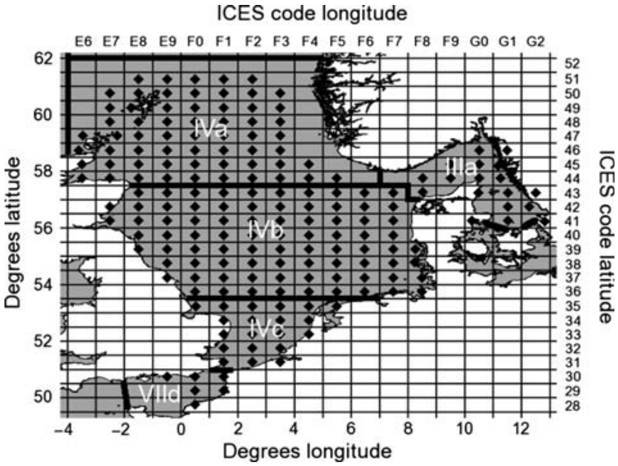

Figure 1. Map showing the area sampled by the IBTS during the first quarter of years 1986–2011. The bold lines delineate ICES Subareas, labelled as IIIa, IVa, IVb, IVc and VIId (ICES, 1977; http://www.fao.org/fishery/area/Area27/en). ICES rectangles marked with a diamond have at least one fish sampled by the IBTS during 1986–2011, according to DATRAS. This figure is based on ERSI shape files downloaded from ICES (http://geo.ices.dk/). Detailed maps of IBTS-sampled rectangles by year and species are available directly from ICES (http://ecosystemdata.ices.dk/Map/).

Greater North Sea region, specifically ICES Subareas IIIa, IV, and VIId (Figure 1). These data are publically available from the ICES Database of Trawl Surveys (DATRAS; http://datras.ices.dk/Home/Default.aspx). The data from DATRAS are for sampled organisms classified into taxanomic groups, mostly to the species level; each sampled organism is also classified by haul and length class. The cpue (catch per unit effort, i.e. the number of organisms caught per hour) is given for each combination of the taxonomic group, haul, and length class. Conversion of these data into LFI values involved several processing steps: removal of data for non-fish organisms and non-demersal fish; deletion of "dubious entries" (Daan, 2001); deletion of entries for Subarea VIId to ensure consistency with Greenstreet *et al.* (2011); conversion of numbers by the taxonomic group, haul, and length class into biomasses using appropriate length–weight regression parameters; and conversion of biomasses into biomass densities. A detailed protocol for these processing steps has not previously been published, and neither have some of the relevant parameters (e.g. length–weight regression parameters).

Below, we first detail the protocol followed in our calculations. It was developed using information available from Greenstreet *et al.* (2011), but in such a way that the LFI can be computed directly from IBTS data available by direct download from DATRAS. In contrast, Greenstreet *et al.* (2011) worked with raw IBTS data obtained directly by a formal request from ICES. To confirm that our approach gives LFI values closely matching those of Greenstreet *et al.* (2011), we then applied our protocol to the first quarter (Q1) IBTS data covering 1986–2008, from DATRAS, to derive a corresponding LFI time-series and compared this series with that of Greenstreet *et al.* (2011). DATRAS data for 1983–1985 were not used because these are not standardized for the same gear (GOV gear). Following the confirmation, we applied our protocol to Q1 IBTS data from 2009 to 2011 to calculate the most recent LFI trend. All DATRAS data were downloaded from the DATRAS website on 22 October 2011, in the format "cpue per length per haul", and 20 November 2011, in the formats "Exchange Data" and "SMALK". The data types used in each of these formats are given below, together with how they were used.

In detail, our protocol consists of the following steps. (i) Organisms were classified as fish or non-fish using the World Register of Marine Species (http://www.marinespecies.org/), enabling the removal of data for non-fish organisms. (ii) Fish were classified as demersal or non-demersal using the classifications of Greenstreet and Hall (1996) and Fraser *et al.* (2007) for the North Sea, supplemented by information from FishBase (Froese and Pauly, 2011), permitting the removal of data for non-demersal fish. (iii) "Dubious entries" were identified following Daan (2001) and either changed or deleted as appropriate. (iv) Entries sampled in ICES Subarea VIId were deleted to be consistent with Greenstreet *et al.* (2011). Note that although Greenstreet *et al.* (2011) stated that data from ICES Subarea IV were used, data from ICES Subarea IIIa were used as well (S. P. R. Greenstreet, in prep.). Subarea VIId entries only occur in 2007–2011 and their inclusion or exclusion has very little effect on the LFI (see Supplementary material for more detail). (v) For each remaining fish taxonomic group, length–weight regression parameter values were computed using DATRAS IBTS length–weight data (given in DATRAS data in the "SMALK" format) where possible. Failing this, North Sea parameter values from other sources were used where possible (Coull *et al.*, 1989; Robinson *et al.*, 2010) and parameter values for other locations were used otherwise (using references from FishBase; Froese and Pauly, 2011). (vi) Using the length–weight parameters, for each taxonomic group, length class, and haul, the number of organisms caught per hour (given in DATRAS data in the "cpue per length per haul" format) was converted into biomass caught per hour:

$$B_{ijkmn} = N_{ijkmn} a_i L_j^{b_i}, \qquad (1)$$

where B_{ijkmn} and N_{ijkmn} are the biomass caught per hour (g h^{-1}) and the number of individuals caught per hour (h^{-1}), respectively, for taxonomic group i, length class j, and haul k by vessel m in year n; a_i and b_i the length–weight regression parameters for taxonomic group i, which convert length (cm) to biomass (g); and L_j the mid-point of length class j (cm).

(vii) The biomasses of organisms caught per hour were converted to biomass densities. For a particular taxonomic group, length class, and haul, the biomass density is equal to the biomass caught divided by the swept-area. The swept-area can be calculated as the fishing gear wingspread multiplied by the distance towed, which is the product of haul duration and vessel groundspeed. Since the biomass caught per hour is the biomass caught divided by the haul duration (in h), this gives the following formula for converting biomass caught per hour to biomass density:

$$\rho_{ijkmn} = \frac{b_{ijkmn}}{A_{kmn}} = \frac{b_{ijkmn}}{S_{kmn} d_{kmn}} = \frac{b_{ijkmn}}{S_{kmn} t_{kmn} v_{kmn}} = \frac{B_{ijkmn}}{S_{kmn} v_{kmn}}, \qquad (2)$$

where ρ_{ijkmn} and b_{ijkmn} are the biomass density (g m^{-2}) and biomass (g), respectively, for taxonomic group i, length class j, and haul k by vessel m in year n; A_{kmn} the swept-area (m^2) of haul k by vessel m in year n; and S_{kmn}, d_{kmn}, t_{kmn}, and v_{kmn} the wingspread (m), towed distance (m), haul duration (h), and groundspeed ($\mathrm{m\,h^{-1}}$) for haul k by vessel m in year n. S_{kmn} values were available (in DATRAS data in the "Exchange Data" format) for 17% of all hauls in 1986–2011, corresponding to 18% of all biomass density entries. For a further 69% of hauls (63% of biomass density entries), S_{kmn} was estimated as the average over the available S_{kmn} values for the same ICES rectangle; the rectangles were given in DATRAS data in the "cpue per length per haul" format. For the remaining 14% of hauls (19% of biomass density entries), S_{kmn} was estimated using the depth of the haul (m), D_{kmn}, and the regression line $S_{kmn} = 6.33(\log_{10} D_{kmn}) + 7.14$ ($n = 1716$, $r^2 = 0.44$, where r is the Pearson's product–moment correlation coefficient), derived using pairs of S_{kmn} and D_{kmn} values from DATRAS data in the "Exchange Data" format. D_{kmn} values were available in DATRAS data in the "cpue per haul per length" format for almost all the remaining hauls. For the <0.1% of hauls without D_{kmn}, this value was estimated as the average over available D_{kmn} values for the same ICES rectangle.

v_{kmn} values were available (in DATRAS data in the "Exchange Data" format) for 47% of all hauls in 1986–2011, corresponding to 51% of all biomass density entries. For a further 36% of hauls (33% of biomass density entries), v_{kmn} was calculated as d_{kmn}/t_{kmn} using d_{kmn} and t_{kmn} values given in DATRAS data in the "Exchange Data" format. For the remaining hauls, v_{kmn} was estimated depending on data availability. Considering one of these hauls, if there was at least one v_{kmn} value for another haul by the same vessel m in year n, then v_{kmn} was estimated as the average of v_{kmn} values for hauls by the same vessel in the same year; this was the case for 1% of hauls (1% of biomass density entries). If there were no v_{kmn} values for the same vessel and year, but there was at least one v_{kmn} value for another haul by the same vessel in a different year, then v_{kmn} was estimated as the average of v_{kmn} values for hauls by the same vessel m in different years; this was the case for 7% of hauls (6% of biomass density entries). If there were no v_{kmn} values for the same vessel in any year, then v_{kmn} was estimated as the average of v_{kmn} values for hauls by different vessels in all years; this was the case for 9% of hauls (9% of biomass density entries).

(viii) For each year considered, the LFI was then calculated by summing the biomass densities of all fish individuals with length >40 cm in the year considered and then dividing the result by the sum of the biomass densities of all fish individuals in the same year:

$$\mathrm{LFI}_n = \frac{\sum_i \sum_{j:L_j>40\mathrm{cm}} \sum_k \sum_m \rho_{ijkmn}}{\sum_i \sum_j \sum_k \sum_m \rho_{ijkmn}}, \tag{3}$$

where LFI_n is the LFI in year n.

To make our method transparent and our results reproducible, we provide, as Supplementary material, a list of all the taxonomic groups considered and their classification as demersal fish, non-demersal fish, or non-fish, together with details of which dubious entries were changed or deleted. Furthermore, we provide a list of synonymous demersal fish species names identified (only one name for each species retained) and a list of all length–weight regression parameters used. For the regression parameters, the corresponding sample sizes, length ranges of the samples, sampling locations, and references are also given, together with a discussion of the quality and relevance of the data used to derive the parameters.

Results

Figure 2 shows the complete LFI time-series we calculated for 1986–2011 and compares it with that calculated by Greenstreet *et al.* (2011) for 1983–2008. A strong correlation between the two time-series ($r^2 = 0.789$, $n = 23$) is evident during the period of overlap 1986–2008. The average absolute difference (over the 23 years) between the two time-series is 0.00984, which we take to be very small. Following the LFI increase in 2007/2008, the trend in the LFI found for 2009–2011 does not support a prediction of continued recovery, but rather shows an apparent stall in recovery, not inconsistent with an unsteady decline (Figure 2).

The years 2007 and 2008 show an anomalous deviation between our LFI values and those calculated by Greenstreet *et al.* (2011). This is explained by an unusually large increase in the proportion of large fish during 2007 and 2008 in the Kattegat and Skagerrak subarea (corresponding to ICES Subarea IIIa) within the data used by Greenstreet *et al.* (2011) (Figure 3). This large increase is not seen in the DATRAS data (Figure 3), which is continuously updated and corrected by an ICES Working Group (ICES, 2011a). If data from Kattegat and Skagerrak in 2007 and 2008 are excluded, then the two LFI time-series calculated using the protocol in this study and the protocol by Greenstreet *et al.* (2011) differ by <0.007 in 2007 and 2008 (S. P. R. Greenstreet, pers. comm.). The datasets differed for Kattegat and Skagerrak in 2007 and 2008 due to the inclusion of entries from ICES rectangle 40G2 in the data of Greenstreet *et al.* (2011) (S. P. R. Greenstreet, in prep.). This square had a high abundance of large cod in the anomalous years, considerably inflating the LFI calculated by Greenstreet *et al.* (2011) for 2007 and 2008 (S. P. R. Greenstreet, in prep.; Figures 2 and 3). However, this square lies outside ICES Subarea IIIa (Figure 1; ICES, 1977; http://www.fao.org/fishery/area/Area27/en) and should therefore be excluded as done in the IBTS data available from DATRAS. There is an excellent fit ($r^2 = 0.956$, $n = 21$) between the LFI series calculated using DATRAS data and that calculated by Greenstreet *et al.* (2011) over

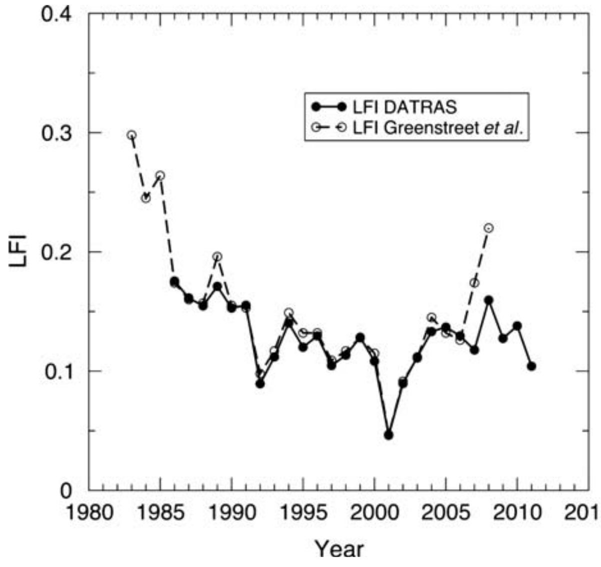

Figure 2. 1986–2011 time-series for the LFI calculated using Q1 IBTS data following the method detailed in this paper (solid line), together with the 1983–2008 time-series for the LFI calculated by Greenstreet *et al.* (2011) (dashed line).

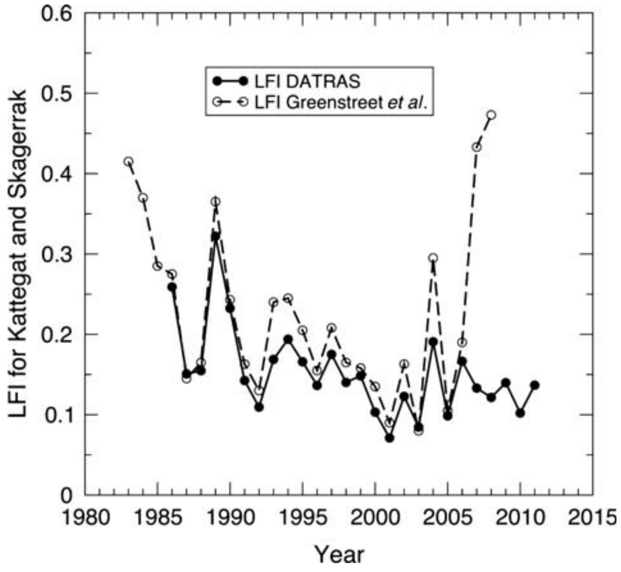

Figure 3. 1986–2011 time-series for the LFI in the Kattegat and Skagerrak subarea (corresponding to ICES Subarea IIIa) calculated using Q1 IBTS data following the method detailed in this paper (solid line); also shown is the corresponding 1983–2008 time-series for the LFI calculated by ICES (2010, Figure 5.5.3) using the data and protocol of Greenstreet *et al.* (2011) (dashed line).

the years 1986–2006, with an average absolute difference of 0.00522.

Discussion

An indicator with wide-ranging policy implications should be robust to minor variations in the protocol used to compute it. Notwithstanding data issues in 2007 and 2008, already discussed, our work confirms this property for the LFI. We worked with an IBTS dataset available by direct download from a public website, whereas Greenstreet *et al.* (2011) used a different, raw IBTS dataset that is not; as expected, this resulted in minor protocol variations. An indicator protocol that is based on free, public data and a simple, published algorithm for computation, as proposed in this paper, has the advantage of allowing all stakeholders to verify the results. The protocol we propose also invites research for further improvement, detailed studies of how management measures could affect the LFI, and updating of LFI values when new catch data become available.

Updating the North sea LFI from 2009 to 2011, together with a recalculation in 2007 and 2008 that includes only ICES rectangles in Subareas IIIa and IV, has shown no evidence of continued recovery in the index beyond 2008. This apparent stall in recovery suggests that meeting GES by 2020, corresponding to an LFI reference level of 0.3, now looks less certain and may take longer than would be expected given data calculated by Greenstreet *et al.* (2011) covering 2006–2008. This expectation was quantified by Greenstreet *et al.* (2011) using seven linear regression models, assuming that the LFI lagged the community-averaged fishing mortality by 12–18 years. The average of these models predicts an increasing LFI trend beyond 2008 so as to nearly reach the reference value by 2020 (Greenstreet *et al.*, 2011). Our update of the time-series for 2009–2011 shows that the 2020 target might be missed by a wider margin. Importantly, the new data (Figure 2) fail to support the prediction of LFI values based on a lagged correlation with the community-averaged fishing mortality—such an extrapolation would have suggested an increasing trend for the LFI in 2009–2011, corresponding to a decreasing trend in the fishing mortality in 1991–1999 (Greenstreet *et al.*, 2011). Recovery may be more complex a process than can be represented by an inverse linear time-lagged relationship between LFI and fishing mortality.

An adequate time interval for updating the LFI values is determined by a balance between the costs of updating and the benefits provided by the added information. Given that IBTS surveys are carried out yearly for other purposes and the data made available on DATRAS soon thereafter, the costs reduce to that of doing the calculations. The protocol described here can be fully automated, so that a yearly LFI update would come at minimal costs. Updating the LFI as often as every year gives rise to the benefit of reducing uncertainties faced by stakeholders planning on the basis of projected LFI trends. Such projections are subject to two kinds of uncertainty. First, the LFI time-series exhibit noticeable year-to-year fluctuations, resulting from a combination of statistical and ecological effects (future studies will need to disentangle and determine the relative strengths of these contributions). Any additional datapoint contributes to an averaging out of fluctuations at the end of the time-series, which can lead to better extrapolations for a given target year. Second, there remains considerable uncertainty regarding the processes driving the long-term dynamics of the LFI and associated response times. Large fish grow slowly relative to small fish, so it is expected that large fish biomass recovers slowly compared with small fish biomass (Hutchings, 2000). Therefore, it might be expected that the LFI also recovers slowly, perhaps approximately decades. However, Hutchings (2000) examined the recovery of 31 stocks of gadoids after 40–100% decreases in reproductive biomass and found that although most of them experienced little to no recovery after 5 years, eight of them recovered by over 20% of their original, pre-decline biomass and two made a full recovery (see Figure 2 in Hutchings, 2000). In addition, North Sea simulations using the FishSUMS model suggest that the LFI can exhibit large increases within 3 years if fishing pressure is low enough, $<60\%$ of 2006 levels (ICES, 2010, Figure 5.4.2.2.1). Currently, there is no generally accepted theory for the processes determining the time-scale of LFI recovery. Annual LFI updates can be useful for differentiating between models predicting different recovery rates, thus further reducing uncertainty for stakeholders using LFI projections. Therefore, we expect that the overall benefits of updating the LFI regularly, even as often as once a year, would outweigh the costs. However, we emphasize that an additional LFI value, arising from a regular update, should be interpreted in conjunction with all preceding LFI values to maximize the reliability of any derived trend—this is implied in our analysis above.

The LFI trend we found over 2009–2011 should be compared with those obtained using alternative protocols (e.g. that of Greenstreet *et al.*, 2011); if the same trend is found across protocols, then this strengthens support for this trend and the robustness of the LFI to protocol variations. Obviously, our updating by another 3 years does not necessarily predict a future trend, but it emphasizes the need for regular updates from now on. In addition, it provides an early indication suggesting that continued recovery of the North Sea demersal fish community to GES may require further (perhaps more sophisticated) management than the reduction in effort achieved so far.

Supplementary material

The following supplementary material is available at *ICESJMS* online: "Processing of ICES DATRAS 1986–2011 North Sea IBTS Data", which includes a list of the taxonomic groups considered and their classification as demersal fish, non-demersal fish, or non-fish; a list of synonymous demersal fish species names identified; details of which dubious entries were deleted or changed following Daan (2001); and a list of all the length–weight regression parameters used for demersal fish.

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Supplementary Material

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Short Communication

Tak Fung, Keith D. Farnsworth, David G. Reid and Axel G. Rossberg

Processing of ICES DATRAS 1986-2011 North Sea IBTS Data

This Supplementary Material details the taxonomic groups considered and their classification as demersal fish, non-demersal fish or non-fish; the synonymous demersal fish species names identified; dubious entries that were deleted or changed following Daan (2001); the effect on LFI of removing entries from ICES subarea VIId; and the length-weight regression parameters used for demersal fish.

Classification of groups and removal of synonymous names

Table S1 below lists all taxonomic groups in the North Sea IBTS data downloaded from the ICES DATRAS website (http://datras.ices.dk/Home/Default.aspx) for the period 1986-2011, together with their classification as demersal fish, non-demersal fish or non-fish. Groups were classified using Greenstreet and Hall (1996), Fraser *et al*. (2007), FishBase (Froese and Pauly, 2011) and the World Register of Marine Species (WoRMS; http://www.marinespecies.org/). Synonymous demersal fish species names were identified using FishBase, as shown in Table S2 below, and only one name for each species retained.

Removal of entries according to Daan (2001)

Daan (2001) examined IBTS data from 1965-1998 and identified dubious entries indicating possible errors. Following this study, the following entries were deleted from or changed in the Q1 1986-1998 data used in our study: (i) the *Raja undulata* entry in 1990 was deleted, (ii) the *Lepadogaster* entry was deleted, (iii) the *Gaidropsarus mediterraneus* entry with length >25 cm was deleted, (iv) the *Trachyrincus murrayi* entry was changed to a *Triglops murrayi* entry, (v) the *Leptoclinus maculatus* with length >20 cm entry was changed to a *Lumpenus lumpretaeformis* entry, (vi) entries corresponding to fish that are unusually small

(Table 4 of Daan (2001)) were deleted and (vii) entries with errors that occurred during data input were corrected (Table 11 of Daan (2001)).

For each year, the total biomass density of the entries deleted according to (i), (ii), (iii) and (vi) was always <0.001% of the total biomass density of entries that were not deleted, such that the deletions have negligible effect on the LFI. Similarly, for each year, the total biomass density of entries that were changed according to (iv), (v) and (vii) was always <0.001% of the total biomass density of entries that were not deleted, such that the changes have negligible effect on the LFI. The IBTS Working Group of ICES, responsible for the continued monitoring and analysis of DATRAS data for quality assurance, has proposed further examination of and changes to entries in the database (ICES, 2008, 2009, 2010*a*, 2011). National laboratories examine these proposals and make appropriate changes by uploading revised data to DATRAS (ICES, 2011). However, the number of entries earmarked for possible change is relatively very small compared to the approx. 850,000 entries used in our study for 1986-2011. In addition, the biomass distributions for the commercial species, which contribute most to the LFI, are unlikely to change by much because of their large sample size and relative ease of identification (ICES, 2007). Thus, we expect that, like the changes we have made following Daan (2001) for 1986-1998, further changes to DATRAS resulting from quality checks will have minor effects on the LFI values we derived in our study. Nevertheless, as DATRAS is updated, the LFI values in our study can be readily updated using the protocol described.

Removal of entries in ICES subarea VIId

After changing the entries according to Daan (2001), the IBTS data downloaded from the ICES DATRAS website contained 4,853 demersal fish entries for ICES subarea VIId. To ensure consistency with the dataset used by Greenstreet *et al.* (2011), which does not include entries from subarea VIId, all entries from VIId were deleted. This was also necessary to ensure consistency of sampled areas across years, since entries from VIId only occurred in 2007-2011. However, this deletion changed LFI in each of the years in 2007-2011 only by very small amounts (<0.005), because these 4,853 entries from VIId make up only <4% of all demersal fish entries in 2007-2011.

Derivation of length-weight regression parameters

Table S3 below lists all the demersal fish taxa remaining after cleaning the entries following Daan (2001), together with their length-weight regression parameters a and b. These parameters relate the weight W (in g) to total length L (in cm) by the equation $W = aL^b$. For each pair of parameters, the sample size, length range of individuals in the sample, sampling location and reference are given in Table S3 as well. In the IBTS, the total lengths of all fish species in Table S3 were measured apart from *Alepocephalus bairdii*, for which the standard length was measured, and *Chimaera monstrosa*, for which the pre-supra caudal fin length was measured (ICES, 2010*b*). Thus, for *A. bairdii*, the lengths from DATRAS (working in cm) were first converted to total lengths by multiplying by 1.116 and subtracting 0.294 (Froese and Pauly, 2011), before converting to weight using the parameters in Table S3. For *C. monstrosa*, conversion factors were not available from FishBase for converting pre-supra caudal fin length to total length. Therefore, a wide range of conversion factors were tested; specifically, it was assumed that the pre-supra caudal fin length is the total length multiplied by a factor c, with c = 0.5, 0.6, 0.7, 0.8, 0.9 and 1 tested. We found that varying c across this wide range changed LFI in a particular year by <0.0002, a tiny amount. Thus, our LFI results are insensitive to c, which was taken to be 0.7.

The IBTS data downloaded from DATRAS in the "CPUE per length per haul" format gives the length class of each sampled organism but not its weight. To convert lengths to weights, length-weight parameter values for each species in Table S3 were derived using 1986-2011 IBTS length-weight data downloaded from DATRAS in the "SMALK" format, Coull *et al.* (1989), Robinson *et al.* (2010) and references from FishBase (Froese and Pauly, 2011). For each species, a set of parameter values a and b derived using the DATRAS IBTS data in the "SMALK" format was preferentially used, since this data has lengths and weights collected by the same survey, in the same quarter, as that used to generate DATRAS IBTS data in the "CPUE per length per haul" format. If a set of parameter values could not be derived using DATRAS IBTS data for a particular species, then a set derived using fish sampled from the North Sea (ICES subarea IV) was preferentially chosen (Coull *et al.*, 1989; Robinson *et al.*, 2010); if there were more than one set of parameters from the North Sea for a particular species, then the one with the largest sample size was chosen.

If there were no North Sea parameter sets for a particular species, then a parameter set for a sampling location within the Greater North Sea region, corresponding to OSPAR region II (http://www.ospar.org/content/content.asp?menu=00470212000000_000000_000000), was chosen; if there were no such sets, then a set from a sampling location closest to the Greater North Sea region by water was chosen (e.g., Bay of Biscay rather than Aegean Sea). The only exception was *Chimaera monstrosa*; the parameter set in Coull *et al.* (1989) for the North Sea and West coast of Scotland was not used because a is unusually high, being five orders of magnitude higher than that derived by Borges *et al.* (2003) using a larger sample size in the Algarve and at least two orders of magnitude higher than the *a* values used for all species in Table S3.

Length-weight parameter sets for 16 species could be derived using DATRAS Q1 IBTS data (Table S3). These 16 species together make up >74% (range of 74.6% to 92.0%) of total demersal fish biomass density in each of the years 1986-2011, for the DATRAS IBTS data used in this study. Thus, the Q1 IBTS LFI time-series presented in this paper was derived using length-weight parameter values that largely reflect the gear, location and season of the survey used. In addition, a total of only 18 species contribute over 95% of total demersal fish biomass density in each of the years 1986-2011 – *Amblyraja radiata*, *Cyclopterus lumpus, Eutrigla gurnardus*, *Gadus morhua*, *Hippoglossus platessoides*, *Limanda limanda*, *Melanogrammus aeglefinus*, *Merlangius merlangus*, *Microstomus kitt*, *Molva molva, Platichthys flesus*, *Pleuronectes platessa*, *Pollachius pollachius*, *Pollachius virens, Raja clavata*, *Scyliorhinus canicula*, *Squalus acanthias* and *Trisopterus esmarkii*. For 9 of these 18 species, parameter sets could be derived using DATRAS IBTS data; for a further 6 species, North Sea parameter sets derived by Coull *et al.* (1989) and Robinson *et al.* (2010) were used; and for the remaining 3 species (*R. clavata*, *S. canicula* and *S. acanthias*), parameter sets derived using data from the Northeast Atlantic, including areas outside the North Sea, were used (Table S3). Thus, the vast majority of the total demersal fish biomass density in each year was computed using length-weight parameter values reflecting the geographic region of the IBTS survey.

As detailed above, >74% of total demersal fish biomass density in each year was computed using length-weight parameter sets derived using Q1 IBTS data, which means that most of the total density in each year was computed using parameter sets reflecting the season in which the Q1 IBTS survey was carried out. However, length-weight regression parameter sets that were derived using fish sampled at other times throughout the year were also used; for example, fish were sampled in the third quarter in the study by Robinson *et al*. (2010). One should note, however, that for each of six North Sea species (*Gadus morhua*, *Melanogrammus aeglefinus*, *Merlangius merlangus*, *Microstomus kitt*, *Pollachius virens* and *Pleuronectes platessa*), the 12 monthly *a* parameter values derived by Coull *et al*. (1989) using fish sampled from the Northeast Atlantic had a small coefficient of variation of <0.05. This suggests that seasonal variation in the length-weight parameters can be assumed to be negligible. Nonetheless, if additional parameter sets derived using only fish sampled during the first quarter become available in the future, then they can be substituted for the corresponding sets in Table S3.

To avoid sex bias, parameter sets for males or females only were not used in isolation; for four species, a parameter set was derived by averaging over two parameter sets, one for males and one for females. Parameter sets for the large majority of species have been published with information on sample size and length range, which was then included in Table S3. This information would help to decide whether to replace any of the parameter sets with new ones in the future, should they become available.

If, for a particular species, parameter values could not be derived using DATRAS IBTS data, Coull *et al*. (1989), Robinson *et al*. (2010) or FishBase, the average values over all North Sea species of the same genus (for which parameter values could be derived) were used. If parameter values were unavailable for all North Sea species of the same genus, the average values over all North Sea species in the same family were used; if parameter values were unavailable for all North Sea species of the same family, then average values over all species in the same genus, regardless of location, were used. If there were no parameter values for all species in the same family, which was the case for the three roundfish species *Echiodon drummondii*, *Liparis liparis* and *Liparis montagui*, then average values over the 10 North Sea roundfish species with nearest maximum lengths (as recorded in the IBTS data downloaded from DATRAS) were used. For taxonomic groups above the species level (i.e., genus or family level), average values taken over all North Sea species at that level were used.

Table S1. List of all taxonomic groups in the North Sea IBTS data downloaded from the ICES DATRAS website, for 1986-2011, together with their classification as demersal fish, non-demersal fish or non-fish. Synonymous names have been removed. For demersal fish, the synonyms deleted are listed in Table S2; for non-demersal fish, no synonyms were identified; and for non-fish, the synonyms *Loligo subulata* (synonymous for *Alloteuthis subulata*) and *Maia squinado* (*Maja squinado*) were deleted.

Taxonomic group	**Classification**
Acentronura	Demersal fish
Aequipecten opercularis	Non-fish
Agonus cataphractus	Demersal fish
Alepocephalus bairdii	Demersal fish
Alloteuthis subulata	Non-fish
Alosa	Non-demersal fish
Alosa agone	Non-demersal fish
Alosa alosa	Non-demersal fish
Alosa fallax	Non-demersal fish
Amblyraja radiata	Demersal fish
Ammodytes	Non-demersal fish
Ammodytes marinus	Non-demersal fish
Ammodytes tobianus	Non-demersal fish
Ammodytidae	Non-demersal fish
Anarhichas lupus	Demersal fish
Anguilla anguilla	Demersal fish
Aphia minuta	Non-demersal fish
Arctica islandica	Non-fish
Argentina	Non-demersal fish
Argentina silus	Non-demersal fish
Argentina sphyraena	Non-demersal fish
Argentinidae	Non-demersal fish
Arnoglossus	Demersal fish
Arnoglossus imperialis	Demersal fish
Arnoglossus laterna	Demersal fish
Artediellus europaeus	Demersal fish
Aspitrigla cuculus	Demersal fish
Atherina presbyter	Non-demersal fish
Austrorossia	Non-fish
Belone belone	Non-demersal fish
Blenniidae	Demersal fish

Bothidae	Demersal fish
Brama brama	Non-demersal fish
Brosme brosme	Demersal fish
Buccinum undatum	Non-fish
Buglossidium	Demersal fish
Buglossidium luteum	Demersal fish
Callionymidae	Demersal fish
Callionymus	Demersal fish
Callionymus lyra	Demersal fish
Callionymus maculatus	Demersal fish
Callionymus reticulatus	Demersal fish
Cancer pagurus	Non-fish
Caproidae	Demersal fish
Capros aper	Demersal fish
Centrolabrus exoletus	Non-demersal fish
Cephalopoda	Non-fish
Chelidonichthys lucernus	Demersal fish
Chimaera monstrosa	Demersal fish
Ciliata mustela	Demersal fish
Ciliata septentrionalis	Demersal fish
Clupea harengus	Non-demersal fish
Conger conger	Demersal fish
Coryphaenoides rupestris	Non-demersal fish
Crangon	Non-fish
Crangon crangon	Non-fish
Crystallogobius linearis	Demersal fish
Ctenolabrus rupestris	Non-demersal fish
Cyclopterus lumpus	Demersal fish
Dicentrarchus labrax	Non-demersal fish
Diplecogaster bimaculata	Demersal fish
Dipturus batis	Demersal fish
Dipturus linteus	Demersal fish
Echiichthys vipera	Demersal fish
Echiodon drummondii	Demersal fish
Eledone cirrhosa	Non-fish
Enchelyopus cimbrius	Demersal fish
Engraulis encrasicolus	Non-demersal fish
Entelurus aequoreus	Demersal fish
Etmopterus spinax	Demersal fish
Eutrigla gurnardus	Demersal fish
Gadiculus argenteus	Non-demersal fish
Gadus morhua	Demersal fish
Gaidropsarus	Demersal fish
Gaidropsarus argentatus	Demersal fish
Gaidropsarus macropthalmus	Demersal fish
Gaidropsarus mediterraneus	Demersal fish

Gaidropsarus vulgaris	Demersal fish
Galeorhinus galeus	Demersal fish
Gasterosteidae	Non-demersal fish
Gasterosteus aculeatus	Non-demersal fish
Glyptocephalus cynoglossus	Demersal fish
Gobiidae	Demersal fish
Gobius	Demersal fish
Gobius cobitis	Demersal fish
Gobius niger	Demersal fish
Gymnammodytes semisquamatus	Non-demersal fish
Helicolenus dactylopterus	Demersal fish
Hippoglossoides platessoides	Demersal fish
Hippoglossus hippoglossus	Demersal fish
Homarus gammarus	Non-fish
Hyperoplus	Non-demersal fish
Hyperoplus immaculatus	Non-demersal fish
Hyperoplus lanceolatus	Non-demersal fish
Illex coindetii	Non-fish
Labrus bergylta	Non-demersal fish
Labrus mixtus	Non-demersal fish
Lampetra fluviatilis	Demersal fish
Lamprididae	Non-demersal fish
Lepadogaster	Demersal fish
Lepidorhombus whiffiagonis	Demersal fish
Leptagonus decagonus	Demersal fish
Leptoclinus maculatus	Demersal fish
Lesueurigobius	Demersal fish
Lesueurigobius friesii	Demersal fish
Leucoraja circularis	Demersal fish
Leucoraja fullonica	Demersal fish
Leucoraja lentiginosa	Demersal fish
Leucoraja naevus	Demersal fish
Limanda limanda	Demersal fish
Liparis	Demersal fish
Liparis liparis	Demersal fish
Liparis montagui	Demersal fish
Lithodes maja	Non-fish
Liza ramada	Non-demersal fish
Loliginidae	Non-fish
Loligo	Non-fish
Loligo forbesii	Non-fish
Loligo vulgaris	Non-fish
Lophius budegassa	Demersal fish
Lophius piscatorius	Demersal fish
Lumpenus lumpretaeformis	Demersal fish
Lycenchelys sarsii	Demersal fish

Lycodes vahlii	Demersal fish
Macropipus puber	Non-fish
Macrorhamphosus scolopax	Demersal fish
Maja	Non-fish
Maja squinado	Non-fish
Maurolicus muelleri	Non-demersal fish
Melanogrammus aeglefinus	Demersal fish
Merlangius merlangus	Demersal fish
Merluccius merluccius	Demersal fish
Microchirus	Demersal fish
Microchirus variegatus	Demersal fish
Micromesistius poutassou	Non-demersal fish
Microstomus kitt	Demersal fish
Molva dypterygia	Demersal fish
Molva molva	Demersal fish
Mugilidae	Demersal fish
Mullus barbatus	Demersal fish
Mullus surmuletus	Demersal fish
Mustelus	Demersal fish
Mustelus asterias	Demersal fish
Mustelus mustelus	Demersal fish
Myoxocephalus quadricornis	Demersal fish
Myoxocephalus scorpioides	Demersal fish
Myoxocephalus scorpius	Demersal fish
Myxine glutinosa	Demersal fish
Nephrops norvegicus	Non-fish
Nerophis ophidion	Demersal fish
Osmerus eperlanus	Non-demersal fish
Pagellus erythrinus	Demersal fish
Palaemon serratus	Non-fish
Pecten maximus	Non-fish
Pegusa lascaris	Demersal fish
Petromyzon marinus	Demersal fish
Pholis gunnellus	Demersal fish
Phrynorhombus norvegicus	Demersal fish
Phycidae	Demersal fish
Phycis blennoides	Demersal fish
Platichthys flesus	Demersal fish
Pleuronectes platessa	Demersal fish
Pollachius pollachius	Demersal fish
Pollachius virens	Demersal fish
Pomatoschistus	Demersal fish
Pomatoschistus lozanoi	Demersal fish
Pomatoschistus microps	Demersal fish
Pomatoschistus minutus	Demersal fish
Pomatoschistus pictus	Demersal fish

Pterycombus brama	Non-demersal fish
Raja	Demersal fish
Raja brachyura	Demersal fish
Raja clavata	Demersal fish
Raja microocellata	Demersal fish
Raja montagui	Demersal fish
Raja undulata	Demersal fish
Rajidae	Demersal fish
Raniceps raninus	Demersal fish
Rossia macrosoma	Non-fish
Salmo salar	Non-demersal fish
Salmo trutta	Non-demersal fish
Sardina pilchardus	Non-demersal fish
Scomber scombrus	Non-demersal fish
Scophthalmus maximus	Demersal fish
Scophthalmus rhombus	Demersal fish
Scorpaena scrofa	Demersal fish
Scyliorhinus canicula	Demersal fish
Scyliorhinus stellaris	Demersal fish
Sebastes	Demersal fish
Sebastes marinus	Demersal fish
Sebastes viviparus	Demersal fish
Sepia	Non-fish
Sepia officinalis	Non-fish
Sepietta oweniana	Non-fish
Sepiola	Non-fish
Sepiola atlantica	Non-fish
Sepiolida	Non-fish
Solea impar	Demersal fish
Solea solea	Demersal fish
Soleidae	Demersal fish
Somniosus microcephalus	Demersal fish
Sparidae	Demersal fish
Spinachia spinachia	Non-demersal fish
Spondyliosoma cantharus	Demersal fish
Sprattus sprattus	Non-demersal fish
Squalidae	Demersal fish
Squalus acanthias	Demersal fish
Stichaeidae	Demersal fish
Symphodus melops	Non-demersal fish
Syngnathidae	Demersal fish
Syngnathus	Demersal fish
Syngnathus acus	Demersal fish
Syngnathus rostellatus	Demersal fish
Syngnathus typhle	Demersal fish
Taurulus bubalis	Demersal fish

Taurulus lilljeborgi	Demersal fish
Teuthida	Non-fish
Thunnus thynnus	Non-demersal fish
Todarodes sagittatus	Non-fish
Todaropsis eblanae	Non-fish
Trachinus draco	Demersal fish
Trachurus trachurus	Non-demersal fish
Trachyrincus murrayi	Demersal fish
Triglidae	Demersal fish
Trigloporus lastoviza	Demersal fish
Triglops murrayi	Demersal fish
Triglops pingeli	Demersal fish
Trisopterus esmarkii	Demersal fish
Trisopterus luscus	Demersal fish
Trisopterus minutus	Demersal fish
Zeiformes	Non-demersal fish
Zeugopterus	Demersal fish
Zeugopterus punctatus	Demersal fish
Zeugopterus regius	Demersal fish
Zeus faber	Non-demersal fish
Zoarces viviparus	Demersal fish
Zoarcidae	Demersal fish

Table S2. List of all demersal fish species with synonyms in the North Sea IBTS data downloaded from the ICES DATRAS website, for 1986-2011. The names on the left-hand column were retained.

Species	**Synonym**
Aspitrigla cuculus	*Chelidonichthys cuculus*
Ciliata mustela	*Ciliata mustella*
Entelurus aequoreus	*Entelurus aequerius*
Lumpenus lumpretaeformis	*Lumpenus lampretaeformis*
Lycenchelys sarsii	*Lycenchelys sarsi*
Scophthalmus maximus	*Psetta maxima*
Dipturus batis	*Raja batis*
Leucoraja fullonica	*Raja fullonica*
Leucoraja naevus	*Raja naevus*
Amblyraja radiata	*Raja radiata*
Enchelyopus cimbrius	*Rhinonemus cimbrius*
Solea solea	*Solea vulgaris*
Echiichthys vipera	*Trachinus vipera*
Chelidonichthys lucernus	*Trigla lucerna*
Phrynorhombus norvegicus	*Zeugopterus norvegicus*

Table S3. List of all demersal groups in the North Sea IBTS data downloaded from the ICES DATRAS website, for 1986-2011, together with their length-weight regression parameters *a* and *b*. These parameters were used to convert total length *L* (cm) to weight *W* (g) using the equation $W = aL^b$. For each set of *a* and *b* values, the corresponding sample size (*N*), length range of individuals, sampling location and reference are shown if they are available. "U" stands for "Unknown" – i.e., no figure was given in the corresponding reference. The reference "DATRAS (2011)" applies to parameter values calculated from DATRAS IBTS data.

Taxonomic group	***a***	***b***	***N***	**Min *L* (cm)**	**Max *L* (cm)**	**Location(s)**	**Reference**
Acentronura	0.0002	3.2326		Average over North Sea species in Syngnathidae			
Agonus cataphractus	0.0091	2.9050	130	2.1	16.2	North Sea	Robinson *et al*. (2010)
Alepocephalus bairdii	0.0028	3.2100	5	12.0	75.0	U	Froese (1998)
Amblyraja radiata	0.0056	3.1210	19	10.6	45.0	North Sea	Robinson *et al*. (2010)
Anarhichas lupus	0.0033	3.2491	58	32.0	84.0	North Sea	Coull *et al*. (1989)
Anguilla anguilla	0.0006	3.3130	957	10.0	60.0	Tadnoll Brook	Mann and Blackburn (1991)
Arnoglossus	0.0047	3.2180		Average over North Sea species in *Arnoglossus*			
Arnoglossus imperialis	0.0028	3.3400	18	9.0	18.0	Cantábrico	Pereda and Villamor (1991)
Arnoglossus laterna	0.0065	3.0960	1,342	1.6	19.4	North Sea	Robinson *et al*. (2010)
Artediellus europaeus	0.0135	3.0641		Average over North Sea species in Cottidae			
Aspitrigla cuculus	0.0045	3.2228	480	12.0	46.0	West coast of Scotland	Coull *et al*. (1989)
Blenniidae	0.0093	3.0000		Average over North Sea species in Blenniidae			
Bothidae	0.0047	3.2180		Average over North Sea species in Bothidae			
Brosme brosme	0.0051	3.1890	7	U	U	U	Bedford *et al.* (1986)

Buglossidium	0.0078	3.1280	Average over North Sea species in *Buglossidium*				
Buglossidium luteum	0.0078	3.1280	3,410	1.2	16.6	North Sea	Robinson *et al*. (2010)
Callionymidae	0.0135	2.6857	Average over North Sea species in Callionymidae				
Callionymus	0.0135	2.6857	Average over North Sea species in *Callionymus*				
Callionymus lyra	0.0086	2.9270	256	2.6	22.8	North Sea	Robinson *et al*. (2010)
Callionymus maculatus	0.0162	2.5781	66	10.0	16.0	North Sea	Coull *et al*. (1989)
Callionymus reticulatus	0.0158	2.5520	33	1.0	17.0	North Sea	Robinson *et al*. (2010)
Caproidae	0.2218	1.9707	Average over North Sea species in Caproidae				
Capros aper	0.2218	1.9707	5	10.5	14.5	North Sea and West coast of Scotland	Coull *et al*. (1989)
Chelidonichthys lucernus	0.0080	3.0610	23	17.0	62.5	North Sea and West coast of Scotland	Coull *et al*. (1989)
Chimaera monstrosa	0.0003	3.4750	22	31.6	93.3	Algarve	Borges *et al.* (2003)
Ciliata mustela	0.0064	3.0000	U	U	U	U	Bauchot and Bauchot (1978)
Ciliata septentrionalis	0.0055	3.1785	351	U	U	Severn Estuary and Bristol Channel	Claridge and Gardner (1977)
Conger conger	0.0002	3.5090	128	30.0	180.0	Bay of Biscay	Dorel (1986)
Crystallogobius linearis	0.0080	3.1614	Average over North Sea species in Gobiidae				
Cyclopterus lumpus	0.0587	2.9390	19	25.0	47.0	North Sea	Coull *et al*. (1989)
Diplecogaster bimaculata	0.0141	2.7370	12	2.0	3.6	North Sea	Robinson *et al*. (2010)
Dipturus batis	0.0036	3.0787	8	25.6	69.8	North Sea and West coast of Scotland	Coull *et al*. (1989)
Dipturus linteus	0.0036	3.0787	Average over North Sea species in *Dipturus*				
Echiichthys vipera	0.0129	2.9470	28	1.7	13.2	North Sea	Robinson *et al*. (2010)
Echiodon drummondii	0.0059	3.1304	Average over 10 North Sea species with closest surveyed maximum *L*				
Enchelyopus cimbrius	0.0035	3.1062	63	11.0	29.0	North Sea	Coull *et al*. (1989)
Entelurus aequoreus	0.0002	3.0000	U	U	U	U	Bauchot and Bauchot (1978)
Etmopterus spinax	0.0019	3.2120	78	11.2	37.2	Algarve	Borges *et al.* (2003)

Eutrigla gurnardus	0.0034	3.2600	240	16.5	40.5	North Sea, Kattegat and Skaggerak	DATRAS (2011)
Gadus morhua	0.0039	3.2434	10,199	4.5	123.5	North Sea, Kattegat and Skaggerak	DATRAS (2011)
Gaidropsarus	0.0072	2.8650	Average over North Sea species in *Gaidropsarus*				
Gaidropsarus argentatus	0.0072	2.8650	Average over North Sea species in *Gaidropsarus*				
Gaidropsarus macropthalmus	0.0063	2.9500	30	10.0	19.0	Cantábrico	Pereda and Villamor (1991)
Gaidropsarus mediterraneus	0.0034	3.0980	413	5.3	18.2	North Evvoikos Gulf and Trikeri Channel	Stergio and Politou (1995)
Gaidropsarus vulgaris	0.0120	2.5470	14	2.6	9.1	North Sea	Robinson *et al*. (2010)
Galeorhinus galeus	0.0098	3.0085	968	85.0	169.0	Uruguay waters	Portela *et al*. (2002)
Glyptocephalus cynoglossus	0.0013	3.4350	391	4.5	45.5	North Sea, Kattegat and Skaggerak	DATRAS (2011)
Gobiidae	0.0080	3.1614	Average over North Sea species in Gobiidae				
Gobius	0.0119	3.0495	Average over North Sea species in *Gobius*				
Gobius cobitis	0.0113	3.1280	526	2.2	8.3	Mar Menor lagoon	Verdiell-Cubedo *et al*. (2006)
Gobius niger	0.0124	2.9710	225	3.6	9.2	Mar Menor lagoon	Verdiell-Cubedo *et al*. (2006)
Helicolenus dactylopterus	0.1510	3.0456	6	15.0	38.5	North Sea	Coull *et al*. (1989)
Hippoglossoides platessoides	0.0070	2.9780	670	1.2	25.0	North Sea	Robinson *et al*. (2010)
Hippoglossus hippoglossus	0.2350	1.7970	8	12.0	23.9	North Sea	Robinson *et al*. (2010)
Lampetra fluviatilis	0.0011	3.1410	7	31.0	45.0	Estonian waters	Saat *et al*. (2003)
Lepidorhombus whiffiagonis	0.0134	2.7460	14	2.5	31.5	North Sea	Robinson *et al*. (2010)
Leptagonus decagonus	0.0091	2.9050	Average over North Sea species in Agonidae				
Leptoclinus maculatus	0.0244	2.0439	Average over North Sea species in Stichaeidae				
Lesueurigobius	0.0026	3.5150	Average over North Sea species in *Lesuerigobius*				
Lesueurigobius friesii	0.0026	3.5150	20	4.0	8.0	Cantábrico	Pereda and Villamor (1991)
Leucoraja circularis	0.0024	3.2330	Average over North Sea species in *Leucoraja*				

Leucoraja fullonica	0.0024	3.2330	Average over North Sea species in *Leucoraja*				
Leucoraja lentiginosa	0.0024	3.2330	Average over North Sea species in *Leucoraja*				
Leucoraja naevus	0.0024	3.2330	276	13.0	70.0	Celtic Sea	Dorel (1986)
Limanda limanda	0.0071	3.1190	1,174	0.9	26.5	North Sea	Robinson *et al*. (2010)
Liparis	0.0207	2.9691	Average over North Sea species in *Liparis*				
Liparis liparis	0.0122	2.9892	Average over 10 North Sea species with closest surveyed maximum *L*				
Liparis montagui	0.0292	2.9490	Average over 10 North Sea species with closest surveyed maximum *L*				
Lophius budegassa	0.0044	3.3450	34	13.6	32.9	Algarve	Borges *et al*. (2003)
Lophius piscatorius	0.0166	2.9776	24	17.5	75.5	North Sea, Kattegat and Skaggerak	DATRAS (2011)
Lumpenus lumpretaeformis	0.0244	2.0439	11	16.0	27.0	North Sea and West coast of Scotland	Coull *et al*. (1989)
Lycenchelys sarsii	0.0417	2.2532	Average over North Sea species in Zoarcidae				
Lycodes vahlii	0.0417	2.2532	Average over North Sea species in Zoarcidae				
Macrorhamphosus scolopax	0.0040	3.1500	34	6.3	14.4	Balearic Islands	Merella et al. (1997)
Melanogrammus aeglefinus	0.0052	3.1560	14,421	5.5	68.5	North Sea, Kattegat and Skaggerak	DATRAS (2011)
Merlangius merlangus	0.0042	3.1842	15,783	5.5	57.5	North Sea, Kattegat and Skaggerak	DATRAS (2011)
Merluccius merluccius	0.0036	3.1469	53	13.5	47.5	North Sea, Kattegat and Skaggerak	DATRAS (2011)
Microchirus	0.0080	3.1410	Average over North Sea species in *Microchirus*				
Microchirus variegatus	0.0080	3.1410	15	2.2	15.5	North Sea	Robinson *et al*. (2010)
Microstomus kitt	0.0042	3.2695	550	11.5	40.5	North Sea, Kattegat and Skaggerak	DATRAS (2011)
Molva dypterygia	0.0019	3.1490	280	69.0	142.0	Western Scotland	Dorel (1986)
Molva molva	0.0010	3.4362	19	20.0	60.0	North Sea	Coull *et al*. (1986)
Mugilidae	0.0107	3.0328	Average over North Sea species in Mugilidae				
Mullus barbatus	0.0139	2.9087	61	11.5	26.5	North Sea, Kattegat and Skaggerak	DATRAS (2011)

Mullus surmuletus	0.0101	3.0201	34	11.5	33.5	North Sea, Kattegat and Skaggerak	DATRAS (2011)
Mustelus	0.0041	2.9185		Average over North Sea species in *Mustelus*			
Mustelus asterias	0.0020	3.0790	67	19.1	117.3	Eastern Adriatic Sea	Pallaoro *et al.* (2005)
Mustelus mustelus	0.0062	2.7580	16	38.0	75.0	Eastern Adriatic Sea	Dulcic and Kraljevic (1996)
Myoxocephalus quadricornis	0.0229	2.9520	352	6.9	23.0	Onezhsky Bay, White Sea	Mukhomediyarov (1967)
Myoxocephalus scorpioides	0.0178	3.0378		Average over North Sea species in *Myoxocephalus*			
Myoxocephalus scorpius	0.0126	3.1235	311	12.0	35.0	North Sea	Coull *et al.* (1989)
Myxine glutinosa	0.0033	2.6990	162	9.2	42.0	North Sea	Robinson *et al.* (2010)
Nerophis ophidion	0.0004	3.0000		Average over North Sea species in *Nerophis*			
Pagellus erythrinus	0.0171	2.9060	103	20.8	40.5	Nazaré to St André	Mendes *et al.* (2004)
Pegusa lascaris	0.0070	3.1300	22	20.3	33.4	Póvoado Varzim to Figueira da Foz	Mendes *et al.* (2004)
Petromyzon marinus	0.0008	3.1956	25	31.5	93.0	North Sea, West coast of Scotland and Faroe Islands	Coull *et al.* (1989)
Pholis gunnellus	0.0043	3.0180	59	15.0	25.0	North Sea	Coull *et al.* (1989)
Phrynorhombus norvegicus	0.0078	3.1457	14	4.0	10.5	North Sea	Robinson *et al.* (2010)
Phycidae	0.0022	3.3892		Average over North Sea species in Phycidae			
Phycis blennoides	0.0022	3.3892	25	19.0	65.0	North Sea and West coast of Scotland	Coull *et al.* (1989)
Platichthys flesus	0.0087	3.0978	178	12.0	38.0	North Sea	Coull *et al.* (1989)
Pleuronectes platessa	0.0078	3.0541	11,551	4.5	56.5	North Sea, Kattegat and Skaggerak	DATRAS (2011)
Pollachius pollachius	0.0061	3.1150	3	40.0	49.5	North Sea, Kattegat and Skaggerak	DATRAS (2011)
Pollachius virens	0.0042	3.1753	2,598	10.5	111.5	North Sea, Kattegat and Skaggerak	DATRAS (2011)
Pomatoschistus	0.0068	3.0965		Average over North Sea species in *Pomatoschistus*			

Pomatoschistus lozanoi	0.0068	3.0965	Average over North Sea species in *Pomatoschistus*				
Pomatoschistus microps	0.0068	3.0965	Average over North Sea species in *Pomatoschistus*				
Pomatoschistus minutus	0.0062	3.1730	967	1.4	7.3	North Sea	Robinson *et al*. (2010)
Pomatoschistus pictus	0.0073	3.0200	34	2.6	5.8	North Sea	Robinson *et al*. (2010)
Raja	0.0035	3.1746	Average over North Sea species in *Raja*				
Raja brachyura	0.0028	3.2330	100	17.0	105.0	English Channel	Dorel (1986)
Raja clavata	0.0032	3.1940	960	10.0	101.0	English Channel	Dorel (1986)
Raja microocellata	0.0049	3.1170	97	15.0	87.0	English Channel	Dorel (1986)
Raja montagui	0.0023	3.2051	87	19.0	66.7	North Sea and North and West coast of Scotland	Coull *et al*. (1989)
Raja undulata	0.0042	3.1240	439	13.0	101.0	English Channel	Dorel (1986)
Rajidae	0.0036	3.1632	Average over North Sea species in Rajiidae				
Raniceps raninus	0.0062	3.2667	21	13.5	30.5	North Sea and West coast of Scotland	Coull *et al*. (1989)
Scophthalmus maximus	0.0046	3.3972	44	27.5	60.5	North Sea, Kattegat and Skaggerak	DATRAS (2011)
Scophthalmus rhombus	0.0055	3.3047	7	25.0	43.0	North Sea and West coast of Scotland	Coull *et al*. (1989)
Scorpaena scrofa	0.0121	3.1240	22	14.3	42.8	Nazaré to St André	Mendes *et al*. (2004)
Scyliorhinus canicula	0.0031	3.0290	376	37.0	103.0	English Channel	Dorel (1986)
Scyliorhinus stellaris	0.0031	3.0290	Average over North Sea species in *Scyliorhinus*				
Sebastes	0.0093	3.1585	Average over North Sea species in *Sebastes*				
Sebastes marinus	0.0071	3.1800	11	10.2	50.0	U	Pauly, Froese and Albert (1998)
Sebastes viviparus	0.0115	3.1369	358	9.0	31.0	North Sea and West coast of Scotland	Coull *et al*. (1989)
Solea impar	0.0834	2.7500	12	25.1	30.3	Northern Adriatic Sea	Dulcic and Glamuzina (2006)
Solea solea	0.0038	3.2751	30	10.5	42.5	North Sea, Kattegat and Skaggerak	DATRAS (2011)

Soleidae	0.0220	3.0848	Average over North Sea species in *Soleidae*				
Somniosus microcephalus	0.0161	2.9300	Average over species in *Somniosus*				
Sparidae	0.1295	2.8380	Average over North Sea species in Sparidae				
Spondyliosoma cantharus	0.0151	3.0233	43	18.5	41.5	North Sea and West coast of Scotland	Coull *et al*. (1989)
Squalidae	0.0034	3.0955	Average over North Sea species in Squalidae				
Squalus acanthias	0.0034	3.0955	U	U	U	Northeast Atlantic	Coull *et al*. (1989)
Stichaeidae	0.0244	2.0439	Average over North Sea species in Stichaeidae				
Syngnathidae	0.0002	3.2326	Average over North Sea species in Syngnathidae				
Syngnathus	0.0001	3.3877	Average over North Sea species in *Syngnathus*				
Syngnathus acus	0.0001	3.5270	4	25.0	33.0	North Sea	Coull *et al*. (1989)
Syngnathus rostellatus	0.0001	3.4140	26	5.2	16.2	North Sea	Robinson *et al*. (2010)
Syngnathus typhle	0.0001	3.2220	31	8.2	12.7	Central Adriatic Sea	Dulcic and Glamuzina (2006)
Taurulus bubalis	0.0154	3.0000	U	U	U	U	Bauchot and Bauchot (1978)
Taurulus lilljeborgi	0.0154	3.0000	Average over North Sea species in *Taurulus*				
Trachinus draco	0.0018	3.4099	29	24.5	35.0	North Sea	Coull *et al*. (1989)
Triglidae	0.0052	3.1457	Average over North Sea species in Triglidae				
Trigloporus lastoviza	0.0049	3.0390	156	6.0	37.0	English Channel	Dorel (1986)
Triglops murrayi	0.0088	3.0000	3	13.5	17.2	U	Pauly, Froese and Albert (1998)
Triglops pingeli	0.0031	3.1810	213	10.0	20.0	Kamchatka coast	Tokranov (1995)
Trisopterus esmarkii	0.0046	3.1405	4,690	7.5	28.5	North Sea, Kattegat and Skaggerak	DATRAS (2011)
Trisopterus luscus	0.0038	3.3665	147	18.0	42.0	North Sea	Coull *et al*. (1989)
Trisopterus minutus	0.0092	3.0265	452	9.0	26.0	North Sea and West coast of Scotland	Coull *et al*. (1989)
Zeugopterus	0.0139	3.1457	Average over North Sea species in *Zeugopterus*				
Zeugopterus punctatus	0.0139	3.1457	28	11.5	23.5	North Sea and West	Coull *et al*. (1989)

						coast of Scotland	
Zeugopterus regius	0.0139	3.1457	Average over North Sea species in *Zeugopterus*				
Zoarces viviparus	0.0417	2.2532	4	19.0	26.0	North Sea	Coull *et al*. (1989)
Zoarcidae	0.0417	2.2532	Average over North Sea species in Zoarcidae				

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