

Changes in species diversity and size composition in the Firth of Clyde demersal fish community (1927–2009)

M. R. Heath* and D. C. Speirs

Marine Population Modelling Group, Department of Mathematics and Statistics, University of Strathclyde, Livingstone Tower, Glasgow G1 1XH, UK

Following the repeal in 1962 of a long-standing ban on trawling, yields of demersal fish from the Firth of Clyde, southwest Scotland, increased to a maximum in 1973 and then declined until the directed fishery effectively ceased in the early 2000s. Since then, the only landings of demersal fish from the Firth have been by-catch in the Norway lobster fishery. We analysed changes in biomass density, species diversity and length structure of the demersal fish community between 1927 and 2009 from scientific trawl surveys, and related these to the fishery harvesting rate. As yields collapsed, the community transformed from a state in which biomass was distributed across numerous species (high species evenness) and large maximum length taxa were common, to one in which 90 per cent of the biomass was vested in one species (whiting), and both large individuals and large maximum length species were rare. Species evenness recovered quickly once the directed fishery ceased, but 10 years later, the community was still deficient in large individuals. The changes partly reflected events at a larger regional scale but were more extreme. The lag in response with respect to fishing has implications for attempts at managing a restoration of the ecosystem.

Keywords: marine fisheries; demersal community; ecosystem state

1. INTRODUCTION

The Firth of Clyde on the southwest coast of Scotland is a large fjordic basin incorporating the estuary of the River Clyde, which has experienced a boom-bust cycle of demersal fisheries. Between 1889 and 1962, the entire Firth was closed to trawlers larger than 8 tonnes in order to protect herring fishing grounds and areas used by small inshore vessels [1]. In 1962, the closure was repealed for waters beyond 3 miles of the coast and, with the resumption of trawling, demersal fish landings increased to a peak in 1973 before starting to decline [2]. Then, in 1984, the waters within 3 miles were also opened to trawling in an attempt to maintain catch levels and exploit inshore Norway lobster (*Nephrops norvegicus*) stocks. However, fish landings continued to decline. In 2001 and each year thereafter, a seasonal prohibition on demersal fish trawling has been implemented in parts of the Clyde to protect spawning cod, but the targeted demersal fishery ceased in about 2005. By the late 2000s, the only demersal fish landed from the Clyde were by-catch from the trawl fishery for Norway lobster.

It has been asserted that the record of demersal fish landings demonstrates that the Clyde is an ‘ecosystem nearing the endpoint of overfishing, a time when no species remain that are capable of sustaining commercial catches’ [1, p. 1]. However, landings data alone are insufficient to diagnose exactly what has happened. The relationship between species landings and abundance in the sea is affected, a range of socio-economic factors in addition to management regulation of fishing effort and opportunities.

We set out to investigate the changes in demersal fish more thoroughly, and report here on a variety of diversity indicators based on survey data collected between the 1927 and 2009, and how these relate to the patterns of harvesting rate.

Abundance-based diversity indices such as species richness (number of taxa present) and evenness (distribution of abundance across taxa) are commonly used to measure biodiversity in both terrestrial and marine habitats [3]. Since the observed number of species typically increases with repeated samples [4], species richness and evenness can be misleading when sampling effort is not standardized. Other measures of diversity have been proposed to overcome such problems, for example, taxonomic diversity and distinctiveness [5], but the main alternatives for marine systems have been size-based measures [6].

Size-spectrum indicators [7,8] and related indices such as proportional stock density [9], mean length and mean maximum length [10] have been developed for marine communities. An operational example of proportional stock density is the large fish indicator (LFI) of the North Sea demersal fish community [11]. The LFI is defined as the ratio of biomass of demersal fish larger than a threshold length relative to the total demersal fish biomass. It combines the influence of large-growing species relative to small ones, and the extent to which large species achieve their maximum size. Both are strongly affected by fishing, which tends to selectively remove large species and individuals. In the North Sea, an LFI value of 0.3, with a 40 cm threshold length, has been set as a target for good status. North Sea trawl survey data show that the LFI declined from around 0.3 in 1980 to 0.1 in 2000, and has since started to increase as community averaged *per capita* fishing mortality rates have been reduced to less than 0.9 yr^{-1} [11].

* Author for correspondence (m.heath@strath.ac.uk).

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2011.1015> or via <http://rspb.royalsocietypublishing.org>.

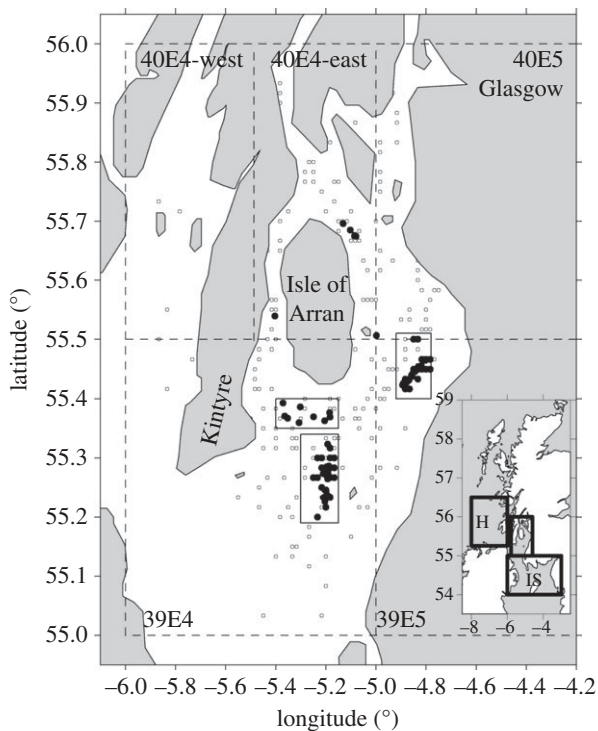


Figure 1. The Firth of Clyde, trawl sampling locations and ICES statistical rectangles used to summarize landings and discard data. Filled symbols indicate the locations of GOV trawl tows and the three rectangular cells show the sub-areas used to filter the remaining non-GOV data (open symbols) so as to correspond spatially with the GOV samples. The outlines of ICES statistical rectangles are shown by dashed lines. Inset shows the Clyde region in relation to the UK, and the domains of the Hebrides (H) and Irish Sea (IS) regions for which comparative data were extracted.

2. MATERIAL AND METHODS

(a) *Firth of Clyde trawl survey data*

Fishing trawl surveys of the west of Scotland shelf sea have been carried out annually during February or March since 1980 by the Scottish Government agency responsible for fish stock assessment, using methodology approved by the International Council for the Exploration of the Sea (ICES). This involves deploying a Grande Overture Verticale (GOV) trawl net at specified locations, and the use of standard procedures to document and analyse the catch [12]. Archived data from 1985 onwards are available at the ICES DATRAS database (<http://datras.ices.dk>). Two trawl locations are in the outer Firth of Clyde, and the post-1985 data comprise the most complete observations on fish abundance and diversity in the Firth. Trawl samples from 1927 to 2006 have also been collected using various gears and locations, and are fully documented at the Marine Scotland Science Laboratory in Aberdeen. The additional sampling since 1960 has been almost exclusively between November and March, but prior to 1960 was confined to the summer months. The standard catch analysis protocol for all surveys involves sorting by species, and measuring the body length of all individuals in the catch or in a random sub-sample (see the electronic supplementary material).

We confined our analysis to demersal fish, excluding invertebrates and pelagic fish, which are not well sampled by demersal trawls. We considered the post-1985 GOV trawl data to be the gold-standard dataset. In order to standardize the remaining data, we first identified three latitude \times longitude cells that enclosed all of the tow locations (figure 1). We

then selected only tows from within these cells that used nets of similar design to the GOV, rejecting data from, for example, prawn trawls or experimental gears. This procedure ensured that, for our main analysis, the fish community was sampled from similar habitats and with similar efficiency over the entire period from 1927 onwards. The rejected data included samples from two dedicated trawl surveys, in 1989 and 1990, of the entire Firth of Clyde. We therefore also conducted a separate analysis of these data which confirmed that the main dataset was representative of the Firth as a whole (see the electronic supplementary material).

To assess the extent to which changes in the Clyde demersal community were symptomatic of changes in neighbouring sea areas, we replicated the assembly and analysis of survey data for the southern part of the Hebrides shelf (8° W, $55^\circ 15' N$ – 6° W, $56^\circ 30' N$), and the northern Irish Sea (6° W, $54^\circ N$ – 3° W, $55^\circ N$; figure 1). All data analysis was performed using the R statistical software environment, v. 2.11.1 [13].

(b) *Abundance*

We sought to calculate the abundance of each taxon in the survey catches in terms of biomass in a given length interval, per unit of swept seabed area. There are three main components of such a calculation, starting with the number of individuals in 1 cm length class intervals from the trawl records. First is the area of seabed swept by the trawl. Second, the conversion of number-at-length to biomass-at-length, and finally accounting for the catchability-at-length of each taxon by the trawl (proportion of fish in the trawl path which are retained by the net).

Since the mid-1990s, underwater sensors have been used to measure the separation distance of the wings of the trawl net so that, given the distance towed, the swept area can be calculated directly [14]. For earlier records, we assumed that the area sweeping rate ($m^2 h^{-1}$) of the net was constant and equal to the mean over instrumented tows, and estimated swept area as the sweeping rate \times tow duration (see the electronic supplementary material). The catch numbers in length intervals were converted to catch weight by applying taxon-specific length–weight conversion functions ($W = aL^b$) with parameters (a , b) sourced from Coull [15] and Fishbase [16]. Where no taxon-specific parameters could be located, values were substituted from morphologically similar species. Catchability-at-length estimates were not available for the Clyde and values for the North Sea [14] were not transferable, since their derivation implicitly included the region-specific accessibility of fish to the survey, in addition to the performance of the gear on the ground. Hence, we assumed a uniform catchability of one recognizing that this resulted in a systematic, but unambiguous, underestimate of absolute abundance.

(c) *Species richness and evenness*

The presence of taxa in each tow was used to derive species richness (S), defined as the cumulative number of taxa found in a given number of tows. Species evenness was expressed by Pielou's index [17],

$$J = \frac{H}{\ln(S)},$$

where H is the Shannon diversity index [18,19],

$$H = -\sum_{i=1}^S p_i \ln(p_i)$$

and where

$$p_i = \frac{B_i}{\sum_{i=1}^S B_i}$$

is the relative biomass of each taxon i . The maximum value of H is $\ln(S)$ so \mathcal{J} has a maximum of 1 when all taxa are equally abundant, decreases towards 0 as the community becomes more concentrated into fewer taxa, and is undefined as the community collapses to a single taxon.

To standardize the sampling effort [20] and assess temporal changes in richness and evenness, we ordered the tows sequentially by date, and derived the richness and evenness in a sliding interval of 20 tows. The derived richness and evenness were then assigned to the median date of tows within the interval and joined by a local polynomial regression smoother (lowess) [21].

(d) Size distribution indicators

The all-time maximum recorded length (L_m) of each species i in the dataset, where m_i was the largest observed length class of species i , was used to derive an L_{\max} index, which expressed the average maximum attainable size of fish in the community,

$$L_{\max} = \sum_{i=1}^S p_i L_{m_i}$$

The L_{\max} index was calculated, as for species richness and evenness, in a sliding window of constant number of tows, and joined using a loess routine.

The mean length of fish in the community (L_{mean}) and LFI were derived from the annual survey abundance data. Mean length was estimated from the length distribution of biomass, rather than of individuals, for consistency with our other indicators and because the former has potentially more relevance in an ecosystem or food web context:

$$L_{\text{mean}} = \frac{\sum_{i=1}^S \sum_{j=1}^{m_i} L_j \cdot B_{ij}}{\left(\sum_{i=1}^S \sum_{j=1}^{m_i} B_{ij} \right)}$$

The LFI was calculated by summing the species length class abundances (t km^{-2}) over the greater than or equal to 40 cm length intervals and expressing as a ratio of total biomass. Additional sub-sets of the LFI were derived for the commercially important species cod, haddock, hake, plaice, saithe and whiting. In addition, for the commercial species, we estimated the proportion of biomass owing to fish larger than the minimum legal landing size (MLS) as defined by EU Council Regulation 850/98 Annex XII [22] (cod 35 cm, haddock 30 cm, hake 27 cm, plaice 30 cm, saithe 35 cm and whiting 27 cm).

(e) Fishery data

Annual landed weights (t yr^{-1}) for the six main commercial demersal taxa (cod, haddock, hake, plaice saithe and whiting) were digitized from compilations of official landings statistics [1]. Series were available for each species from 1960 to 2009 for an area referred to as the wider Clyde, defined by a set of four ICES 1° longitude \times 0.5° latitude statistical rectangles (denoted 39E4, 39E5, 40E4 and 40E5) which included parts of the North Channel and the Sound of Jura (figure 1). The sea surface area of these rectangles was estimated by geographic information system

(GIS) planimetry of coastline data, and the landed weights normalized to sea surface area ($\text{t km}^{-2}\text{yr}^{-1}$).

Assessing the weight and composition of fish that were caught but not landed was difficult since discards are not officially monitored. However, tabulated records of data collected by observers aboard Norway lobster trawlers in the Firth of Clyde between 1982 and 1998 provide information on annual discarded weights, and the mean species composition of discards [23]. We assumed that the proportion by weight of commercial species in discards was related to the proportion of $<$ MLS fish in the demersal community as a whole. By further assuming that total discards were proportional to Norway lobster landings [24], we obtained a crude estimate of annual aggregated discards of the commercial species from 1960 to 2009 (see the electronic supplementary material).

The ratio of annual fishery catch (W) to biomass (B) referred to as the harvest ratio (HR , yr^{-1}) represents a measure of the annual fishing mortality. Assuming that discarded fish of the commercial species were exclusively smaller than the respective MLS, which the available data indicate to be principally the case [23], we estimated the HRs

$$\text{HR}_x = \frac{(W_{\text{discard}} + W_{\text{landed}})}{B_x},$$

where $x \in \{\text{total}, <\text{MLS}, \geq\text{MLS}\}$ denotes whether the calculation is for all commercial species, or partial HRs for commercial species below or above the MLS.

3. RESULTS

(a) Taxonomic richness, evenness and maximum length

The filtered Clyde trawl survey dataset consisted of 19 868 taxon \times length class records from 138 tows conducted in 46 of the years in the period 1927–2009 (i.e. no data in 37 years, mainly pre-1960). The number of tows per year in the three latitude \times longitude cells varied between 2 and 14 (mean = 3, s.d. = 2.17), and the cumulative dataset contained records of the occurrence of 70 taxa, 59 of which were demersal fish (electronic supplementary material, table S2). Thirty-four (57%) of the total demersal fish taxa at the sampling sites were recorded as being present in the first 20 (14%) tows. Previously unrecorded taxa continued to be discovered up to 2009 (figure 2). More data were available from the Hebrides shelf and northern Irish Sea regions (Hebrides: 52 514 taxon \times length class records from 392 tows in 56 years; northern Irish Sea: 26 863 taxon \times length class records from 220 tows but in only 18 years). The cumulative numbers of taxa discovered were also higher in these regions (Hebrides: 115 taxa, 93 demersal; northern Irish Sea: 94 taxa, 79 demersal).

The standardized species richness of the Clyde demersal fish community (figure 2) showed fluctuations with time but no long-term linear trend ($p > 0.05$). Mean richness over 20 tows, averaged over the period 1927–2009, was 35 taxa (s.d. 2.4), compared the cumulative known taxa in the dataset of 59. Richness was slightly higher and increasing ($p < 0.001$) in the Hebrides shelf region, and similar in the Irish Sea where the data were too sparse to diagnose a trend.

Species evenness in the Clyde was between 0.5 and 0.6 throughout the period from 1927 to around 1980. Between 1980 and 2000, evenness declined to a minimum of less than 0.2, and then increased towards 0.4 by 2009

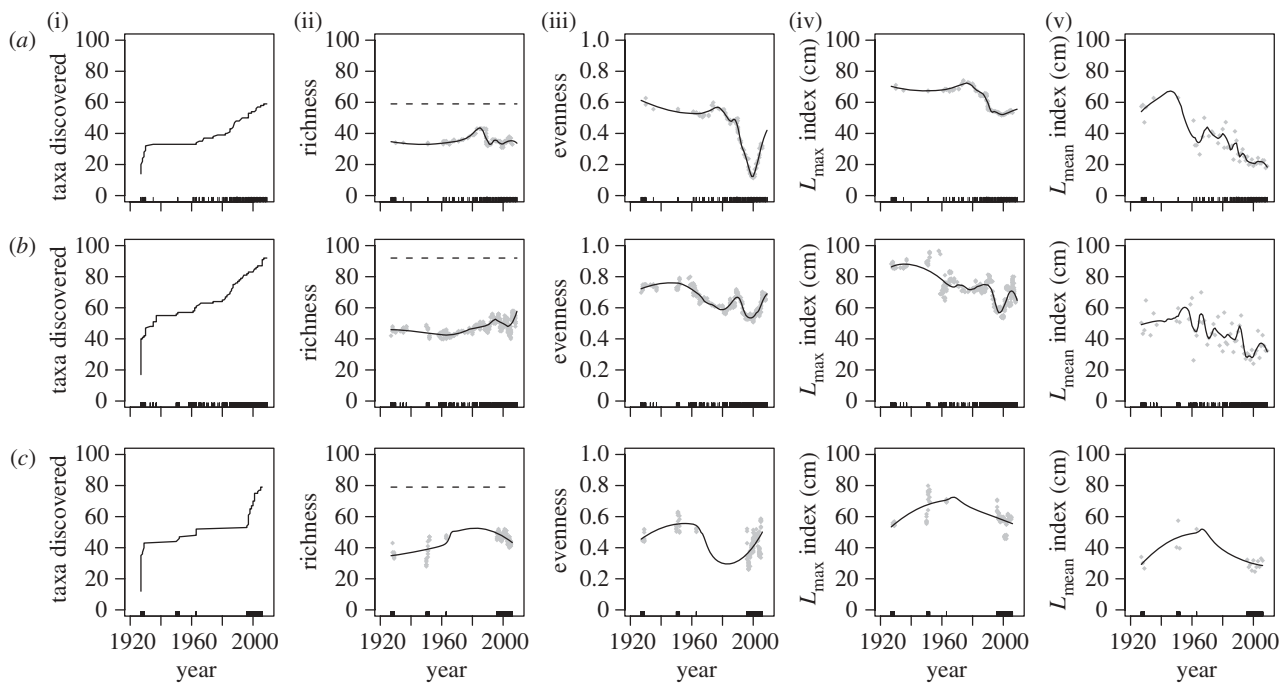


Figure 2. (a) Time series of demersal fish community metrics for the Clyde, (b) Hebrides and (c) northern Irish Sea regions. (i) cumulative number of demersal fish species identified in trawl samples; (ii) species richness per 20 tows; (iii) species evenness per 20 tows; (iv) annual L_{\max} index and (v) annual mean length L_{mean} index. Symbols represent estimates for the mid-year of a 20-haul sliding window or for a given year, and the solid lines show the loess smoothers through the data. The dashed line in the richness panel shows the cumulative number of species identified in the surveys between 1927 and 2009. Tick-marks above the x-axes indicate sampling occasions.

(figure 2). Between 1927 and 1959, 13 taxa accounted for 95 per cent of the average biomass, with spurdog, hake and cod each accounting for greater than 10 per cent of biomass (table 1). By contrast, during 1995–2004, only four taxa accounted for 95 per cent of the biomass, and whiting alone accounted for greater than 80 per cent. By 2005–2009, the number of taxa accounting for 95 per cent of biomass had risen to 8, but whiting still accounted for greater than 70 per cent. By comparison, evenness remained greater than 0.5 throughout the surveyed period in the Hebrides shelf region, and greater than 0.3 in the Irish Sea.

The L_{\max} indicator in the Clyde showed a step-change between pre-1980 and post-1995 from approximately 70 cm to less than 55 cm. Prior to 1980, apart from the main commercial species, a variety of taxa with all-time maximum body lengths exceeding 70 cm formed a significant component of the community biomass (anglerfish, spurdog, lesser spotted dogfish, thornback ray and tope). After 1980, few of these taxa appeared in the subset forming 95 per cent of total biomass, and other non-commercial species with maximum lengths smaller than 30 cm assumed higher ranking in terms of biomass (Norway pout, long rough dab and poor cod). L_{\max} in the Hebrides shelf region was consistently higher than the Clyde and declined more steadily over the period. Data from the Irish Sea were too sparse to discern a temporal pattern, but were possibly similar to the Clyde.

The mean length of demersal fish biomass (L_{mean}) in the Clyde declined steeply from 60 cm in the 1920s to less than 20 cm in 2009. The indicator also decline in the Hebrides shelf region but less steeply, being greater than 30 cm in 2009. In the Irish Sea, L_{mean} was 20–40 cm in the 1920s and remained so in the 1990s.

(b) Changes in community abundance and the large fish indicator

There was no statistically significant linear trend ($p > 0.05$) in total biomass density of demersal fish in the Clyde over the 83-year period. However, a loess smoother fitted through the data indicated two main peaks in abundance, the first around 1960, and more recently around 2000 (figure 3). Similarly, the total biomass of the six main commercial species (cod, haddock, hake, plaice, saithe and whiting) showed no significant linear trend, and peaks in abundance around 1960 and 2000 (figure 3). However, the remaining species, which we refer to as the non-commercial species, showed a strongly declining trend ($p < 0.001$), and the proportion of total biomass accounted for by the six commercial species increased from approximately 0.5 prior to 1960, to consistently greater than 90 per cent after 1993. This pattern was largely owing to the biomass dominance of whiting from 1995 onwards (table 1).

The LFI for the whole demersal community in the Clyde was highly correlated with L_{mean} (r^2 0.93, $n = 46$) and declined from greater than 0.6 pre-1960 to less than 0.02 in 2000, with evidence of a slight recovery thereafter. The changes in the LFI were mainly driven by a significantly decreasing trend ($p < 0.001$) in the biomass of fish greater than or equal to 40 cm. Prior to 1980, a variety of commercial and non-commercial species made up 95 per cent of the biomass of greater than or equal to 40 cm individuals, in particular cod, spurdog and saithe (table 2). During 1980–1995, cod dominated the greater than or equal to 40 cm biomass (greater than 80%), but after 2004, spurdog and other non-commercial taxa re-appeared among the subset of taxa making up the majority of the greater than or equal to 40 cm biomass. As a consequence, by 2005, the LFI for the non-commercial

Table 1. Species cumulatively accounting for 95% of total demersal biomass averaged over periods of years (Dab = Lough Rough Dab, Pout = Norway Pout, Gurnard = Grey Gurnard, Thornback = Thornback Ray).

1920–1959		1960–1979		1980–1994		1995–2004		2005–2009	
common name	% biomass	common name	% biomass	common name	% biomass	common name	% biomass	common name	% biomass
spurdog	22.71	whiting	42.61	whiting	43.86	whiting	87.27	whiting	71.90
hake	14.02	saithe	18.43	cod	23.68	haddock	4.14	haddock	12.23
cod	13.47	haddock	9.54	pout	9.02	cod	2.92	pout	4.05
gurnard	7.91	cod	8.55	haddock	7.22	hake	1.48	cod	2.08
whiting	7.32	hake	7.17	saithe	5.38			hake	1.62
saithe	6.00	spurdog	4.04	hake	3.55			poor cod	1.54
thornback	5.91	poor cod	1.46	dab	2.26			plaice	1.52
haddock	5.16	pout	1.25	poor cod	1.88			dab	1.02
dab	3.76	dab	1.15						
witch	2.76	dogfish	0.99						
tope	2.75								
plaice	2.54								
anglerfish	1.85								

species had risen to approximately 0.2, compared with the LFI for the commercial subset of species of which remained at approximately 0.02 (figure 3).

The total and commercial species biomass in the Hebrides region followed a similar pattern to that in the Clyde; less than 40 cm biomass increased post-1960 while greater than or equal to 40 cm biomass decreased (see electronic supplementary material, figure S7). However, non-commercial biomass comprised a higher proportion of the total than in the Clyde (greater than 50% as opposed to less than 30%). Hebrides non-commercial species biomass did not decline to the very low values observed in the Clyde during the 2000s and the non-commercial LFI remained greater than 0.3 through the study period. Data for the Irish Sea (see electronic supplementary material, figure S8) were too sparse to reach firm conclusions, but possibly indicated that the changes in LFI and distributions of biomass were similar to the Hebrides region and did not show the steep decline in non-commercial species seen in the Clyde.

(c) Changes in the fishery extraction rate of commercial species

The combined biomass density of >MLS individuals of the six main commercial species in the Clyde declined from a peak loess smooth value of 2.59 t km⁻² in 1962 to less than 0.15 t km⁻² in 2009. However, commercial fish smaller than their respective MLS increased in abundance (figure 4). After 1960, landings peaked at 1.82 t km⁻²yr⁻¹ in 1973 and then declined to less than 0.01 t km⁻²yr⁻¹ by 2009 (figure 4). Our estimates of discarded weights were reliable for the period 1982–1998, but only crudely estimated for earlier and later years. In addition, we were only able to estimate discards from the Norway lobster trawl fishery, and not from the demersal fisheries that were prevalent prior to the late 1980s. However, we estimated that discards rose from approximately 0.05 t km⁻²yr⁻¹ prior to 1965 to greater than 0.45 t km⁻²yr⁻¹ by 2009. For the >MLS component of the community, the loess smoothed HR showed a peak of 1.23 yr⁻¹ in 1985, with low values (approx. 0.2 yr⁻¹) during the early 1960s and declining to less than 0.1 yr⁻¹ by 2009 (figure 4). The HR for <MLS fish also increased from 1960 to a peak of 0.27 in 1986, then declined to a minimum of 0.08 in 1999, followed by an increase through the 2000s to a maximum of 0.3 in 2008. The total HR for the whole commercial community peaked in 1979 (0.84 yr⁻¹), declined to a minimum of 0.13 yr⁻¹ in 1998, and then rose to approximately 0.25 by 2008.

4. DISCUSSION

(a) Do the changes in the Clyde simply reflect those over the wider region?

Declines in the LFI and changes in other community indicators of demersal fish are well documented at the regional scale for waters all around the UK [25], and we would expect to see these reflected in the Clyde. The issue here is whether the changes in the Clyde are more extreme than in neighbouring areas. Our analyses indicate this to be the case. Changes in species evenness, mean length L_{mean} and the proportion of non-commercial species were all more extreme in the Clyde than in the neighbouring areas. The implication is that the Clyde

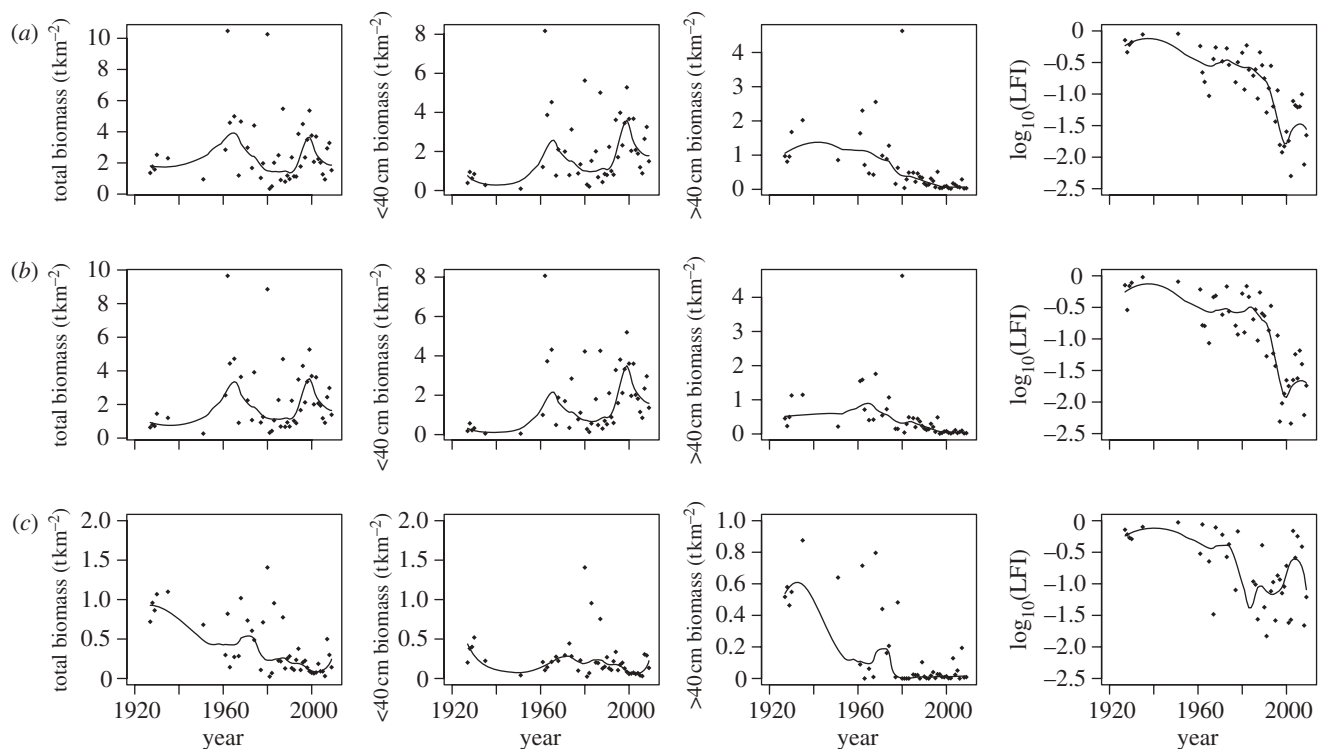


Figure 3. (a) Whole demersal community biomass density, biomass of fish smaller than 40 cm, biomass of fish larger than 40 cm and the LFI (log scale). (b) Same for the six main commercial species (cod, hake, haddock, plaice, saithe and whiting). (c) Same for the non-commercial species. Symbols represent data points for individual years, lines represent loess smoothers through the data.

community is sufficiently isolated from the neighbouring shelf regions to display a distinct local response to harvesting, and potentially also to environmental conditions.

For some species, such as dogfish, tagging data suggest that migratory exchange between the Clyde and neighbouring areas probably occurs [26,27]. For others, there is clear evidence of restricted exchange. For example, out of 7049 cod tagged around Scotland between November 1960 and August 1984, 204 were subsequently recaptured in the Clyde [28] and of these almost all (197, 96.6%) had been tagged locally. Only 2.5 per cent of cod tagged in the Clyde (five out of 202 recovered fish) were recaptured elsewhere, from the Hebrides (1), Irish Sea (2) and North Sea (2). Similarly, there is a distinct component of herring which are local to the Clyde [29], though this species is pelagic and not included in the community analysis. Hence, there is good supporting evidence that the Clyde is capable of supporting local populations of fish species, and hence that the community is spatially distinct and susceptible to local impacts of fishing.

(b) *Development of the Firth of Clyde fishery and state of the demersal community*

There may be additional components of catch that we were not able to take into account in our analysis of harvesting rates in the Clyde, such as discards from the fisheries which targeted demersal fish, and recreational angling. In addition, our methodology for analysing the trawl survey data underestimated the biomass density, since we assumed 100 per cent catchability for all species and length classes. There is a further uncertainty in that the trawl surveys post-1960 were restricted to the winter months, while

those pre-1960 were confined to the summer, so none of the survey data really reflected annually averaged abundances of species. However, none of these factors should materially affect the post-1960 temporal patterns of HR over time or the community health indicators. As a result, we can now identify the main phases in the development of the fishery and the demersal fish community in the Firth of Clyde (table 3).

Prior to the opening of the Firth to trawling in 1962, the data are sparse, but all the sampling indicates a community in which the biomass was distributed across a range of taxa and which included a number of large L_{max} species such as tope and spurdog. After opening to trawling, the extraction rate escalated to a maximum in the mid-1980s followed by a rapid reorganization of the species complement to a state in which the majority of the biomass was invested in whiting and to a lesser extent haddock, instead of the previous mix of functionally different species. At this point, boats probably began to leave the fishery and the extraction rate declined to a minimum in 1999/2000. Concurrently, the biomass density of small demersal fish (less than 40 cm) increased to a maximum. We can speculate that this was due to the relaxation of predation pressure as the abundance of large fish in the community declined. By the late 2000s, the demersal fish extraction was low and almost entirely owing to by-catch in the Norway lobster trawl fishery.

Despite the large changes in the fishery since the 1920s, the survey data suggest little detectable impact on demersal fish species richness. However, this is not to say that there were no effects on individual species, with some species which were originally prevalent becoming rare or absent (e.g. spurdog and saithe), and vice-versa (e.g. snake

Table 2. Species cumulatively accounting for 95% of biomass of demersal fish > 40 cm averaged over periods of years. (dogfish, lesser spotted dogfish; thornback, thornback ray; cuckoo, cuckoo ray).

common name	1920–1959		1960–1979		1980–1994		1995–2004		2005–2009	
	common name	% biomass	common name	% biomass	common name	% biomass	common name	% biomass	common name	% biomass
spurdog		32.44	saithe	34.29	cod	86.04	cod	70.23	cod	41.36
cod		19.00	cod	27.22	saithe	8.17	cuckoo	6.01	nurse hound	19.58
hake		13.47	spurdog	13.69	haddock	1.06	haddock	5.41	dogfish	17.48
saithe		8.61	hake	9.45			dogfish	5.27	spotted ray	8.52
thornback		9.97	dogfish	3.30			spotted ray	4.65	spurdog	5.81
tope		3.94	tope	2.90			hake	3.47	haddock	3.15
anglerfish		2.55	whiting	2.56						
haddock		2.24	ray	2.39						

blenny). This result adds to those from a growing list of studies which have found demersal fish species richness to be temporally insensitive to exploitation despite clear trends in abundance and size composition [25,30,31]. Species continued to be discovered by the surveys in both the Clyde and neighbouring areas throughout the study period, and the cumulative number of species was approximately double the richness measured over 20 tows. From this, we suggest that the continuing discovery rate was primarily a function of rarefaction but we cannot rule out turn-over of the species complement.

In contrast to species richness, species evenness declined steeply as the extraction rate reached its peak in the mid-1980s, and also increased rapidly as the extraction rate declined to minimum values around 1999–2000. However, the species that reappeared among the subset comprising 95 per cent of the community biomass in the 2000s were not those which had been important prior to the 1960s. Rather than large-growing taxa, such as spurdog and rays, the re-emerging species were Norway pout, long rough dab and poor cod. These species had been present throughout but at lower ranking abundances. Different patterns in species richness and evenness have been well documented in the terrestrial plant literature (e.g. [32]). Evenness has been related to environmental stress [33,34] though generally in a spatial rather than temporal context. However, there is growing evidence that regeneration of ecosystem function following environmental or human impact requires restoration of species evenness, rather than just richness [35].

Although species evenness and the subset of species comprising 95 per cent of the biomass during 2005–2009 were very similar to those during 1980–1994, the recovering system was clearly deficient both in large fish (1980–1994 LFI = 0.20; 2005–2009 LFI = 0.03) and individuals of species capable of exceeding 40 cm at maximum length (post-1990 L_{\max} index < 60 cm). A large part of the reduction in LFI which began in the 1960s was due to the steeper decline in abundance of large hake and spurdog relative to small individuals. Cod, the other main large maximum length species, declined overall but large cod were still present at 30–50% of total cod biomass even during the 2000s. With the decline and near-cessation of demersal fish landings post-1995, the biomass of commercial species <MLS increased, further suppressing the LFI. The increasing abundance of <MLS commercial fish was almost entirely owing to whiting and haddock, and not apparent among the other commercial species. However, this escalating abundance of <MLS fish did not propagate through to increasing biomass of larger individuals despite the low fishing mortality rates.

(c) Lags in the response of demersal community metrics to harvesting

The LFI, L_{\max} index, evenness and abundance clearly showed a lagged response to harvesting rate since the changes that occurred following the cessation of directed fishing were not simply a reversal of those that occurred over the period of collapse. A 15-year lagged response of the LFI has also been suggested in the North Sea [11].

Multi-species food web models can exhibit discontinuous changes in abundance, hysteresis in community configuration during reversal of an external forcing pressure,

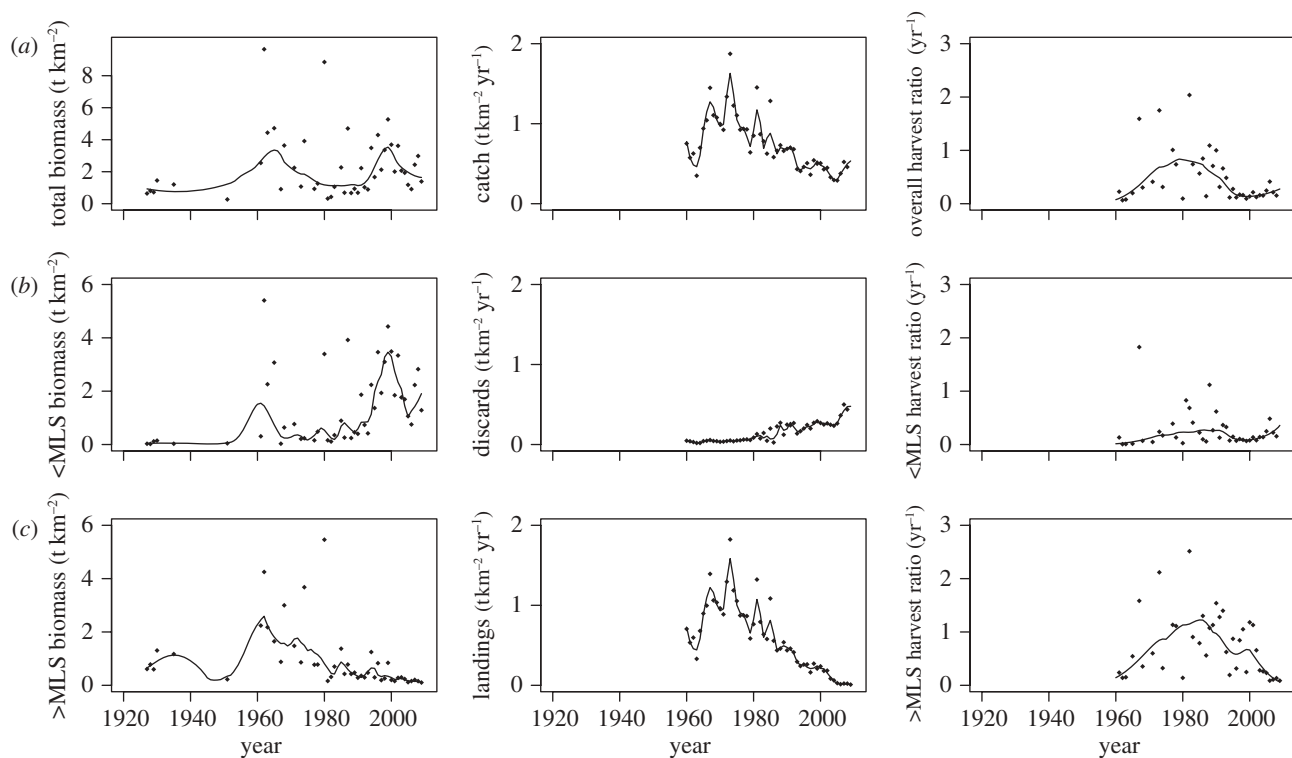


Figure 4. (a) Biomass density, removals and harvest ratio (HR) for all sizes of the six main commercial species (cod, hake, haddock, plaice, saithe and whiting). (b) Same for fish smaller than their respective MLS. (c) Same for fish larger than their respective MLS. Symbols represent data for individual years, lines represent loess smoothers through the data.

Table 3. Phases of development of the Firth of Clyde demersal fish community defined in terms of the geometric means of various measures derived from the data analysis. The row labelled $N_{95\%}$ indicates the number of species, from those with the highest biomass to the lowest, required to account for 95% of the biomass, while the corresponding numbers in parenthesis indicate the number of those species which have an $L_{\max} > 40$ cm. ?, no information.

fishery characteristics	pre-1960 Firth closed to large trawlers	1960–1979 waters beyond 3 miles opened to trawling in 1962	1980–1994 inshore waters open to trawling in 1984. Peak exploitation and collapse	1995–2004 vessels convert to Norway lobster fishing	2005–2009 remaining trawl fishery targeting only Norway lobster
landings ($\text{t km}^{-2} \text{ yr}^{-1}$)	?	0.932	0.601	0.191	0.019
discards ($\text{t km}^{-2} \text{ yr}^{-1}$)	?	0.044	0.159	0.247	0.391
harvest ratio (HR, yr^{-1})	?	0.473	0.623	0.155	0.229
biomass ≥ 40 cm (t km^{-2})	1.253	0.891	0.295	0.079	0.062
biomass < 40 cm (t km^{-2})	0.523	1.786	1.140	2.848	1.857
evenness (\mathcal{J})	0.553	0.538	0.457	0.193	0.322
L_{\max} index (Λ)	68.2	69.4	63.2	53	53.2
large fish indicator (LFI)	0.611	0.306	0.200	0.028	0.032
$N_{95\%}$ ($L_{\max} > 40$ cm)	13 (12)	10 (7)	8 (5)	4 (0)	8 (5)
whiting biomass (% of total)	7	43	44	87	72

and sometimes alternative equilibrium states under the same forcing conditions, depending on the initial conditions [36–38]. Nonlinearity in the predator–prey coupling between species is the main process that gives rise to such phenomena. The most notable predator species to have

suffered a large decline in prevalence regionally and in the Clyde following the exposure to trawling was spurdog [27]. The survey data and anecdotal fishery evidence [1] indicate that this small pelagic shark species were extremely abundant in the Clyde and neighbouring waters prior to the

1960s and were presumably a significant predator on <MLS demersal teleost fish.

Another mechanism that might explain why a community could exist in different configurations at the same extraction rate is a change in environmental conditions affecting the vital rates (growth and maturation). This is a plausible theory in this case since sea temperatures in the Firth have shown a strong warming trend since 1985 [39], and eutrophication impacts in the upper estuary owing to anthropogenic nutrients from the Glasgow conurbation have been significantly reduced [40]. Together, these might be expected to result in changes in productivity of the Firth as a whole, but there is no evidence of changes in fish growth on a scale which would account for the observed shift in community structure.

(d) Conservation and management implications

Biodiversity, the status of commercially exploited species and food web integrity are three aspects of environmental quality, which requires national assessment and monitoring under the EU Marine Strategy Framework Directive. The types of measurements that might be appropriate, the geographical scale over which they should be collected, and the criteria for defining acceptable status are all subject to debate [41–44]. In anticipation of implementing the Directive, the UK has conducted an evaluation of a variety of biodiversity measures for assessing the regional status of demersal marine fish communities in UK waters [25]. Our study is an example of the type of further analysis that will be required to relate changes in community status to exploitation, as a prelude to delivering advice on restorative measures.

Our results show that management measures developed at the regional scale (e.g. the whole of the west of Scotland) are not guaranteed to protect locally distinct communities such as in the Clyde, and that additional local measures will be necessary. Based on landings data alone, it has been suggested that removal of the ban on trawling in inshore waters of the Clyde in 1984 was instrumental in the demise of the demersal fisheries, and hence that reimposition of such restrictions might be an effective restoration measure [1]. However, our analysis shows no dynamic features that might be associated with the removal of the inshore trawling ban. If anything, the removal of the restriction on inshore trawling coincided with the onset of decline in harvesting rates. The changes in demersal community properties had their origins much earlier in the 1960s when the Clyde as a whole was opened up to demersal trawling.

5. CONCLUSIONS

The statement referring to the Clyde, that ‘no species remain that are capable of sustaining commercial catches’ [1, p. 1], gives the impression that commercially important species are no longer present. On the contrary, our analysis shows that biomass of the six main commercial species in the late 2000s was approximately double that prior to the onset of trawling in the 1960s (figure 4). However, the size structures of these species were dramatically different, being markedly deficient in large commercially marketable individuals after the period of peak harvesting rates in the 1980s. The same was true of non-commercial species, and in addition, the incidence

of species with a maximum attainable length greater than 40 cm declined precipitously and did not recover during the period of low harvesting rates after the late 1990s. It is likely that this lag in demersal community state with respect to harvesting was at least partly owing to internal predator–prey dynamics. Diagnosing the exact species interaction which were responsible, the likely persistence of the state change, and delivering advice on how it might be reversed, would require analysis of fish diet compositions in conjunction with multi-species models to simulate the community responses to the observed patterns of fishing and environmental change (e.g. [45,46]).

Data not publicly available from the ICES DATRAS database were provided by the Marine Scotland Science (MSS) Marine Laboratory in Aberdeen under research project MF0762, as part of a Memorandum of Understanding between MSS and the University of Strathclyde. This work received funding from the MASTS pooling initiative (The Marine Alliance for Science and Technology for Scotland) and their support is gratefully acknowledged. MASTS is funded by the Scottish Funding Council (grant reference HR09011) and contributing institutions.

REFERENCES

- 1 Thurstan, R. H. & Roberts, C. M. 2010 Ecological meltdown in the firth of clyde, scotland: two centuries of change in a coastal marine ecosystem. *PLoS ONE* **5**, e11767. (doi:10.1371/journal.pone.0011767)
- 2 Hislop, J. R. G. 1986 The demersal fishery in the Clyde Sea Area. *Proc. R. Soc. Edinb. B* **90**, 423–437.
- 3 Gaston, K. L. 1996 Species richness: measure and measurement. In *Biodiversity. A biology of numbers and difference* (ed. K. J. Gaston) pp. 77–113. Oxford, UK: Blackwell Science.
- 4 Hortal, J., Borgesm, P. A. V. & Gaspar, C. 2006 Evaluating the performance of species richness estimators: sensitivity to sample grain size. *J. Anim. Ecol.* **75**, 274–287. (doi:10.1111/j.1365-2656.2006.01048.x)
- 5 Warwick, R. M. & Clarke, K. R. 1995 New biodiversity measures reveal a decrease in taxonomic distinctness with increasing stress. *Mar. Ecol. Prog. Ser.* **129**, 301–305. (doi:10.3354/meps129301)
- 6 Greenstreet, S. P. R. 2008 Biodiversity of North Sea fish: why do the politicians care but marine scientists appear oblivious to this issue? *ICES J. Mar. Sci.* **65**, 1515–1519. (doi:10.1093/icesjms/fsn102)
- 7 Shin, Y.-J., Rochet, M.-J., Jennings, S., Field, J. G. & Gislason, H. 2005 Using size-based indicators to evaluate the ecosystem effects of fishing. *ICES J. Mar. Sci.* **62**, 384–396. (doi:10.1016/j.icesjms.2005.01.004)
- 8 Petchey, O. L. & Belgrano, A. 2010 Body-size distributions and size-spectra: universal indicators of ecological status? *Biol. Lett.* **6**, 434–437. (doi:10.1098/rsbl.2010.0240)
- 9 Willis, D. W., Murphy, B. R. & Guy, C. S. 1993 Stock density indices: development, use, and limitations. *Rev. Fish. Sci.* **1**, 203–222. (doi:10.1080/10641269309388542)
- 10 Jennings, S., Greenstreet, S. P. R. & Reynolds, J. D. 1999 Structural change in an exploited fish community: a consequence of differential fishing effects on species with contrasting life histories. *J. Anim. Ecol.* **68**, 617–627. (doi:10.1046/j.1365-2656.1999.00312.x)
- 11 Greenstreet, S. P. R., Rogers, S. I., Rice, J. C., Piet, G. J., Guirey, E. J., Fraser, H. M. & Fryer, R. J. 2010 Development of the EcoQO for the North Sea fish community. *ICES J. Mar. Sci.* (doi:10.1093/icesjms/fsq156)
- 12 ICES. 2010 Manual for the International Bottom Trawl Surveys in the Western and Southern Areas Revision III. In *Int. Bottom Trawl Survey Working Group 22–26*

- March 2010, Lisbon 64 pp. Copenhagen: Denmark: International Council for the Exploration of the Sea. See <http://datras.ices.dk/Documents/Manuals/Manuals.aspx> (accessed 20 September 2010).
- 13 RDevelopment Core Team. 2008 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. (www.R-project.org).
 - 14 Fraser, H. M., Greenstreet, S. P. R. & Piet, G. J. 2008 Taking account of catchability in groundfish survey trawls: implications for estimating demersal fish biomass. *ICES J. Mar. Sci.* **64**, 1800–1819. (doi:10.1093/icesjms/fsm145)
 - 15 Coull, K. A., Jermyn, A. S., Newton, A. W., Henderson, G. I. & Hall, W. B. 1989 Length/weight relationships for 88 species of fish encountered in the North East Atlantic. *Scot. Fish. Res. Rep.* **43**, 80.
 - 16 Froese, R. & Pauly, D. (eds) 2010 *FishBase*. World Wide Web electronic publication. www.fishbase.org, version (07/2010).
 - 17 Pielou, E. C. 1966 The measurement of diversity in different types of biological collections. *J. Theor. Biol.* **13**, 131–134. (doi:10.1016/0022-5193(66)90013-0)
 - 18 Magurran, A. E. 1988 *Ecological diversity and its measurement*. Princeton, NJ: Princeton University Press.
 - 19 Sokal, R. R. & Rohlf, F. J. 1995 *Biometry* 3rd edn. New York, NY: W. H. Freeman and Company.
 - 20 Greenstreet, S. P. R. & Piet, G. J. 2008 Assessing the sampling effort required to estimate species diversity in the groundfish assemblages of the North Sea. *Mar. Ecol. Prog. Ser.* **364**, 181–197. (doi:10.3354/meps07499)
 - 21 Cleveland, W. S., Grosse, E. & Shyu, W. M. 1992 Local regression models. In *Statistical models* (eds J. M. Chambers & T. J. Hastie). Blemont, CA: S Wadsworth & Brooks/Cole.
 - 22 EC. 1998 Council Regulation (EC) No 850/98 of 30 March 1998 for the conservation of fishery resources through technical measures for the protection of juveniles of marine organisms, pp. 1–36. (OJEU L125, 27.4.1998).
 - 23 Stratoudakis, Y., Fryer, R. J., Cook, R. M., Pierce, G. J. & Coull, K. A. 2001 Fish bycatch and discarding in *Nephrops* trawlers in the Firth of Clyde (west of Scotland). *Aquat. Living Resour.* **14**, 283–291. (doi:10.1016/S0990-7440(01)01135-4)
 - 24 ICES. 2009 *Nephrops* in Division VIa. (ICES Advice 2009 Book 5, Section 5.4.33). Copenhagen: Denmark: International Council for the Exploration of the Sea. See <http://www.ices.dk/products/Adviceoverview>. (accessed 12 November 2010).
 - 25 Greenstreet, S. P. R., Fraser, H. M., Cotter, J. & Pinnegar, J. 2010 UK Biodiversity in Your Pocket 2010—Assessment of the State of the Demersal Fish Communities in UK waters. JNCC Technical annex. 34 pp. See http://www.jncc.gov.uk/docs/biyp2010_13TechBackground.doc. (accessed 20 September 2010).
 - 26 Gauld, J. A. 1982 The dogfish; an ocean rover. *Scot. Fish. Bull.* **47**, 13–16.
 - 27 Pawson, M. G., Ellis, J. R. & Dobby, H. 2011 The evolution and management of spiny dogfish (Spurdog) fisheries in the Northeast Atlantic. In *Biology and management of dogfish sharks* ch. 31, pp. 373–390. Bethesda, MD: American Fisheries Society.
 - 28 Wright, P. J., Galley, E., Gibb, I. M. & Neat, F. C. 2006 Fidelity of adult cod to spawning grounds in Scottish waters. *Fish. Res.* **77**, 148–158. (doi:10.1016/j.fishres.2005.10.008)
 - 29 Bailey, R. S., Morrison, J. A. & Saville, A. 1982 The biological basis of the Clyde herring fishery. *Scot. Fish. Bull.* **47**, 16–22.
 - 30 Lorange, P. 1998 Structure du peuplement ichthyologique du talus continental à l'ouest des Iles Britanniques et impact de la pêche. *Cybium* **22**, 209–231.
 - 31 Campbell, N., Neat, F., Burns, F. & Kunzlik, P. 2010 Species richness, taxonomic diversity, and taxonomic distinctness of the deep-water demersal fish community on the Northeast Atlantic continental slope (ICES Subdivision VIa). *ICES J. Mar. Sci.* **68**, 365–376. (doi:10.1093/icesjms/fsq070)
 - 32 Cerabolini, B., Pierce, S., Luzzaro, A. & Ossola, A. 2010 Species evenness affects ecosystem processes in situ via diversity in the adaptive strategies of dominant species. *Plant Ecol.* **207**, 333–345. (doi:10.1007/s11258-009-9677-1)
 - 33 Crain, C. M. & Bertness, M. D. 2006 Ecosystem engineering across environmental gradients: implications for conservation and management. *Bioscience* **56**, 211–218. (doi:10.1641/0006-3568(2006)056[0211:EE AEGI]2.0.CO;2)
 - 34 Scrosati, R. & Heaven, C. 2007 Spatial trends in community richness, diversity, and evenness across rocky intertidal environmental stress gradients in eastern Canada. *Mar. Ecol. Prog. Ser.* **342**, 1–14. (doi:10.3354/meps342001)
 - 35 Crowder, D. W., Northfield, T. D., Strand, M. R. & Snyder, W. E. 2010 Organic agriculture promotes evenness and natural pest control. *Nature* **466**, 109–113. (doi:10.1038/nature09183)
 - 36 May, R. M. 1977 Thresholds and breakpoints in ecosystems with a multiplicity of stable states. *Nature* **269**, 471–477. (doi:10.1038/269471a0)
 - 37 Beisner, B. E., Haydon, D. T. & Cuddington, K. 2003 Alternative stable states in ecology. *Front. Ecol. Environ.* **1**, 376–382. (doi:10.1890/1540-9295(2003)001[0376: ASSIE]2.0.CO;2)
 - 38 Petraitis, P. S. & Dudgeon, S. R. 2004 Detection of alternative stable states in marine communities. *J. Exp. Mar. Biol. Ecol.* **300**, 343–371. (doi:10.1016/j.jembe.2003.12.026)
 - 39 Hughes, S. L. (ed.) 2007 Scottish ocean climate status report 2004 and 2005. Aberdeen, fisheries research services, 40pp. See <http://www.scotland.gov.uk/Uploads/Documents/Ocean%2004-05v1.pdf>. (accessed 12 November 2010).
 - 40 Ross, D., Thompson, K. R. & Donnelly, J. E. 2009 The state of the Clyde: environment baseline report. SSMEI Clyde Pilot Project, Scottish Sustainable Marine Environment Initiative, 96 pp. See <http://clydeforum.com/ssmei>. (accessed 15 November 2010).
 - 41 Rochet, M.-J. & Trenkel, V. M. 2003 Which community indicators can measure the impact of fishing? A review and proposals. *Can. J. Fish. Aquat. Sci.* **60**, 86–99. (doi:10.1139/f02-164)
 - 42 Jennings, S. & Dulvy, N. K. 2005 Reference points and reference directions for size-based indicators of community structure. *ICES J. Mar. Sci.* **62**, 397–404. (doi:10.1016/j.icesjms.2004.07.030)
 - 43 Greenstreet, S. P. R. & Rogers, S. I. 2006 Indicators of the health of the North Sea fish community: identifying reference levels for an ecosystem approach to management. *ICES J. Mar. Sci.* **63**, 573–593. (doi:10.1016/j.icesjms.2005.12.009)
 - 44 Rogers, S. *et al.* 2010 Marine Strategy Framework Directive Task Group 4 Report. Food webs. EUR Scientific and Technical Research series, EUR 24343 EN, 55 pp. Luxemburg, Germany: Office for Official Publications of the European Communities. (doi:10.2788/87659)
 - 45 Andersen, K. H. & Pedersen, M. 2010 Damped trophic cascades driven by fishing in model marine ecosystems. *Proc. R. Soc. B* **277**, 795–802. (doi:10.1098/rspb.2009.1512)
 - 46 Speirs, D. C., Guirey, E. J., Gurney, W. S. C. & Heath, M. R. 2010 A length structured partial ecosystem model for cod in the North Sea. *Fish. Res.* **106**, 474–494. (doi:10.1016/j.fishres.2010.09.023)