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Long-term changes in deep-water fish populations in the northeast Atlantic: a deeper reaching effect of fisheries?

D. M. Bailey[1,*], M. A. Collins[2], J. D. M. Gordon[3], A. F. Zuur[4] and I. G. Priede[5]

[1]*Faculty of Biomedical and Life Sciences, University of Glasgow, Graham Kerr Building, Glasgow G12 8AA, UK*
[2]*British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, UK*
[3]*Dunstaffnage Marine Laboratory, Scottish Association for Marine Science, Oban PA37 1QA, UK*
[4]*Highland Statistics Ltd, 6 Laverock Road, Newburgh, Aberdeenshire AB41 6FN, UK*
[5]*Oceanlab, University of Aberdeen, Newburgh, Aberdeenshire AB41 6AA, UK*

A severe scarcity of life history and population data for deep-water fishes is a major impediment to successful fisheries management. Long-term data for non-target species and those living deeper than the fishing grounds are particularly rare. We analysed a unique dataset of scientific trawls made from 1977 to 1989 and from 1997 to 2002, at depths from 800 to 4800 m. Over this time, overall fish abundance fell significantly at all depths from 800 to 2500 m, considerably deeper than the maximum depth of commercial fishing (approx. 1600 m). Changes in abundance were significantly larger in species whose ranges fell at least partly within fished depths and did not appear to be consistent with any natural factors such as changes in fluxes from the surface or the abundance of potential prey. If the observed decreases in abundance are due to fishing, then its effects now extend into the lower bathyal zone, resulting in declines in areas that have been previously thought to be unaffected. A possible mechanism is impacts on the shallow parts of the ranges of fish species, resulting in declines in abundance in the lower parts of their ranges. This unexpected phenomenon has important consequences for fisheries and marine reserve management, as this would indicate that the impacts of fisheries can be transmitted into deep offshore areas that are neither routinely monitored nor considered as part of the managed fishery areas.

Keywords: marine fishes; deep water; Atlantic Ocean; fisheries

1. INTRODUCTION

A diverse fish assemblage exists in the depths between the continental shelf edge (200 m) and the abyssal plains (depths of more than 3000 m; Haedrich & Merrett 1988). Each species is found in a discrete depth band, thus forming an overlapping sequence of different species across the continental margins. Spatial patterns in fish species presence and abundance have been widely studied (Haedrich & Merrett 1988), but temporal patterns are not at all clear.

What long-term data exist are predominantly provided by deep-water fishery landings (Morato *et al.* 2006). While useful, such data tell us little about the normal functioning of deep-water communities, provide no information on non-target species and cover only the depths that are commercially fished. When Bailey *et al.* (2006) examined long-term trends in Pacific fishes living in areas deeper than commercial fishing, they discovered that populations varied greatly from year to year. The changes in prey availability, which apparently drove the changes in fish abundance, were probably a result of natural changes in oceanic regime (Ruhl & Smith 2004). The magnitude of the changes observed and the apparent 'bottom-up' control underlying them were quite unexpected, and contrasted with the findings of studies based on the fisheries data (Worm & Myers 2003).

Many deep-water fish species are the targets of fisheries, but a shortage of ecological and life-history information makes deep-water fisheries notoriously difficult to manage, and as a result major declines in stock size have occurred (Roberts 2002). What data exist generally show that deep-water fishes are longer lived and mature later than most commercial species (Morato *et al.* 2006), compounding an already difficult problem.

Technology and economics restrict most commercial fishing in water less than approximately 1600 m (Basson *et al.* 2002). The majority of the seafloor (with an average ocean depth of 3790 m) therefore remains untouched, suggesting that those species with all or part of their range extending deeper than 1600 m would be, to a variable degree, protected from the effects of fishing. In our study area to the west of Ireland, the deep-water fishery targets roundnose grenadier (*Coryphaenoides rupestris*), black scabbardfish (*Aphanopus carbo*), orange roughy (*Hoplostethus atlanticus*) and some deep-water sharks. The commercial catch per unit of effort for ICES subarea VII (which includes the study area) showed a decline for several target species from the start of the fishery in *ca* 1989 (Lorance & Dupouy 2001).

Apart from vent and seep systems, deep-water habitats have no primary productivity, and most fish species are predators and/or scavengers. Marine predator removal

* Author for correspondence (d.bailey@bio.gla.ac.uk).

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can have powerful effects that cascade down the trophic levels (Heithaus *et al.* 2008). Although we know that both oceanographic changes and fishing have the potential to change deep-water fish populations (Koslow *et al.* 2000; Roberts 2002; Ruhl & Smith 2004; Bailey *et al.* 2006), the role of deep-water fishes in structuring communities is almost completely unknown at this point (Bailey *et al.* 2006). At present, we know very little about how most deep-water fish communities vary naturally, or in response to anthropogenic disturbance, and this is a major problem for our understanding of deep-water systems. The present study is the first to investigate long-term changes in the majority of the fish communities from the upper slope to the abyssal plain.

2. MATERIAL AND METHODS

Since 1977, we have surveyed the Porcupine Seabight and Abyssal Plain area of the northeast Atlantic Ocean (approx. 50° N, 13° W), at depths of 800–4865 m. The 'early' period (1977–1989; 97 trawls) is before and during the development of the commercial fishery, while the 'late' period (1997–2002; 64 trawls) is considered post-commercial fishing.

(a) *Trawling*

Sampling was undertaken using semi-balloon otter trawls (OTSB 14; Marinovich Trawl Co. Biloxi, MS, USA), fished on a single warp. This small trawl had an estimated wing-end spread of 8.6 m (11.4 m headline length) and caught a wide range of species, but because of its limited herding action, large and highly mobile species such as sharks and black scabbardfish were poorly represented in the catch (Merrett *et al.* 1991; Gordon *et al.* 1996). Bottom times (and thus swept areas) are estimates based on tilt switches in the trawl doors and the warp tension data used to indicate that the net was in contact with the seafloor.

Substantial overlaps in the personnel present on the trawl cruises ensured consistent trawl technique and fish identification. Voucher specimens of fishes whose identification was uncertain were retained and verified with reference to museum collections. Trawl locations are provided in figure 1. Full trawl metadata (locations, dates, depths, etc.) have been lodged with the Pangaea database (www.pangaea.de) and are available as the electronic supplementary material. All fishes were retained, capturing 32 954 individuals, out of which 32 892 were identified to species (110 species).

(b) *Data analysis*

Trawls shallower than 800 m were not used in the analyses as no trawls at those depths had been used in the late period. Abundances were calculated from the trawl swept area (calculated from time on bottom, vessel speed and door spread), and pelagic and mesopelagic fishes were excluded. A subset of eight trawls from the late period lacked 'time on bottom' data and were thus not available for analyses where abundance km^{-2} were calculated. No robust catchability data are available for these species and gears so these estimates are approximate, but any errors are consistent across the survey.

Q4 Additive mixed models (GAMMs; Wood 2006; Zuur *et al.* 2007) were used to describe the abundance of fishes and species richness with respect to 'depth' (mean water depth of the trawl while it was on the seabed) and to compare between the two time 'periods'. Initial data exploration using Cleveland dot- and boxplots revealed outliers in most abundance datasets (total abundance and individual species abundances per trawl). This required square-root transformation prior to analysis. Species richness data did not require further transformation. Examination of multi-panel scatterplots indicated likely interactions between period and depth in some datasets, so interactions were included within the models.

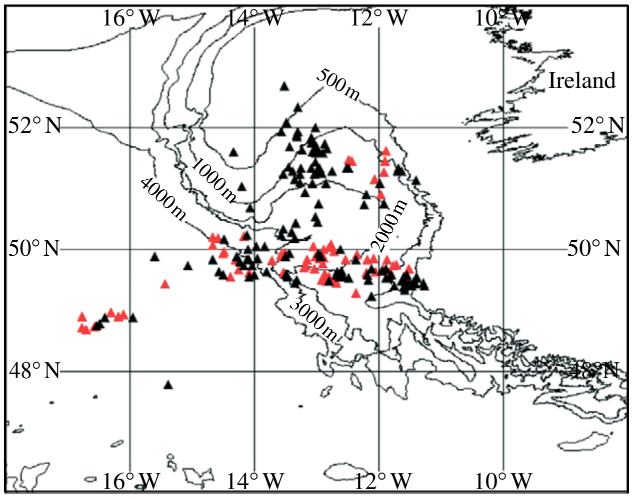

Figure 1. Trawl locations in the Porcupine Seabight and Porcupine Abyssal Plain area southwest of Ireland. Black triangles are the 'early' period and red triangles are the 'late' period. Contours are labelled at 500, 1000, 2000, 3000 and 4000 m depths below sea level.

The models were fitted using the mgcv (Wood 2006) and nlme (Pinheiro *et al.* 2007) packages in R software (R Development Core Team 2007; mgcv's full title is 'GAMs with GCV smoothness estimation and GAMMs by REML/PQL', nlme is 'linear and nonlinear mixed effects models').

The explanatory variables considered in the analysis were trawl 'period' (early or late), depth and interactions between period (nominal) and depth (fitted as a smoother)

$$\sqrt{\text{abundance}_{ij}} = \alpha + f(\text{depth}_i) : \text{factor}(\text{period}_{ij}) + \varepsilon_{ij},$$

where α is an intercept; f is the smoothing function; and ε is independently, normally distributed noise with expectation 0 and variance σ^2. Variance was allowed to vary with both depth and period (see below). The interaction between depth (smoother) and period (categorical variable) was fitted using the 'by' command in the mgcv package. It applies a depth smoother on the data for each period. Where this interaction was not significant the following model was fitted:

$$\sqrt{\text{abundance}_{ij}} = \alpha + f(\text{depth}_i) + \text{factor}(\text{period}_j) + \varepsilon_{ij}.$$

The effects of temporal autocorrelation were investigated using variograms with respect to 'day of series', the number of days since the first trawl (the autocorrelation function cannot be used because the data are irregularly spaced). The x–y coordinates (in km from the centre of study area) were used to assess the effects of spatial autocorrelation visually using bubble plots (Pebesma 2004). No spatial or temporal autocorrelation was detected. The appropriate degrees of freedom of the smoothers were selected automatically using cross validation (Wood 2006). Statements about changes in abundance are based on the significance of the main effect period, and not on the interaction between period and depth.

The model was optimized by first looking for the optimal random structure, and then for the optimal fixed structure (Zuur *et al.* 2007). The principal tool was comparison of

Table 1. GAMM summary results for the 15 most abundant species (95% of all individuals). (Significance, $p>0.01$, n.s., $*p<0.01$, $**p<0.001$, $***p<0.0001$. Depth ranges are based on observations in the present study. Records separated by more than 500 m from the rest of the species' distribution were not included in the analysis. Species marked '+' did not show significant differences between periods when 'outside' trawls were not included (see §2).)

rank	species	depth range in analysis (m)	MDO (m)	maximum depth of occurrence (m)	depth (m)	period (early/late)	interaction depth by period
	all species pooled	800–5000	n.a.	n.a.	***	***	***
1	*Synaphobranchus kaupii*	800–2500	407	2500	***	***	n.s.
2	*Coryphaenoides guentheri*+	1100–3000	1200	2875	***	*	n.s.
3	*Lepidion eques*	800–1600	506	2420	***	n.s.	n.s.
4	*Nezumia aequalis*	800–1700	472	2058	***	**	**
5	*Coryphaenoides rupestris*+	800–2000	706	1932	***	**	n.s.
6	*Coryphaenoides armatus*	2000–5000	2016	4865	***	n.s.	*
7	*Antimora rostrata*+	800–3000	853	2970	***	*	***
8	*Polyacanthonotus rissoanus*	900–2600	740	2500	***	**	n.s.
9	*Halosauropsis macrochir*	1400–3500	1440	3500	***	***	n.s.
10	*Coryphaenoides mediterraneus*	1200–2700	743	2700	***	***	n.s.
11	*Caelorinchus labiatus*	800–2000	472	1900	***	**	n.s.
12	*Trachyrincus murrayi*	1200–1700	1205	1600	***	***	n.s.
13	*Bathypterois dubius*	1000–2000	1016	2434	***	n.s.	n.s.
14	*Hoplostethus atlanticus*	900–1700	960	1677	**	***	*
15	*Coryphaenoides leptolepis*	2500–5000	1993	4865	***	n.s.	**

Akaike information criteria for each model. Visual inspection of residual plots for the models indicated violation of homogeneity in most cases, requiring the use of particular variance structures (generalized least squares) that allow the residual spread to vary with respect to depth and/or period (Pinheiro *et al.* 2007; Zuur *et al.* 2007). Once the optimal model was found (in terms of the random structure), further selection was applied by rejecting any remaining non-significant explanatory variables.

Some of the hauls in the 800–2000 m range in the early period were obtained in an area to the northwest of the main survey area. When the abundances of fishes in 800–2000 m trawls obtained 'inside' the main survey area ($n=23$) and 'outside' it (to the north and west of 51° N, 13° W, $n=29$; see figure 1) were compared using the same GAMM procedure as above, there was no significant difference. Omitting the outside points from the analyses used to compare abundances between periods resulted in three weakly significant tests dropping below the $p<0.01$ significance threshold used in this paper, but the majority were unaffected (table 1). On the basis of this and previous studies showing little difference in the fish communities between the two sides of the Porcupine Seabight (Gordon *et al.* 1996), it was decided to use all the available trawls and thus maximize the power of the analyses.

3. RESULTS

(a) *All species pooled*

Fish abundances were the highest at depths of 1000–1800 m, reaching 20 000–30 000 fishes km^{-2}, declining to less than 1000 fishes km^{-2} on the abyssal plain (figure 2*a*) and fell significantly between periods (figure 2*b* and table 1). Comparisons of the smoothers (non-parametric curves) generated by the additive mixed modelling for the two time periods showed significant declines in abundances at all depths down to approximately 2500 m, but no significant difference deeper than this.

Species richness peaked at 23 species per trawl at 1500 m in both study periods, declining with increasing depth until at depths of more than 4500 m, and the maximum number of species caught was eight in both study periods (figure 2*c*). There was no significant difference in species richness between periods (figure 2*d*).

(b) *Individual species*

Strongly significant declines in abundance were observed in 9 out of the most common 15 species, with weakly significant reductions in a further two (table 1). Abundances of a main target species roundnose grenadier (*C. rupestris*) declined by 41 per cent. Declines were also observed in non-target species (e.g. *Polyacanthonotus rissoanus*, down by 77%). The deepest living fish to exhibit a significant change was *Halosauropsis macrochir*, which had a maximum depth of occurrence of 3500 m, with occasional individuals to 4226 m (table 1). Similarly, abundances of *Synaphobranchus kaupii*, *Antimora rostrata* and *Coryphaenoides mediterraneus* all declined significantly across their depth ranges (table 1). All species with statistically significant declines had minimum depths of occurrence (MDO) of less than 1500 m (MDO for each species was defined as the depth of the shallowest trawl to capture the species). Abundances of fishes recorded in trawls shallower than 1500 m declined by an average of 69.7 per cent, while deeper species (MDO of 1500–3000 m) declined by only 19.9 per cent. Interactions between depth and period were rarely seen in individual species abundances (table 1), but changes in the overall pattern of fish abundance with depth were seen when all species were pooled (table 1; figure 2*a*).

4. DISCUSSION

We considered two explanations for the differences between the early and late periods; changes in food availability and the effects of fishing on the upper slope. Studies of abyssal plain fish populations indicate that they can respond to changes in prey availability (Bailey *et al.* 2006), which can, in turn, be linked to oceanographically

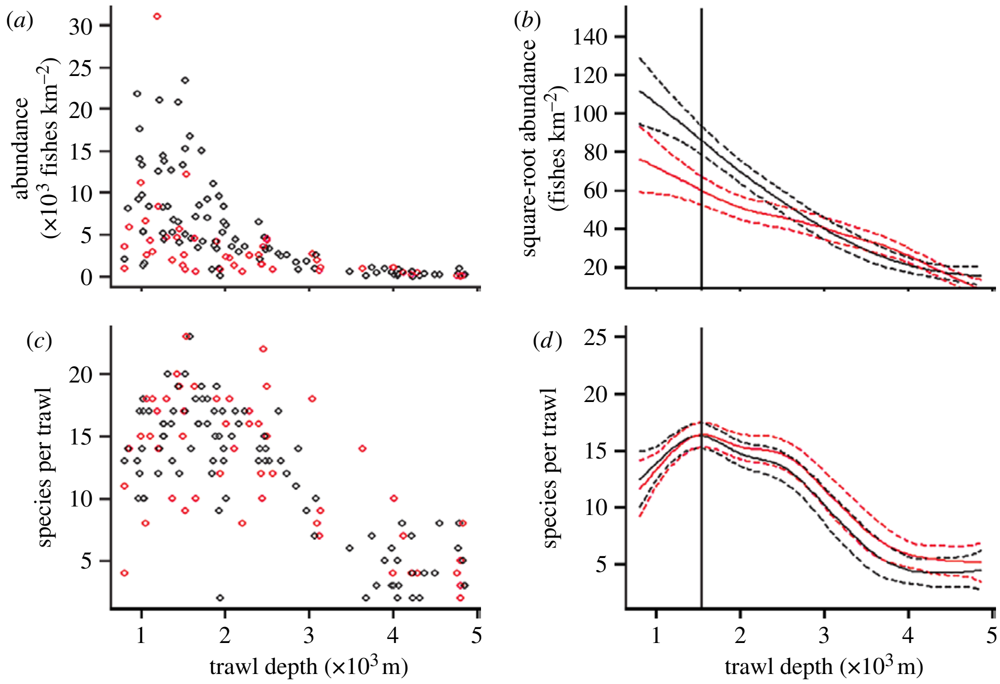

Figure 2. (*a–d*) Trends in fish community characteristics with depth. Black circles/lines: 'early' trawls; red circles/lines: 'late' trawls. (*a*) Abundance (all species pooled), (*b*) smoothers for abundance, (*c*) species per trawl and (*d*) smoothers for species per trawl. Dashed lines on smoother plots are 95% CIs. The vertical line in (*b*,*d*) indicates the approximate maximum depth of commercial fishing in this area.

driven changes in surface primary production (Ruhl & Smith 2004). Phytoplankton colour data (an indicator of phytoplankton biomass) collected for the surface waters overlying our study area show an increase in phytoplankton in the years between the study periods (Edwards *et al.* 2001). Sediment trap measurements at the deepest end of the survey area show no long-term changes in fluxes from the surface (Lampitt *et al.* 2001), but with a single year of very high particle flux in 2001 (Billett *et al.* 2009), while trawls show increases in benthic animal abundance in the years between the trawl periods (Billett *et al.* 2001), being the highest in 1997 and 2002 (Billett *et al.* 2009). These changes in abundance did not affect biomass, as they were characterized by changes in fauna from large to small species (especially *Amperima rosea*). It is possible that a change in prey species composition could affect fish populations, even without a decrease in total benthic invertebrate biomass, so it is not possible to rule out a role for oceanographic effects on the fish community.

However, in the only long-term study of abyssal fish abundance, Bailey *et al.* (2006) showed that it was total megafaunal invertebrate abundance that was correlated with fish abundance. Also, similar declines (table 1) are seen in fishes with widely different lifestyles (e.g. scavenging and non-scavenging fishes; Collins *et al.* 2005), making it seem less likely that a change in prey species composition could cause such a widespread effect. It is also unlikely that changing carrion availability has had a significant long-term effect.

The depth-related declines in abundance are, however, consistent with the effects of deep-water fishing. Significant changes in abundance were detected only in fishes whose depth ranges fell at least partly within the fishing grounds, in both target and non-target species. This pattern of widespread declines in abundance can be best explained by high rates of mortality among the fishes that escape through the net, as well as those that are brought to the surface and subsequently discarded (Basson *et al.* 2002). It is also possible that habitat modification by trawling has effects on a wide range of fish species by changing the availability of refugia and food (Collie *et al.* 1997). Species richness and its relationship with depth were not affected, probably because fishing mortality affects all species to a similar extent.

While commercial fishing occurred to a depth of 1500 m in this area, the majority of bottom trawls were shallower than 1000 m (Hopper 1995). It is possible that the effects of fishing are transmitted down the slope, resulting in significant changes in overall abundance to 2500 m. The affected species include those with maximum depths of occurrence of over 3000 m, making it possible for impacts in one part of their range to be manifested at greater depths. Some common species normally move down the slope as they age (Collins *et al.* 2005), providing one mechanism for the downslope transmission of fishery effects if removal of these fishes from the upper slope reduces the number of fishes that are available to move down to greater depths. As the effect is also observed in fishes that show little or no ontogenetic migration (e.g. *Nezumia aequalis*, *H. macrochir*, *C. rupestris*; Collins *et al.* 2005), it is possible that these other species move up and down the slope during normal activity, periodically bringing them within the reach of fishing. Depending on the steepness of the continental slope, fishing effects may extend a horizontal distance of more than 70 km beyond the limits of fishing.

5. CONCLUSIONS

If the above theory is correct, the effects of fisheries now reach the lower slope (approx. 2500 m), leaving only the abyssal and hadal zones unaffected. Although the magnitude of the change in abundance is relatively small compared with those described in other deep-water systems (Devine *et al.* 2006), it is important that the apparent impacts of fishing extend deeper than the reach of fishing gear. As the fishes whose abundances have declined include the apex predators in these habitats, ecosystem-level changes are possible, but the relative importance of predator pressure in structuring deep-water communities remains unclear (Bailey *et al.* 2006). The possible vulnerability of deep-water communities to impacts, which are occurring in shallower waters, implies that proposals for future deep-water marine protected areas are likely to be of limited effectiveness unless fleet fishing effort is controlled in the surrounding areas.

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