

Long-term changes in the benthos on a heavily fished ground off the NE coast of England

C. L. J. Frid*, R. A. Clark, J. A. Hall**

University of Newcastle upon Tyne, Dove Marine Laboratory, Cullercoats, North Shields NE30 4PZ, United Kingdom

ABSTRACT: Long-term monitoring of 2 benthic stations off the Northumberland coast, NE England, at 80 and 55 m depth, has been carried out since 1971. The 80 m station is located within a *Nephrops norvegicus* fishing ground, while the 55 m station is located outside of the main fished area. In this study we compare the fauna of the heavily fished site with that of the shallower site over a period during which fishing effort changed. Changes in macrofaunal abundance at the station outside the fishing ground reflected changes in organic input. This was also the case at the fished station except during the period of highest fishing activity when this relationship broke down. This suggests that the dynamics of the macrobenthos at this station were influenced by fishing activity. Individual taxa were categorised *a priori*, based on literature accounts of their response to fishing. At the site outside the fishing ground the proportion of individuals predicted *a priori* to increase and that predicted to decrease in response to the direct effects of fishing did not vary. At the heavily fished station the increase in fishing effort in the early 1980s did not alter the abundance of the taxa predicted to decline, but the abundance of individuals in taxonomic groups predicted to increase did change in the predicted direction. The differences in the dynamics of the 2 stations, which differed in their fishing intensity, provide some evidence for a role of direct effects of fishing in determining the abundance and composition of coastal macrofauna.

KEY WORDS: Benthos · Fishing impacts · Time series · Macrofauna · Species composition

INTRODUCTION

There is no doubt that, as a result of fishing activity, significant changes have taken place in the abundances and species composition of fish communities in the North Sea (e.g. Serchuk et al. 1996). However, there is less evidence that the activities of commercial fishing fleets have caused changes in other marine communities (Gislason 1994). Fishing using mobile gears results in direct and indirect impacts upon the benthos (Messieh 1991, Dayton et al. 1995). A decrease in benthic infaunal population densities occurs immediately after the passage of gears due to mortalities resulting from damage caused by the gear (Tuck et al. 1998). Individuals disturbed but not killed by the gears may be left at the surface, where they are prone to predation. Shortly after the disturbance has taken place, scavengers may move into the fished area (Kaiser & Spencer

1994, Ramsay et al. 1996). Fishing may also indirectly affect benthic communities by disturbing the sediment, causing reduction in habitat complexity (Auster et al. 1995), and by increasing suspended solids in the water column (Churchill 1989). These changes in the physical environment have the potential to affect the recolonisation of trawled areas (Gislason 1994).

Although the direct effects of fishing on the benthos are becoming known, the broader impacts of fishing activities which may cause profound changes, even at the ecosystem level, are less well understood. However, these more widespread, ecosystem level effects are difficult to study. Effects at this level may operate through the removal by the fishing nets of the larger individuals present in both fish and benthic communities. This has the effect of reducing the abundances of predatory fish species such as cod, haddock, plaice and sole in fish populations (Serchuk et al. 1996), as well as large predatory crustaceans, echinoderms and molluscs in benthic populations (Dayton et al. 1995). Fishing disturbance may also destroy meta-populations that act as sources of larvae, and thus affect benthic

*E-mail: c.l.j.frid@ncl.ac.uk

**Present address: Baroid Ltd, St. Magnus House, Guild Street, Aberdeen AB11 6NJ, United Kingdom

communities that are reliant on a supply of propagules from fished areas, even if they are not fished directly (Thrush et al. 1995). All of these changes in communities are expected to be reflected in knock-on effects within trophic cascades (Anonymous 1995).

Before-After Control-Impacted (BACI) type experimental programmes (Underwood 1991) or short-term manipulations of the benthos in experimental areas have been used to observe the direct impacts of fishing. Unfortunately, the results of such studies do not lend themselves to extrapolation to the much larger spatial and temporal scale of the fishing ground (Thrush et al. 1995). Additionally, the type of experimental approaches applied does not fully address the less readily recognisable indirect impacts of fishing. As ecological changes due to fishing impacts occur over large areas and time scales, they may only be detected by comparing long time series that have been collected in fished areas and unfished areas. This is particularly important as other natural factors may be changing over the time period observed. These could include changes in density dependence, climate, hydrography and other biotic factors (Buchanan & Moore 1986a, Buchanan et al. 1986). The problem is that few areas of the North Sea are unfished and undamaged by trawling

This paper compares time series data from 2 stations off the NE coast of England. One (Stn P) is located within a *Nephrops norvegicus* (Dublin Bay prawn) fishing ground (Fig. 1) and the other (Stn M1) outside of the main fished area. Previous analysis of the Stn M1 time series has related abundances of benthic individuals to changes in phytoplankton abundance ($r^2 = 0.55$), suggesting that the dynamics of the community were largely controlled by changes in the food supply

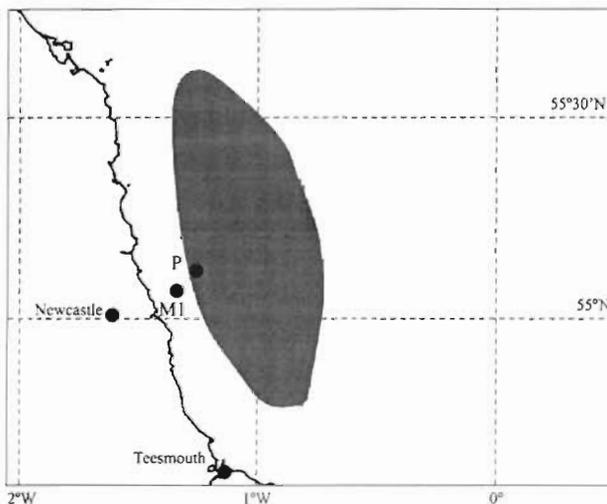
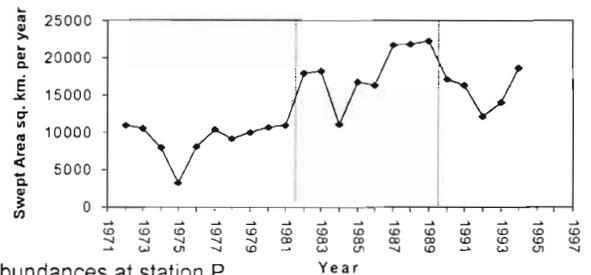


Fig. 1. Map showing locations of benthic sampling Stns P and M1 off the NE coast of England

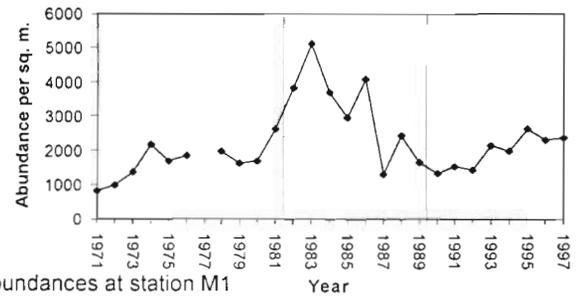
during this period (Buchanan 1993). No such relationship was detected at Stn P.

The intensity of trawling in the area considered in this study (ICES statistical rectangle 39E8) varied considerably from the early 1970s to the early 1990s (Fig. 2a). From 1972 until 1981 the area of 39E8 swept by fishing gear was approximately $10000 \text{ km}^2 \text{ yr}^{-1}$, while in the period from 1982 to 1986 it was around $15000 \text{ km}^2 \text{ yr}^{-1}$. After this, there was a period when the

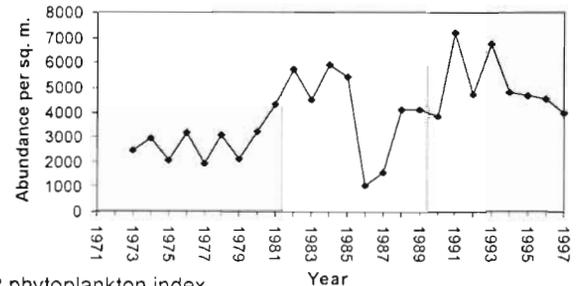
a) Swept area ICES rectangle 39E8



b) Abundances at station P



c) Abundances at station M1



d) C2 phytoplankton index

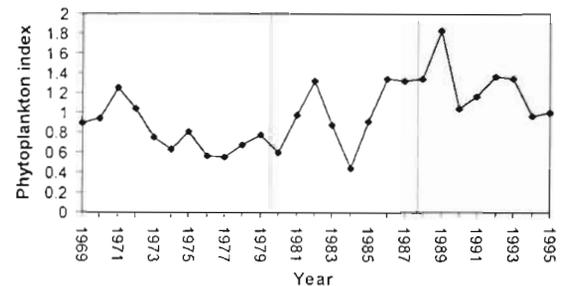


Fig. 2. Time series plots of (a) fishing impact measured as swept area per year over the period 1972 to 1994; (b) abundance of individuals at Stn P; (c) abundance of individuals at Stn M1; (d) CPR phytoplankton index for the years 1971 to 1995. In all cases vertical lines separate the 3 defined phases corresponding to low, high and mid periods of fishing

area swept exceeded 20 000 km² yr⁻¹ until 1989, since when it has dropped to around 15 000 km² yr⁻¹. Since ICES statistical rectangles at this latitude cover 3091 km², but only 51 % of the area of ICES statistical square 39E8 is water, this is equivalent to trawlers sweeping the seabed approximately 12.9 times yr⁻¹ in the most heavily impacted period. Rijnsdorp (1998) described the distribution of fishing activity at a resolution of 1 × 1 nautical mile. The fishers were found to behave in a non-random fashion and trawl only 60 % of the available area. Therefore, on the fishing grounds the benthos may have been impacted as often as 20 times yr⁻¹!

Over time, the communities at Stns M1 and P would be expected to change in response to differing environmental conditions. For example, steadily increasing productivity over time would result in trends in the benthos across the entire observation period. These may include for example increased numbers of opportunists (Pearson & Rosenberg 1978) and increased abundances of deposit feeding species (Beukema 1992a). In contrast, on the fishing grounds, the increasing, then declining level of fishing intensity may cause changes during the period of greatest fishing activity which mask the changes taking place due to fluctuations in organic input. This paper examines temporal changes in the macrobenthic community at the 2 stations over the last 27 yr. Our premise is that the fauna

at Stn M1 (outside the main fishing ground) would be controlled by the organic flux over the entire time period, while at Stn P (within the fishing ground) the dynamics would be altered during the period of high fishing effort (1981 to 1990). Based on literature accounts of the direct impacts of fishing (e.g. Pope & Macer 1996, Rijnsdorp et al. 1996) (see 'Study site and methods', below) we hypothesise *a priori* that the errant polychaetes and ophiroid and asteroid echinoderms will respond positively to fishing (Lindley et al. 1995, Frid & Clark 1999) while sedentary polychaetes, echinoid echinoderms and large (>50 mm) bivalves would be negatively impacted (see Table 1). We therefore examine changes in the proportion of the fauna in these groups and changes in their abundance over 3 periods of differing fishing intensity.

STUDY SITE AND METHODS

In the early 1970s, time series were established at 2 benthic stations off the Northumberland coast, north east England (Stns M1 and P; Fig. 1). These stations are both located in ICES statistical rectangle 39E8 and close to or within a *Nephrops norvegicus* (Dublin Bay Prawn) fishing ground (BODC 1992) where otter trawling is the predominant technique. The accumulated

Table 1. Categorisation of recorded prey classes into groups for which *a priori* hypotheses could be formulated for their responses to fishing effects

Predicted decrease		No prediction		Predicted increase			
Phylum	Genus	Phylum	Genus	Phylum	Genus		
Annelida	<i>Ampharete</i>	Cnidaria	<i>Virgularia</i>	Annelida	<i>Capitella</i>		
	<i>Anobothrus</i>		Crustacea		<i>Chaetozone</i>		
	<i>Levinsenia</i>	<i>Ampelisca</i>			<i>Commensodorum</i>		
	<i>Minuspio</i>	<i>Diastylis</i>			<i>Diplocirrus</i>		
	<i>Myriochele</i>	<i>Ericthonius</i>			<i>Exogone</i>		
	<i>Owenia</i>	<i>Eudorella</i>			<i>Glycera</i>		
	<i>Prionospio</i>	<i>Harpinia</i>			<i>Glycinde</i>		
	<i>Rhodine</i>	<i>Leucon</i>			<i>Goniada</i>		
	<i>Spionid</i>	Mollusca			<i>Photis</i>	<i>Heteromastus</i>	
	<i>Spiophanes</i>				<i>Abra</i>	<i>Lumbrineris</i>	
	<i>Synelmis</i>				<i>Chamelea</i>	<i>Magelona</i>	
	<i>Terebellidae</i>		<i>Lucinoma</i>		<i>Magelona</i>		
	<i>Terebellides</i>		<i>Mysella</i>		<i>Mediomastus</i>		
	<i>Thelepus</i>		<i>Nuculoma</i>		<i>Nephtys</i>		
	Echinodermata	<i>Echinocardium</i>	Nemertea		<i>Tellimya</i>	Echinodermata	<i>Ophelina</i>
	Mollusca	<i>Acanthocardia</i>			<i>Thyasira</i>		<i>Paramphinome</i>
Phoronida	<i>Phoronis</i>	Platyhelminthes	<i>Nemertea</i>	<i>Pholoe</i>			
			<i>Polycladida</i>	<i>Praxillella</i>			
				<i>Praxillella</i>			
				<i>Pseudeurythoe</i>			
				<i>Scalibregma</i>			
				<i>Tharyx</i>			
				<i>Amphiura</i>			
				<i>Ophiuroidea</i>			
				<i>Oligochaeta</i>			

data were analysed at intervals during collection (Buchanan et al. 1974, 1986, Buchanan & Moore 1986a, b, Buchanan 1993, Frid et al. 1996). However, until now, the data have not been examined with regard to the possible effects of fishing

Stn P is situated at 55°07' N, 01°15' W (Fig. 1). It lies 11.5 miles (18.5 km) offshore and is in 80 m of water. The sediment has a silt-clay content of greater than 50%, of which 20% is faecal pellets. The community at the station is the *Brissopsis lyrifera* - *Amphiura chiajei* variant of the *Amphiura filiformis* community type (Petersen & Boysen-Jensen 1911). The station lies within the *Nephrops norvegicus* ground and was initially sampled in January 1971.

Stn M1 lies at 55°04' N, 01°20' W (Fig. 1), 6.5 miles (10.5 km) offshore outside of the *Nephrops norvegicus* ground. It has a predominantly sandy sediment, with a 20% silt clay content and lies in 55 m of water. The community is, *sensu* Petersen & Boysen-Jensen (1911), the *Amphiura filiformis*-*Echinocardium cordatum* variant of the *Amphiura filiformis* community type. Sampling commenced in September 1972.

Sampling at Stn P is routinely carried out in January and at Stn M1 in March of each year. On all sampling occasions, a van Veen grab removing an area of 0.1 m² and a 0.5 mm mesh sieve were used. At least 5 grab samples were taken on each occasion. The 1977 sample from Stn P has not been included in the study as weather and operational constraints prevented sampling until June of that year and the sample is therefore not comparable with the rest of the time series. Buchanan & Warwick (1974) and Buchanan & Moore (1986b) describe the methods of sampling at each station in detail.

Time series analysis. Data on level of fishing effort in 39E8 were obtained from MAFF, North Shields, UK. The time series was divided into 3 phases corresponding to the level of fishing effort. These phases were: low fishing effort, 1972–1981; high fishing effort, 1982–1989; and moderate fishing effort, 1990–1994 (Fig. 2a). The benthic time series were also divided into the 3 periods corresponding to the level of fishing effort operating at any one time.

Each genus in the data set was defined on the basis of literature accounts (de Groot & Lindeboom 1994, Lindeboom & de Groot 1997) as being (1) likely to increase, (2) likely to decrease, or (3) one for which no *a priori* prediction could be made (see Table 1). Category 3 included taxa with diverse life histories as well as ones for which no experimental data were available to form a prediction. Taxa in Category 1 were essentially errant or mobile polychaetes and asteroid echinoderms. Category 2 was characterised by sedentary or fragile taxa such as echinoid echinoderms, large bivalves (defined as max size ≥50 mm), and sedentary

polychaetes. Due to the lack of information on specific taxa, we have assumed that all species in a genus respond in a similar fashion, and where data were lacking for a genus, we believe that it would behave in a similar manner to taxa with comparable life histories.

The statistical package PRIMER (Plymouth Marine Lab, Plymouth, UK), was used to calculate Bray-Curtis similarity indices between annual means (of the 5 grabs), and for non-metric multiple dimensional scaling (MDS) analyses of data (Clarke & Warwick 1994). Analyses of long term changes in community structure were carried out at the genus level using a 4th root transformation to reduce the effect of dominant species. MDS ordination was used to show changes in species composition of the community. Analysis at the genus level avoided any problems due to errors of misidentification at the species level, or changes in taxonomy leading to problems with homonyms. Somerfield & Clarke (1995) demonstrated that such aggregations of data to higher taxonomic levels causes minimal loss of information. Therefore, this method was considered to be robust.

Analysis of bootstrapped means. The total number of individuals and proportion of individuals in the predicted increasing and predicted decreasing categories was examined over the 3 periods. In addition, abundances were examined separately for each taxonomic group within each category (see Fig. 5). For each category, and the taxonomic group within each category, we obtained bias-corrected, bootstrapped estimates of the mean abundance and 95% confidence intervals in each of the 3 periods. Bootstrapping was carried out with 10000 samples of the original data. For each of the 10000 samples, the mean was calculated and from the resulting distributions, bias-corrected 95% confidence intervals were obtained. The calculations were carried out using the Simstat for Windows package.

RESULTS

Changes in infaunal abundance and genera composition

At Stn P, within the fishing ground, benthic abundances in the decade 1971–1980 varied between 825 and 2195 m⁻² (Fig. 2b), while at Stn M1 abundances fluctuated between 2000 and 3000 m⁻² in a biennial cycle (Fig. 2c). From 1981 abundances at both stations increased. These shifts were also manifest in the genera composition of the macrofauna which altered between 1980–1981 at both sites (Fig. 3a, b).

From 1982 to the end of the series, fluctuations in macrofaunal abundance at Stn M1 were correlated with the abundance of phytoplankton 2 yr previously

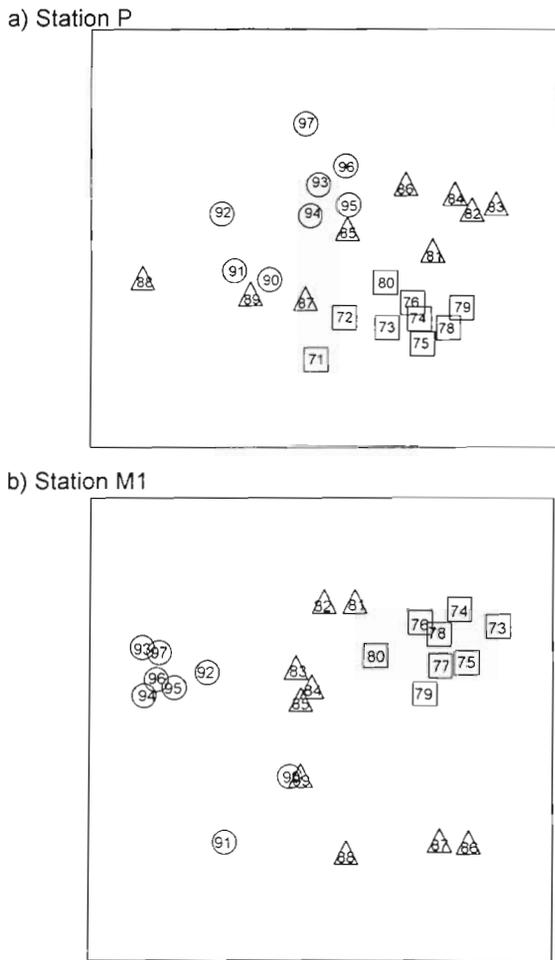


Fig. 3. (a) MDS plot produced after calculation of Bray-Curtis similarity index on double root transformed benthic faunal data from Stn P (MDS stress value = 0.16). (b) MDS plot produced after calculation of Bray-Curtis similarity index on double root transformed benthic faunal data from Stn M1 (MDS stress value = 0.12). (□) Low fishing phase; (△) high fishing phase; (○) midfishing phase

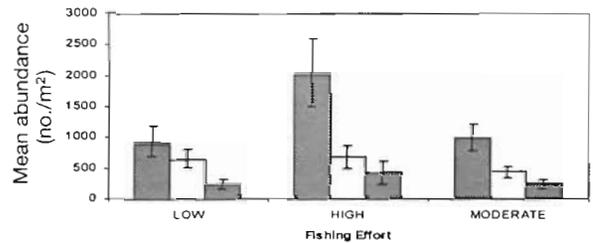
($r^2 = 0.277$) (see Fig. 2c, d). During the decade 1981–1991, genera composition varied considerably, but from 1992 to the end of the time series (1997), interannual variation in genera composition was small (Fig. 3b). The latter period coincides with a period of relative stability in macrobenthic abundance (Fig. 2c).

At Stn P, from 1982 until 1986, when fishing intensity increased, macrobenthic abundances did not track phytoplankton abundance, remaining over 0.73 standard deviations above the mean of the entire time series. Genera composition (Fig. 3a) during this period showed no obvious trend. With the decline in fishing in this area from 1989, interannual variation in macrofaunal abundance decreased while genera composition remained variable.

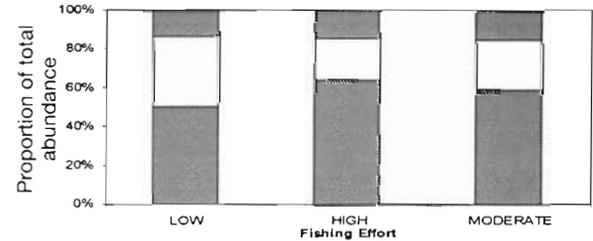
Changes in sensitive groups

The total abundance of individuals in the taxonomic groups identified *a priori* as likely to respond positively to fishing increased significantly at Stn P (within the fishing ground) between the period of low fishing activity and the period of high activity (Fig. 4a). They subsequently declined when fishing decreased. The total number of individuals in taxa identified *a priori* as likely to decline in response to fishing impacts did not

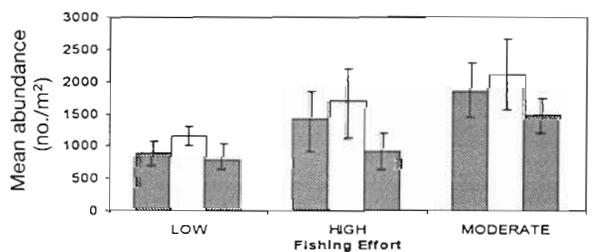
a) Total abundances: Station P



b) Proportions: Station P



c) Total abundances: Station M1



d) Proportions: Station M1

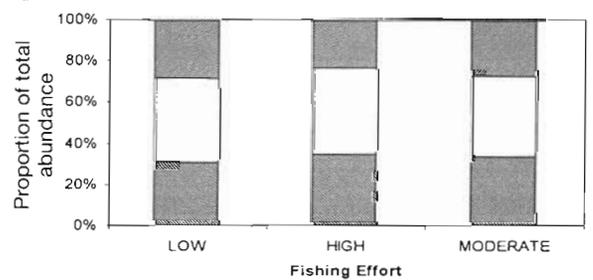


Fig. 4. (a, c) Bootstrapped means and 95% confidence intervals for total abundance of predicted increase, decrease and no prediction groups in low, high and mid fishing effort phases at (a) Stn P and (c) Stn M1. (b, d) Proportions of predicted increase, decrease and no prediction groups in low, high and mid fishing effort phases at (b) Stn P and (d) Stn M1. (■) Predicted increasers; (□) predicted decrease; (▨) no prediction

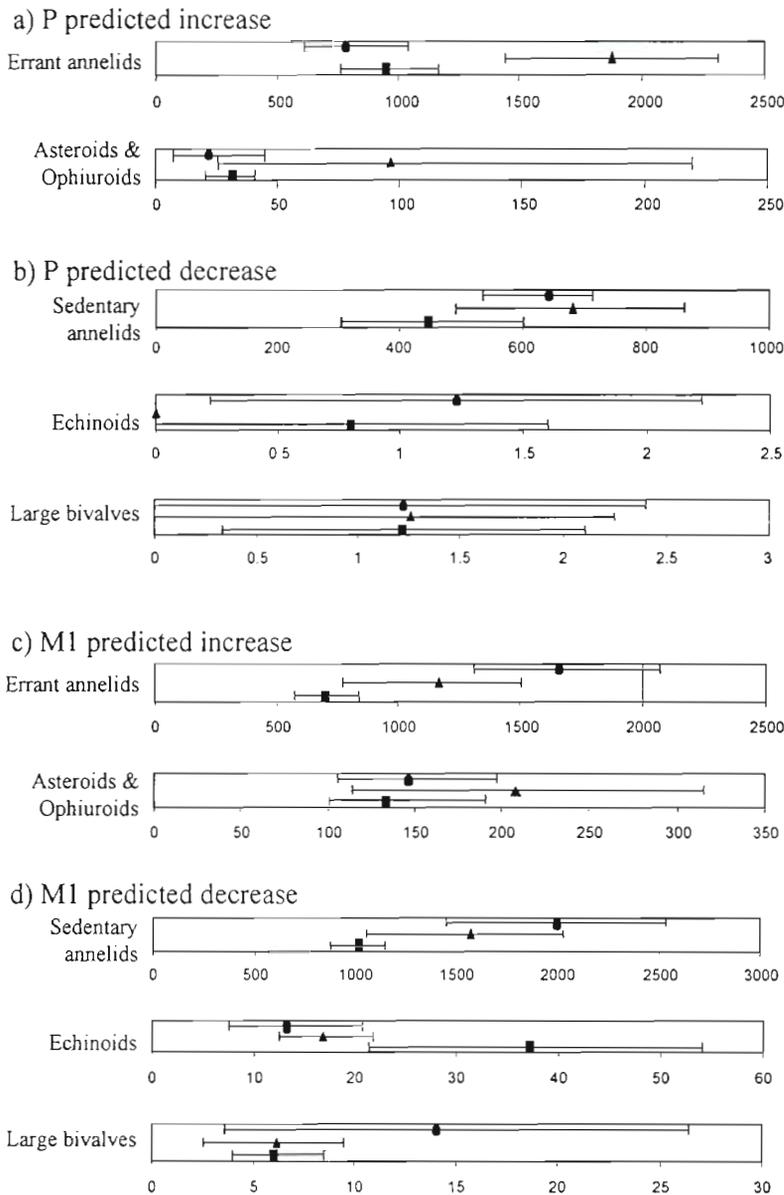


Fig. 5. Bootstrapped means and 95 % confidence limits for phyla from (a) Stn P predicted increase group, (b) Stn P predicted decrease group, (c) Stn M1 predicted increase group, (d) Stn M1 predicted decrease group. Means identified as follows: (■) Low fishing effort phase (1972–1980); (▲) high fishing effort phase (1981–1989); (●) mid fishing effort phase (1990–1994)

vary significantly between time periods (Fig. 4a). At Stn M1, outside the fishing ground, all the groups showed considerable increases over time (Fig. 4c) in response to the increasing inputs of organic material from the phytoplankton (Fig. 2d).

At Stn P, the proportion of the individuals in the community belonging to taxa predicted to increase as a result of fishing, increased during the period of high fishing effort and declined when fishing declined (Fig. 4b). Those taxa predicted to decline did show a

reduction in their proportion followed by an increase when fishing, decreased. In contrast, at Stn M1 there were no notable changes in the proportions of each group in the macrobenthic community over time, even though total abundance had increased (Fig. 4d).

Considering the changes in individual taxonomic groups, at Stn P we observed (Fig. 5a,b) changes in the predicted direction in 3 of the groups (errant polychaetes, asteroids and ophiroids, and echinoids), of which 2 (errant polychaetes and echinoids) were significant changes. The 2 categories which did not vary in the predicted direction had both been predicted to decline and showed no significant change in abundance between the 3 periods. At Stn M1, outside the fishing ground, none of the groups changed significantly between periods (Fig. 5c,d).

DISCUSSION

It would be expected that, despite differences in depth and slight differences in community structure, Stns M1 and P would follow similar trends in the timing of large changes in community structure and productivity, and these would be largely determined through changes in organic input (Pearson & Rosenberg 1986). Sedimentation of phytoplankton from the pelagos to the benthos is the major source of organic matter at these sites. Phytoplankton productivity is in turn controlled by climatic factors (e.g. Gieskes & Kraay 1975, Reid 1978, Reid et al. 1998), and thus long-term trends in climatic variables do affect the macrobenthos. Parallel trends in macrofaunal abundance between the 2 sites were observed until 1982. However, after this time, abundance at Stn M1 continued to reflect the trends in phytoplankton input while the dynamics at P were influenced by an increase in fishing activity. Other observations of faunal changes in the North Sea have shown that macrobenthic abundances increased in the early 1980s in the Wadden Sea, eastern North Sea (Beukema 1992b), in the Skaggeak (Austen et al. 1991) and Kattegat (Josefson et al. 1993), which have also been linked to climate change or eutrophication of the pelagos (Hickel et al. 1993).

It is unlikely, at least in the North Sea, that unfished benthic communities have ever been observed (Frid & Clark 1999). In this study we compare the fauna of a lightly fished area with a more heavily fished area over a period in which fishing effort changed. At the lightly fished site (Stn M1) the proportion of individuals predicted *a priori* to either increase or decrease in response to the direct effects of fishing did not vary even though productivity increased in response to increasing inputs of phytoplankton. At the heavily fished station the increase in fishing effort in the early 1980s did not alter the abundance of the small number of taxa predicted to decline. This could be due to the long history of fishing at this site already having caused declines in sensitive taxa (Frid & Hall 1998). In contrast, the abundance of individuals in taxonomic groups predicted to increase did so and thus caused a consequent shift in the proportion of taxa predicted to decline.

During the last 27 yr, phytoplankton levels off the Northumberland coast have been increasing (Frid et al. 1996). The importance of organic flux in determining benthic community dynamics is well established (see Pearson & Rosenberg 1986). We therefore expect to see this trend in the benthic time series. While genera composition at both sites does tend to show this trend across the time period (Fig. 3a,b), at Stn M1, community changes generally occurred with changes in total abundance at the site. Abundance at the site over much of the time series was generally controlled by changes in organic input (Buchanan 1993). The changing levels of phytoplankton input to the benthos would also be expected to affect the community at the fished site, Stn P. The similarity in year-to-year changes at the fished site to those of Stn M1 in the periods 1972–1980 and 1990–1997 provides evidence of the role of organic inputs to the dynamics at Stn P (Fig. 3a,b). The decoupling of the dynamics of the 2 stations at the time when fishing intensity increased provides circumstantial evidence of a role for fishing disturbance in influencing the dynamics of this system. At Stn P, the interannual variability in genera composition was greatest from 1982 to 1984, when fishing was at its most intense. Increased variability in composition is considered to be indicative of a stressed community (Warwick & Clarke 1993).

Differences in the dynamics of the predicted *a priori* groups also suggest that different mechanisms were at work at the 2 sites. At Stn M1 there was an increase in errant polychaetes which occurred through the 3 phases, yet at Stn P their abundances increased during the high fishing period and subsequently decreased when fishing activity decreased. Kröncke (1990) and Reise (1982) attributed the long-term (greater than 10 yr) increased abundance of polychaetes in some

areas of the North Sea to fishing activity and human disturbances of the sediment, respectively.

The use of time series to establish causality is fraught with difficulty (Underwood 1997). In this case many of the predicted changes in individual taxa due to fishing (Tuck et al. 1998) could also have been predicted from increased organic inputs (Pearson et al. 1986). The differences in the dynamics of these 2 stations, which differ in their fishing intensity, during the period of increased fishing, provides some evidence for a role of direct effects of fishing in determining the abundance and composition of coastal macrofauna. Re-analysis of other benthic time series is now required to determine the generality of our findings.

LITERATURE CITED

- Anonymous (1995) Report of the study group on the ecosystem effects of fisheries. ICES Co-operative Research Report 200, ICES, Copenhagen
- Austen MC, Buchanan JB, Hunt HG, Josefson AB, Kendall MA (1991) Comparison of long-term trends in benthic and pelagic communities of the North Sea. *J Mar Biol Assoc UK* 71:179–190
- Auster PJ, Malatesta RJ, Larosa SC (1995) Patterns of microhabitat utilization by mobile megafauna on the southern New England (USA) continental shelf and slope. *Mar Ecol Prog Ser* 127:77–85
- Beukema JJ (1992a) Expected changes in the Wadden Sea benthos in a warmer world: lessons from periods with milder winters. *Neth J Sea Res* 30:73–79
- Beukema JJ (1992b) Long-term and recent changes in the benthic macrofauna living on tidal flats in the western part of the Wadden Sea. *Neth J Sea Res* 20:135–141
- BODC (1992) United Kingdom digital marine atlas. British Oceanographic Data Centre, Bidston
- Buchanan J, Warwick R (1974) An estimate of benthic macrofaunal production in the offshore mud of the Northumberland coast. *J Mar Biol Assoc UK* 54:197–222
- Buchanan JB (1993) Evidence of benthic pelagic coupling at a station off the Northumberland coast. *J Exp Mar Biol Ecol* 172:1–10
- Buchanan JB, Moore JJ (1986a) A broad review of variability and persistence in the Northumberland benthic fauna. *J Mar Biol Assoc UK* 66:641–657
- Buchanan JB, Moore JJ (1986b) Long-term studies at a benthic station off the coast of Northumberland. *Hydrobiologia* 142:121–127
- Buchanan JB, Kingston PF, Shearer M (1974) Long-term population trends of the benthic macrofauna in the offshore mud of the Northumbrian coast. *J Mar Biol Assoc UK* 54:785–795
- Buchanan JB, Brachi R, Christie G, Moore JJ (1986) An analysis of a stable period in the Northumberland benthic fauna. *J Mar Biol Assoc UK* 66:659–670
- Churchill JH (1989) The effect of commercial trawling on sediment resuspension and transport over the Middle Atlantic Bight continental shelf. *Cont Shelf Res* 9:841–864
- Clarke KR, Warwick RM (1994) Change in marine communities: an approach to statistical analysis and interpretation. Plymouth Marine Laboratory, Plymouth
- Dayton PK, Thrush SF, Agardy MT, Hofman RJ (1995) Environmental effects of marine fishing. *Aquat Conserv Mar Freshw Ecosyst* 5:205–232

- de Groot SJ, Lindeboom H (1994) Environmental impact of bottom gears on benthic fauna in relation to natural resources management and protection of the North Sea. Netherlands Institute for Sea Research, Texel
- Frid CLJ, Clark RA (1999) Long-term changes in North Sea benthos: discerning the role of fisheries. In: Kaiser M (ed) *Ecosystem effects of fishing*. Blackwell, Oxford, p 198–216
- Frid CLJ, Hall SJ (1998) Long term trends in benthic communities on North Sea fishing grounds. Report to E.C. from University of Newcastle upon Tyne, Newcastle upon Tyne
- Frid CLJ, Buchanan JB, Garwood PR (1996) Variability and stability in the benthos: twenty-two years of monitoring off Northumberland. *ICES J Mar Sci* 53:978–980
- Gieskes WWC, Kraay GW (1975) The phytoplankton spring bloom in Dutch coastal waters of the North Sea. *Neth J Sea Res* 9:166–196
- Gislason H (1994) Ecosystem effects of fishing activities in the North Sea. *Mar Pollut Bull* 29:520–527
- Hickel W, Mangelsdorf P, Berg J (1993) The human impact in the German Bight: eutrophication during three decades (1962–1991). *Helgol Meeresunters* 47:243–263
- Josefson AB, Jensen JN, Aertebjerg G (1993) The benthos community structure in the late 1970s and early 1980s—a result of a major food pulse. *J Exp Mar Biol Ecol* 172:31–45
- Kaiser MJ, Spencer BE (1994) Fish scavenging behavior in recently trawled areas. *Mar Ecol Prog Ser* 112:41–49
- Kröncke I (1990) Macrofauna standing stock of the Dogger Bank—a comparison. 2. 1951–1952 versus 1985–1987 are changes in the community of the northeastern part of the Dogger Bank due to environmental changes. *Neth J Sea Res* 25:189–198
- Lindeboom H, de Groot SJ (1997) The effects of different types of fisheries on the North Sea and Irish Sea benthic ecosystems. European Commission, Brussels
- Lindley J, Gamble J, Hunt H (1995) A change in the zooplankton of the central North Sea (55° to 58° N): a possible consequence of changes in the benthos. *Mar Ecol Prog Ser* 119:299–303
- Messieh S (1991) Fluctuations in Atlantic herring populations in the north western atlantic, with particular emphasis on the Gulf of St Lawrence stocks. In: Kawasaki T, Tanaka S, Toba Y, Taniguchi A (eds) *Long-term variability of pelagic fish populations and their environment*. Pergamon Press, Oxford, p 155–163
- Pearson TH, Rosenberg R (1978) Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanogr Mar Biol Annu Rev* 16:229–311
- Pearson TH, Rosenberg R (1986) Feast and famine: structuring factors in marine benthic communities. In: Gee JHR, Gill PS (eds) *Organization of communities*. Blackwell Scientific, Oxford, p 373–398
- Pearson TH, Duncan G, Nuttall J (1986) Long-term changes in the benthic communities of Loch Linnhe and Loch Eil (Scotland). *Hydrobiologia* 142:113–119
- Petersen CGJ, Boysen-Jensen P (1911) Valuation of the sea. I. Animal life of the sea bottom, its food and quantity. *Rep Dan Biol Stat* 10:1–76
- Pope JG, Macer CT (1996) An evaluation of the stock structure of North Sea cod, haddock and whiting since 1920, together with a consideration of the impacts of fisheries and predation effects on their biomass and recruitment. *ICES J Mar Sci* 53:1157–1169
- Ramsay K, Kaiser MJ, Hughes RN (1996) Changes in hermit crab feeding patterns in response to trawling disturbance. *Mar Ecol Prog Ser* 144:63–72
- Reid PC (1978) Continuous plankton records: large-scale changes in the abundance of phytoplankton in the North Sea from 1958 to 1973. *Rapp PV Réun Cons Int Explor Mer* 172:384–389
- Reid P, Edwards M, Hunt HG, Warner AJ (1998) Phytoplankton change in the North Atlantic. *Nature* 391:546
- Reise K (1982) Long-term changes in the macrobenthic invertebrate fauna of the Wadden Sea—are polychaetes about to take over? *Neth J Sea Res* 16:29–36
- Rijnsdorp AD, van Leeuwen PI, Daan N, Heessen HJL (1996) Changes in abundance of demersal fish species in the North Sea between 1906–1909 and 1990–1995. *ICES J Mar Sci* 53:1054–1062
- Rijnsdorp AD, Buys AM, Storbeck F, Visser EG (1998) Micro-scale distribution of beam trawl effort in the southern North Sea between 1993 and 1996 in relation to the trawling frequency of the sea bed and the impact on benthic organisms. *ICES J Mar Sci* 55:403–419
- Serchuk FM, Kirkegaard E, Daan N (1996) Status and trends of the major roundfish, flatfish and pelagic fish stocks in the North Sea: thirty-year overview. *ICES J Mar Sci* 53:1130–1145
- Somerfield PJ, Clarke KR (1995) Taxonomic levels, in marine community studies, revisited. *Mar Ecol Prog Ser* 127:113–119
- Thrush SF, Hewitt JE, Cummings VJ, Dayton PK (1995) The impact of habitat disturbance by scallop dredging on marine benthic communities: what can be predicted from the results of experiments? *Mar Ecol Prog Ser* 129:141–150
- Tuck ID, Hall SJ, Robertson MR, Armstrong E, Basford DJ (1998) Effects of physical trawling disturbance in a previously unfished sheltered Scottish sea loch. *Mar Ecol Prog Ser* 162:227–242
- Underwood A J (1991) Beyond BACI—experimental designs for detecting human environmental impacts on temporal variations in natural populations. *Aust J Mar Freshw Res* 42:569–587
- Underwood AJ (1997) *Experiments in ecology*. Cambridge University Press, Cambridge
- Warwick RM, Clarke KR (1993) Increased variability as a symptom of stress in marine communities. *J Exp Mar Biol Ecol* 172:215–226

Editorial responsibility: John Gray (Contributing Editor), Oslo, Norway

*Submitted: February 15, 1999; Accepted: June 2, 1999
Proofs received from author(s): October 21, 1999*