Structural change in an exploited fish community: a consequence of differential fishing effects on species with contrasting life histories

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Summary

1. An understanding of the links between life histories and responses to exploitation could provide the basis for predicting shifts in community structure by identifying susceptible species and linking life-history tactics with population dynamics.

2. We examined long-term trends in the abundance of species in the North Sea bottom-dwelling (demersal) fish community. Between 1925 and 1996 changes in species composition led to an increase in mean growth rate, while mean maximum size, age at maturity and size at maturity decreased. The demersal fish community was increasingly heavily fished during this period.

3. Trends in mean life-history characteristics of the community were linked to trends in abundance of component species. An approach based on phylogenetic comparisons was used to examine the differential effects of fishing on individual species with contrasting life histories.

4. Those species that decreased in abundance relative to their nearest relative, matured later at a greater size, grew more slowly towards a greater maximum size and had lower rates of potential population increase. The phylogenetically based analyses demonstrated that trends in community structure could be predicted from the differential responses of related species to fishing.

5. This is the first study to link exploitation responses of an entire community to the life histories of individual species. The results demonstrate that fishing has greater effects on slower growing, larger species with later maturity and lower rates of potential population increase. The comparative approach provides a basis for predicting structural change in other exploited communities.

Key-words: community structure, fisheries exploitation, life history, North Sea, phylogeny.

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Introduction

The intensive exploitation of marine fish has led to substantial reductions in the abundance of some target species (Myers, Hutchings & Barrowman 1996) and changes in the structure and species composition of fish communities (Greenstreet & Hall 1996). Species from higher trophic levels (Koslow, Hanley & Wicklaud 1988; Russ 1991; Jennings, Grandcourt & Polu-

nin 1995; Jennings & Polunin 1996; Pauly *et al.* 1998) and large or slow-growing species with late maturity (Adams 1980; Roff 1984; Kirkwood, Beddington & Rossouw 1994) often decline in abundance more rapidly than their smaller and faster-growing counterparts. Indeed, many large or slow-growing species have become scarce following intensive exploitation, even when they are not primary targets of the fishery (Brander 1981; Vince 1991; Walker & Heessen 1996; Jennings & Kaiser 1998; Sutherland & Reynolds 1998). Such observations were substantiated by a comparative analysis of population trends in stocks directly targeted by north-east Atlantic fisheries (Jennings, Reynolds & Mills 1998b). After accounting for

differences in fishing mortality, those species which had decreased in abundance were shown to be larger, mature later and have lower rates of potential population increase. Such responses imply that community changes following fishing may be caused by differential abundance trends in species with different life histories. However, linkages between life histories and structural changes in entire communities have not been explored because life history and time series abundance data for all non-target species in an exploited community have not been available.

The North Sea is an intensively fished marine ecosystem. The entire North Sea was fished by 1900 (Cushing 1988; Smith 1994), and with the possible exception of periods during the First and Second World Wars (Beverton & Holt 1957), fishing effort has increased steadily since that time (Holden 1978; Anon 1993; Rijnsdorp & van Leeuwen 1996; Rijnsdorp *et al.* 1996; Jennings *et al.* 1999). The demersal (bottom-dwelling) fish community is targeted by many gears, in particular otter trawls, beam trawls and seine nets. Fishers currently remove over 20% of the standing stock biomass of many demersal species on an annual basis (Anon 1993; Gislason 1994). In addition, many non-target species suffer high levels of mortality because they are caught incidentally and discarded (Alverson *et al.* 1994; Gislason 1994).

Decreases in the abundance of commercially important North Sea demersal species are well known (Cook, Sinclair & Stefannson 1997), but recent analyses of catch-per-unit-effort (CPUE) data from scientific trawl surveys suggest that other species have increased in abundance despite increased fishing effort (Greenstreet & Hall 1996; Heessen 1996; Heessen & Daan 1996). The North Sea, therefore, provides an ideal system in which to test for the differential effects of fishing on species with different life-history parameters. Intensive and long-term study of the North Sea demersal fish community means that life history and abundance trend data are now available for most target and non-target species. In this paper we describe temporal changes in the mean life-history characteristics of the North Sea demersal fish community and long-term changes in the abundance of individual species. The species under consideration accounted for 99% of all individuals caught during scientific trawl surveys in the northern North Sea from 1925 to 1996. A phylogenetic comparative approach is used to examine the differential effects of fishing on species with contrasting life histories.

Methods

STUDY AREA

We studied the demersal fish community in a region of $\approx 91\,000\,\text{km}^2$ to the east of the Shetland Islands in the northern North Sea (Fig. 1). Fishing effort in this region increased steadily from 1960 (Fig. 2) and was assumed to have increased steadily before 1960 as a result of continued improvements in the seaworthiness of vessels and the development of offshore fisheries (Greenstreet *et al.* 1999b). The region is usually fished by UK registered vessels which land their catches in Scotland. For the years 1990–95, when international trawling effort data were available (Greenstreet *et al.* 1999b; Jennings *et al.* 1999), such vessels accounted for > 90% of total trawling effort. It is reasonable to assume, therefore, that the trends indicated by the Scottish effort database are a reliable indication of trends in international effort in this region. There are no international records of seine netting effort, but the technique is used almost exclusively by Scottish vessels and any effort attributable to other countries would have no effect on overall trends (Greenstreet *et al.* 1998b).

TRENDS IN ABUNDANCE

Catch rates (CPUE) of demersal species caught by Scottish fishery research vessels were used as indices of relative abundance. Mean catch rates were calculated for 19 groups of years that covered the period 1925–96. Year groups ranged from one to four consecutive years and were selected to ensure that the spatial coverage of the combined hauls was similar in each group. The analyses of Greenstreet, Spence & McMillan (1999a) indicated that it was essential to group years in this way because significant spatial variation in catch rates could obscure temporal trends in community structure. Abundance trends were described as the slope of the relationship between ln-transformed abundance and time, based on a linear model fitted using a least squares procedure. While the linear model did not necessarily describe trends in abundance before or after the period covered, it provided a general description of trends for comparative purposes. Time series analyses and other more powerful statistical techniques were not used to describe trends because the grouping of years violated the assumptions of these methods.

The mesh size and net dimensions remained the same throughout the survey period and minor modifications to other aspects of the design would have had little effect on sampling efficiency (Greenstreet & Hall 1996). However, the power of successive Scottish research vessels increased from 400 to 1540 usable horse power in the period 1925–96 and there was a concomitant increase in net towing speed from 2·25 to 4·25 knots (Greenstreet *et al.* 1999a). Because the net fishes a greater area of seabed when towed at higher speeds, we multiplied early abundance estimates by the appropriate conversion factors to account for differences in the area trawled. Further discussion of the procedures for standardizing datasets is provided by Rush & Ferro (1984), Greenstreet & Hall (1996) and Greenstreet *et al.* (1999a).

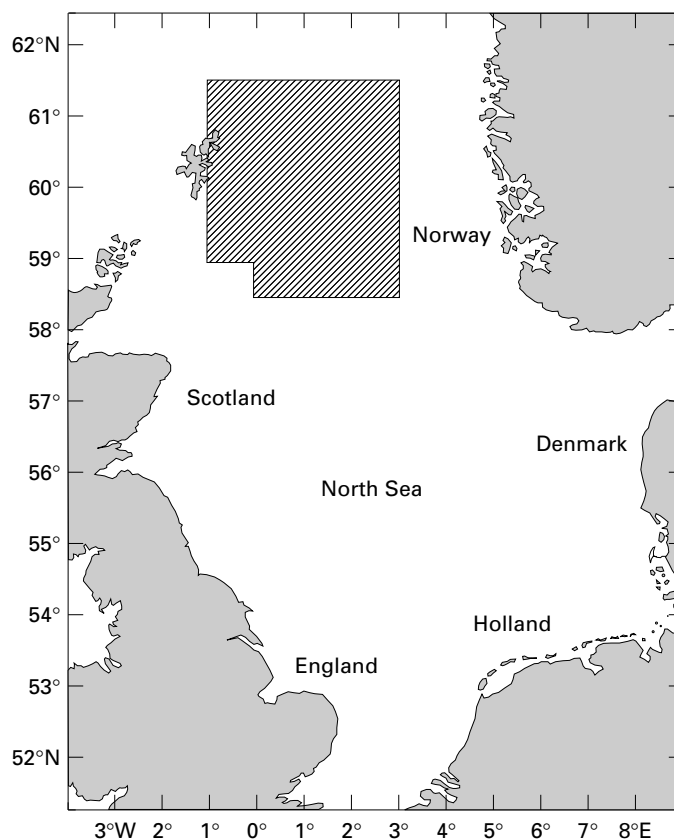Increased towing speed will result in the net catch-

Fig. 1. The area in the northern North Sea (hatched) for which abundance trends were reported.
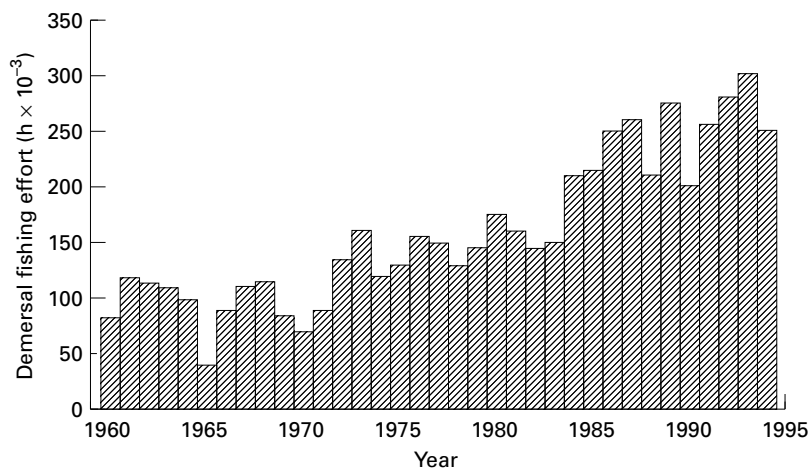

Fig. 2. Demersal fishing effort by Scottish vessels fishing in the study area.

ing faster-swimming species more effectively. Accordingly, we excluded the only fast swimming, demersal species found in this region, the saithe [*Pollachius virens* (L.)] from the analysis. We also excluded pelagic fish and fish associated with wrecks or reefs which were caught incidentally and any species for which there were less than three records in the entire survey period. The 23 species retained accounted for over 99% of all individuals caught during surveys.

DESCRIPTION OF LIFE HISTORIES

Growth rate, maximum length and the age and length at maturity of each exploited species was described parametrically. The growth rate and maximum length of fish in each stock were described using the parameters K and L_∞ of the von Bertalanffy growth equation:

$$L_t = L_\infty [1 - e^{-K(t-t_0)}].$$

Where L_t is the length at age t, L_∞ is the asymptotic length, K is the rate of growth towards the asymptotic length and t_0 is the time at which length is zero on the modelled growth trajectory (Beverton & Holt 1957). Age and length at maturity were the mean age (years) or length (cm) at which 50% of the stock attained maturity. Data were collated from the sources listed in Table 1. If life-history parameters for northern North Sea populations of each species were not available, then we used parameters for populations in adjacent areas such as the central and southern North Sea. When life-history data for male and female fish were presented separately, or when several estimates from different studies were available, then mean parameters were calculated. We described trends in community based life-history parameters by calculating a mean value for all individuals, of all species, caught in each year group.

ANALYSES

We used a phylogenetic comparative approach to test the null hypothesis that differences in length or age at maturity, growth rate and maximum size of component species did not correspond with differences in abundance trends. Phylogenetically based analyses overcome the fact that related taxa may share traits resulting from common ancestry (Harvey & Pagel 1991; Martins 1996). Thus, data on life histories of different taxa are not statistically independent. To overcome this we calculated phylogenetically independent differences (contrasts) in life-history traits within pairs of closely related species (Felsenstein 1985; Harvey & Pagel 1991). For each pair of taxa we subtracted the value of the life-history trait for the species that had increased in relative abundance from the value of the trait for the species that decreased in relative abundance. Phylogenetic relationships among taxa were determined from published morphological and molecular evidence (Wheeler 1969; Lauder & Liem 1983; Moser, Chen & Kendall 1984; Nelson 1984; Cohen 1989; Israelsson *et al.* 1991; Verneau *et al.* 1994; Lee *et al.* 1995).

We also analysed the same data without accounting for the phylogenetic relatedness between stocks. In these traditional cross-species analyses we used linear

Table 1. Abundance trends and life-history parameters for species in the North Sea fish community. Trend: slope of linear relationship between standardized catch rate (numbers h^{-1}) and time (years), L_∞: asymptotic (maximum) length, K: growth rate, T_m: age at maturity, L_m: length at maturity. Calculation of parameters is described in the text. ND indicates that no data were available. The sequence and grouping of species reflects their phylogenetic relationships (see Fig. 4)

Species	Common name	Trend	L_∞ (cm)	K (y^{-1})	T_m (y)	L_m (cm)	Reference
Raja naevus Müller & Henle	Cuckoo ray	−0·027	92	0·11	9·0	59	7
Raja radiata Donovan	Starry ray	+0·013	66	0·23	4·0	46	21
Raja batis L.	Common skate	−0·030	254	0·06	11·0	130	7
Squalus acanthias L.	Spurdog	−0·051	90	0·15	6·5	67	9
Scyliorhinus canicula (L.)	Lesser spotted dogfish	+0·002	88	0·20	5·0	58	19
Eutrigla gurnardus (L.)	Grey gurnard	−0·015	46	0·16	3·0	23	6, 19
Sebastes viviparus Krøyer	Norway haddock	−0·005	36	0·07	ND	ND	12
Callionymus lyra L.	Dragonet	−0·024	23	0·47	2·5	13	20
Melanogrammus aeglefinus (L.)	Haddock	+0·004	68	0·19	2·5	34	11
Merlangius merlangus (L.)	Whiting	+0·005	42	0·32	1·5	20	11
Gadus morhua L.	Cod	+0·007	123	0·23	3·8	70	11
Trisopterus minutus (L.)	Poor cod	−0·007	20	0·51	2·0	15	19
Trisopterus esmarkii (Nilsson)	Norway pout	+0·012	23	0·52	2·3	19	11
Brosme brosme (Ascanius)	Torsk	−0·000	89	0·08	7·0	50	3, 4
Enchelyopus cimbrius (L.)	Four-bearded rockling	+0·009	36	0·20	3·0	25	1, 16
Lophius piscatorius L.	Anglerfish	−0·015	106	0·18	4·5	61	2, 5
Glyptocephalus cynoglossus (L.)	Witch	−0·020	44	0·20	4·5	29	14, 19
Microstomus kitt (Walbaum)	Lemon sole	−0·003	37	0·42	4·0	27	17
Pleuronectes platessa L.	Plaice	−0·005	54	0·11	2·5	27	11
Limanda limanda (L.)	Dab	+0·005	27	0·26	2·3	13	18
Hippoglossus hippoglossus (L.)	Halibut	−0·015	204	0·10	5·8	83	8, 10
Hippoglossoides platessoides (Fabricius)	Long rough dab	−0·005	25	0·34	2·6	15	15
Lepidorhombus whiffiagonis (Walbaum)	Megrim	−0·022	54	0·12	3·0	23	13, 19

References: 1 Albert (1993); 2 Alfonso-Dias & Hislop (1996); 3 Bergstad (1988); 4 Bergstad & Hareide (1996); 5 Crozier (1989); 6 Damm (1987); 7 Du Buit (1977); 8 Haug (1990); 9 Holden & Meadows (1962); 10 Jakupsstovu & Haug (1988); 11 Jennings, Reynolds & Mills (1998); 12 Kosswig (1974); 13 Moguedet & Perez (1988); 14 Nilsen *et al.* (1991); 15 Ntiba (1989); 16 Quero (1984); 17 Rae (1965); 18 Rijnsdorp, Vethaak & van Leeuwen (1992); 19 unpublished data; 20 Van der Veer *et al.* (1990); 21 Vinther (1989)

regressions to determine the significance of relationships between abundance trends and life-history parameters.

Results

There were marked temporal trends in the community-based life-history parameters for the northern North Sea demersal fish community. From 1925 to 1996, mean growth rate of all fish combined tended to increase, while mean age at maturity, length at maturity and maximum length (L_∞) decreased (Fig. 3). The statistical significance of these trends cannot be calculated because the time-series data will be autocorrelated and because artificial groupings of years were needed to ensure consistent spatial coverage over time (Greenstreet *et al.* 1999a).

Of the 23 species included in the analyses, 15 decreased in abundance in the period 1925–96 (Table 1). The phylogenetic analysis (Table 1; Fig. 4) indicated that nine comparisons could be made between pairs of closely related species that exhibited different population trends during the period of increasing fishing intensity. In each comparison, the value of the life-history parameter for the species that had declined less was subtracted from that which had declined more. The null expectation was that the incidence of positive and negative values of the paired contrasts would not be significantly different from random. However, in eight of the nine pairs of taxa, the species that declined in abundance relative to its nearest rela-

tive had a larger body size (Fig. 5a; binomial test, $P = 0.020$). These species were also slower growing (Fig. 5a; binomial tests, $P = 0.020$). Similarly, contrasts in age and size at maturity indicated that species that decreased in abundance with respect to their closest relatives were larger and older at maturity (Fig. 5b; binomial tests, $P = 0.035$).

The traditional cross-species analyses showed the same trends but most did not reveal statistically significant relationships between abundance trends and maximum length ($F_{1,21} = 2.63$, $P = 0.120$), growth rate ($F_{1,21} = 2.74$, $P = 0.113$) or length at maturity ($F_{1,20} = 2.64$, $P = 0.120$). However, the analysis suggested that abundance trends were related to age at maturity ($F_{1,20} = 8.43$, $P = 0.009$).

Estimates of fecundity (number of eggs produced per year) were available for five of the species pairs used in the analysis (Table 2). These estimates, in conjunction with age at maturity (Table 1), allowed the potential rate of population increase (r'; Jennings *et al.* 1998) to be calculated as:

$$r' = (\log \text{fecundity at } L_m)/T_m$$

where L_m and T_m are the mean lengths and ages at which 50% of the stock attain maturity. Contrasts in log fecundity at L_m and in r' indicated that those species that decreased in abundance relative to their nearest phylogenetic relatives did not have significantly lower fecundity (Fig. 6; binomial test, $P = 0.50$), but they did have significantly lower poten-
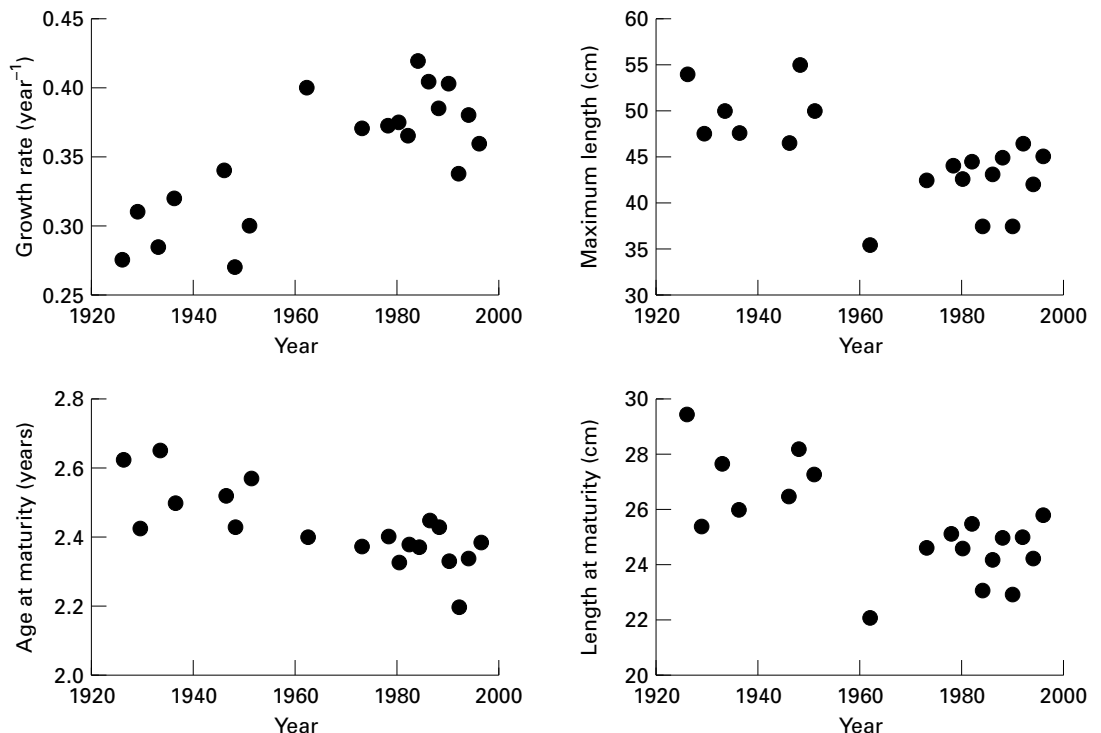
Fig. 3. Trends in the mean growth rate, maximum length, age at maturity and length at maturity of North Sea demersal fish from 1925 to 1996.
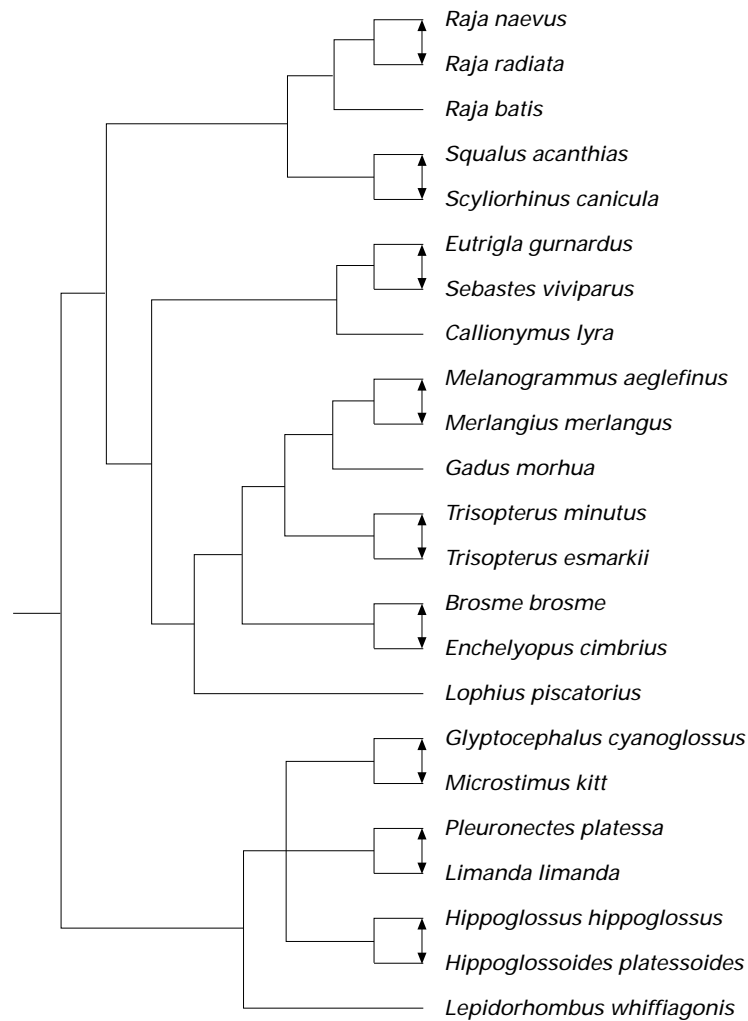
Fig. 4. Phylogenetic relationships among North Sea fish. Paired comparisons between species that exhibited contrasting population trends are indicated by vertical bars. Branch lengths were set to unity.
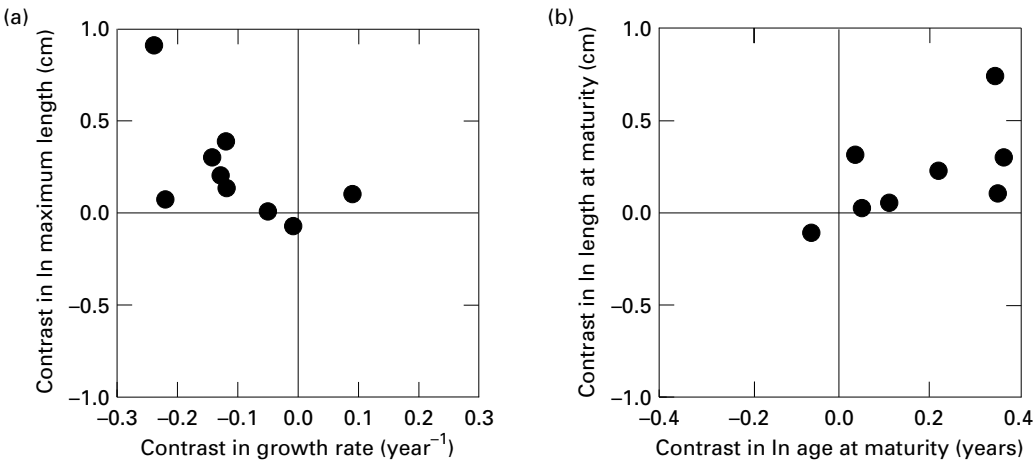

Fig. 5. Differences in (a) the maximum length and growth rate and (b) the age and length at maturity between pairs of related species that exhibited opposing population trends. In calculating each contrast the value of the life-history parameter for the species which had declined least was subtracted from that which had declined most.

Table 2. Annual fecundity at the length of maturity and potential rate of population increase (r^t) for five species-pairs in the North Sea fish community. The sequence and grouping of species reflects their phylogenetic relationships (Fig. 4)

Species	Fecundity	r^t	Reference
Spurdog	5	0·11	Gauld (1979)
Lesser spotted dogfish	23	0·27	Wourms, Grove & Lombardi (1988)
Haddock	160 800	2·08	Hislop & Shanks (1979)
Whiting	83 900	3·28	Hislop & Hall (1974)
Witch	100 000	1·11	Bagenal (1965)
Lemon sole	95 000	1·24	Newton & Armstrong (1974)
Plaice	69 700	1·94	Horwood, Bannister & Howlett (1986)
Dab	80 500	2·13	Lee (1972)
Halibut	171 200	0·90	Haug & Gulliksen (1988)
Long rough dab	21 100	1·66	Ntiba (1989)
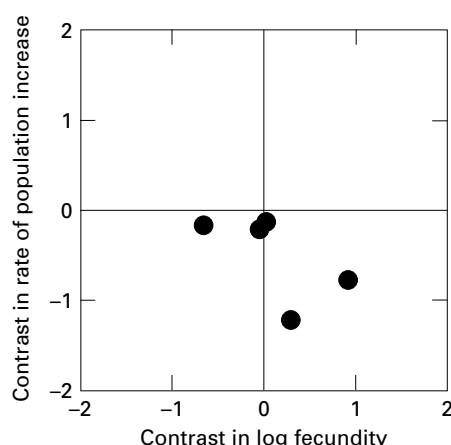
Fig. 6. Differences in log fecundity and potential rate of population increase between five pairs of related species that exhibited opposing population trends. In calculating each contrast the value of the life-history parameter for the species that had declined least was subtracted from that which had declined most.

tial rates of population increase (Fig. 6; binomial test, $P = 0·031$).

Discussion

The comparative approach indicates that changes in the structure of the North Sea fish community were determined by the differential effects of fishing on species with different life-history parameters. There has been a shift towards small species with fast life histories as fishing effort increased. This is the first assessment to link the responses of both target and by-catch species, in a single community, to characteristics of their life histories. The results provide quantitative evidence to support speculation that fishing has had greater effects on slower-growing, larger species with late maturity (Holden 1968, 1978; Brander 1981; Walker & Heessen 1996).

Studies of the size structure of the entire North Sea fish community have demonstrated that the proportion of fish in larger size classes decreased in the period 1974–92 (Rice & Gislason 1996). The present results suggest that this change should be attributed not only to the loss of larger individuals of all targeted species (Rice & Gislason 1996) but to a decrease in the relative abundance of species which have the capacity to grow to large sizes. Because species with faster life histories have higher production : biomass ratios (Beddington & Cooke 1983), changes in mean life-history parameters for the whole community suggest that increases in potential yields per unit biomass will follow increases in fishing intensity. This effect would partly compensate for any reduction in the total biomass of an exploited community. However, in economic terms, many smaller species are less desirable and are used in the manufacture of fish meal for animal feeds rather than for human consumption.

Our analyses are based on ascribing fixed life-history parameters to individual species, when theoretical and empirical studies demonstrate that the values of these parameters will change in response to fishing (Law 1991; Buxton 1993; Rijnsdorp 1993a, 1993b; Rowell 1993; Rijnsdorp & van Leeuwen 1996). These changes may be a result of phenotypic plasticity, but in the longer term the selective pressure of fishing may lead to genetic changes (Law 1991; Rowell 1993). Long-term studies of commercially important North Sea fish such as cod and plaice demonstrate that growth rate has increased while age at maturity has decreased (Rijnsdorp 1993a, 1993b; Rijnsdorp & van Leeuwen 1996). Ideally, we would examine these changes in life histories in all component taxa but, unfortunately, long-term studies of life-history shifts in other species are not available. The use of fixed life-history parameters is, however, a conservative approach; for example, if increased fishing mortality led to intraspecific increases in the growth of other species, then the mean growth rates of individuals in the community would increase. Thus increased growth rates with time would magnify, rather than nullify, the trends we have reported.

Consistent relationships between increased fishing effort and the long-term abundance trends suggest that fishing had the dominant effect on abundance

(Hempel 1978; Jakobsson *et al.* 1994; Daan & Richardson 1996). Environmental changes are unlikely to explain the results for two reasons. First, while short-term trends in the abundance of individual species can be attributed to environmental change, these trends are subsumed within long-term (decades) population trajectories (Daan & Richardson 1996; Hempel 1978). Second, long-term abundance trends of all larger species are consistent with changes in fishing effort but not with changes in salinity, temperature or pollutants, which would have different effects on species with different environmental preferences (Hempel 1978; Anon 1993; Jakobsson *et al.* 1994). Thus both torsk [*Brosme brosme* (Ascanius)] and starry ray (*Raja radiata* Donovan) have more northerly distributions than their closest relatives, the four-bearded rockling [*Enchelyopus cimbrius* (L.)] and cuckoo ray (*Raja naevus* Müller & Henle) (Wheeler 1969; Fig. 4), but the torsk has decreased in relative abundance while the starry ray has increased.

Those species of fish that decreased in abundance compared to their nearest relatives mature significantly later at a greater size, and grow more slowly towards a greater maximum size. For three of these parameters this significant result could not be duplicated using a traditional cross-species analysis. An examination of species that are exceptions in the cross-species trends demonstrates the strength of the comparative method; for example two flat fish, witch [*Glyptocephalus cynoglossus* (L.)] and plaice (*Pleuronectes platessa* L.), have decreased in abundance, while the larger starry ray (an unrelated species with similar morphology) has not. This appears to be an exception to the central hypothesis as the starry ray is larger and has later maturity than the flatfish. However, when we account for phylogenetic relatedness it is clear that the closest relative of the starry ray, the cuckoo ray, has decreased in abundance during the same period. The cuckoo ray is both larger and older at maturity and grows more slowly to a greater maximum size than the starry ray. Such differential responses to fishing can only be revealed by analyses within a phylogenetic framework because these eliminate many spurious differences among unrelated taxa (Harvey 1996).

There are a number of reasons why species with different life histories may respond differently to fishing pressure; for example, the faster life histories of smaller species enable them to sustain higher instantaneous mortality rates than larger species (Jennings *et al.* 1998) and they may suffer lower fishing mortality because they are less desirable and less accessible targets in a size-selective fishery. As information on the fishing mortality rates of all non-target species is not available in this or any other fishery, it is not possible to partition the roles of mortality and life history. However, flatfish and rays, with similar morphology and habitat preferences, are targeted on the same grounds with the same fishing gears, and yet starry rays and dabs have increased in abundance while their phylogenetic and ecological counterparts, cuckoo rays and plaice, have not.

While fecundity data were not available for all species in the community, analyses were completed for five of the nine potential species pairs (Table 2, Fig. 4). The results suggest that fecundity is not an important predictor of the response to exploitation, whereas the potential rate of population increase is lower for the species that have decreased in relative abundance. The potential rate of population increase (r') is analogous to the intrinsic rate of natural increase (r) reported for many unexploited populations (Jennings *et al.* 1998). In this study, r' is preferred because the egg production and cohort generation time estimates needed to calculate r would be biased by the reduced lifespans of individuals in exploited stocks.

Growing interest in marine conservation (Nelson & Soulé 1987; Ludwig, Hilborn & Walters 1993; Reynolds & Jennings 1999) and the wider effects of fishing on non-target fish and invertebrate communities (Norse 1993; Dayton *et al.* 1995; Jennings & Cotter 1998; Jennings & Kaiser 1998) has stimulated the development of methodologies for identifying those species that are most susceptible to fishing (Hudson & Mace 1996). Reliable estimates of fishing mortality will never be available for most non-target species, given the investments of time and money needed to collect such data. However, the present study suggests that trends in abundance of non-target species could be predicted without direct knowledge of fishing mortality using existing knowledge of phylogenetic relationships and life histories. This approach has particular application in many tropical fisheries where the knowledge of taxonomic relationships between fish is good but basic population data are often lacking. Moreover, even age-based life-history parameters may not be needed for such analysis because parameters describing the growth, maturation, reproduction and natural mortality of fish are closely interrelated (Alm 1959; Beverton & Holt 1959; Beverton 1963, 1992; Pauly 1980; Jennings & Beverton 1991; Charnov 1993). As such, an easily measured parameter such as length at maturity or maximum size (which is correlated with theoretical asymptotic length L_∞) may be sufficient to predict which non-target species are more vulnerable to overexploitation and how the community may shift as a result.

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