

Life history correlates of responses to fisheries exploitation

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We use an approach based on phylogenetic comparisons to identify life history correlates of abundance trends in 18 intensively exploited fish stocks from the north-east Atlantic. After accounting for differences in fishing mortality, we show that those fishes that have decreased in abundance compared with their nearest relatives mature later, attain a larger maximum size, and exhibit significantly lower potential rates of population increase. Such trends were not evident in a more traditional cross-species analysis. This is the first phylogenetically independent evidence to link life histories with abundance trends, and provides a quantitative basis for assessing vulnerability of fish populations to exploitation. Our approach can be applied to the conservation and management of other exploited taxa.

Keywords: conservation; exploitation; fishes; fisheries; life history; phylogeny

1. INTRODUCTION

Recent analyses suggest that most fished stocks are fully or over-exploited (Botsford *et al.* 1997). The most dramatic results of intensive fishing have been the economic extinction of some commercially important stocks such as cod, *Gadus morhua*, and herring, *Clupea harengus* (Beverton 1990; Hutchings & Myers 1994; Myers *et al.* 1996). These collapses typically followed long-term declines in abundance, such as those reported for North Sea cod (Cook *et al.* 1997) and many tropical groupers (Epinephelinae) (Bannerot *et al.* 1987). In contrast to these cases, some fished stocks have continued to withstand high fishing pressure, and their abundance has increased in recent years (Daan 1996; Greenstreet & Hall 1996; Jennings & Kaiser 1998).

Theoretical analyses suggest that large, slow-growing and late-maturing species should suffer greater population declines for a given mortality rate (Adams 1980; Beddington & Cooke 1983; Roff 1984; Kirkwood *et al.* 1994; Trippel 1995). However, there have been no phylogenetically based comparisons of the role of life histories in determining responses to exploitation, although there is some evidence that such relationships may exist (Bannerot *et al.* 1987; Trippel 1995). The phylogenetic comparative approach helps to eliminate spurious correlations among the life histories of related taxa and yields data which are statistically independent (Harvey & Pagel 1991; Harvey *et al.* 1995). This approach, therefore, can test the hypothesis that taxa with late maturity, slow growth, large body size, and low potential rates of population increase will decline more quickly under exploitation than related taxa with 'faster' life histories. Furthermore, it will help identify stocks or species which are vulnerable to fishing (Hudson & Mace 1996), predict shifts in fish community structure (Greenstreet & Hall 1996), and

establish links between life histories and population dynamics (Sutherland & Reynolds 1998).

In this paper we describe changes in the abundance of exploited fish stocks in the north-east Atlantic and use a comparative approach to test whether these responses to fishing are related to life history. Fisheries are typically exploited, assessed, and managed on a stock by stock basis. Stocks are intraspecific populations with characteristic life history attributes (Beverton 1963; Cushing 1967) and sufficient spatial or temporal integrity to be treated as self-perpetuating management units (Carvalho & Hauser 1994; Pawson & Jennings 1996). If theoretical predictions about the effects of exploitation on fishes with different life histories are correct (Adams 1980; Roff 1984; Stokes *et al.* 1993; Kirkwood *et al.* 1994) then this should be evident in comparisons among stocks or species. Our results provide a simple quantitative basis for predicting vulnerability to fishing mortality and linking the life histories and dynamics of exploited populations.

2. METHODS

(a) *Abundance trends and fishing mortality*

Abundance, fishing mortality, and life history data were obtained from a literature survey and assessments done by working groups of the International Council for the Exploration of the Seas (ICES) using virtual population analysis (VPA) (Pope 1972; Darby & Flatman 1994). We obtained data for a 20-year period for seven intraspecific pairs of stocks, and for 12- and 13-year periods for two pairs of related species (table 1). Where data for more than two intraspecific stocks were available we chose the two stocks with the most divergent abundance trends.

Abundance trends were described as the slope of the relation between \ln -transformed abundance and time. Slopes for each stock were determined from a linear model fitted using a least squares procedure. While a linear model cannot necessarily describe historic and future changes in abundance, it provided a short-term description of abundance trends for comparative

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purposes. Fishing mortality was expressed as the annual mean instantaneous fishing mortality for the period over which abundance trends were calculated. Fishing mortality (F) is related to survivorship such that

$$S = e^{-(F+M)},$$

where S is the survival rate per unit time (1 year) and M is the instantaneous rate of natural mortality.

(b) Growth parameters

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, 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). Growth parameters were calculated from mean length at age using data from the VPA assessments during the same time period as our abundance estimates. The age at which 50% of the stock attained maturity (T_m) was determined from a logistic curve fitted to the relation between age and the proportion of sexually mature individuals.

(c) Potential rate of population increase

We cannot calculate the intrinsic rate of natural increase (r) because stock assessment has invariably followed exploitation, and the necessary data for egg production and cohort generation time are available only after stocks have been exploited. This biases r through reduced lifespans of individuals. Instead, we calculated a surrogate, r' , which we call the potential rate of population increase:

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

where L_m is the mean length at which 50% of the stock attain maturity. Fecundity at L_m provides an index of reproductive output and T_m gives an index of cohort generation time. Fecundity was estimated from published fecundity to weight or length relationships (table 1) with conversions between length and weight based on Bedford *et al.* (1986), Coull *et al.* (1989) and unpublished sources. Fecundity data were taken from the period during which abundance trends and life history parameters were estimated (table 1) with the exception of three cases for which data from an earlier period were used. If fecundity estimates for different years were available, we calculated mean fecundity per year.

(d) Comparative analyses

We calculated differences between related stocks or species in abundance trends and each life history component (table 1). The resultant 'contrasts' yield data which are phylogenetically and statistically independent, analogous to the advantages of a paired design in an experiment. They therefore offer finer resolution than traditional cross-species comparisons by controlling for spurious differences among unrelated taxa (Felsenstein 1985; Harvey & Pagel 1991; Harvey *et al.* 1995; Martins 1996). We controlled for differences in fishing mortality (F) by taking residuals from a regression between the contrast in abundance change and contrast in mean fishing mortality over the same period. The contrasts in life history parameters were then

regressed against these residuals for significance testing with regressions forced through the origin (Harvey & Pagel 1991; Purvis & Rambaut 1995).

3. RESULTS

A total of 11 of the 18 stocks declined in abundance during the period of assessment (table 1) and in figure 1 the contrasts in life history parameters between pairs of stocks have been set positive. The panels show that stocks tended to decline more than expected from their rates of fishing mortality when they had the following life history characteristics: high ages at maturity (figure 1a, $F_{1,8} = 4.87$, $p=0.06$), large maximum size (figure 1c, $F_{1,8} = 5.05$, $p=0.06$), and low potential rates of population increase (figure 1d, $F_{1,6} = 6.47$, $p=0.04$). However, stocks with lower growth rates (figure 1b, $F_{1,8} = 2.67$, $p=0.14$) and lower fecundity ($F_{1,6} = 0.36$, $p=0.57$; not shown) did not decline significantly more than expected. When the analyses were restricted to the seven intraspecific comparisons (table 1), exploited stocks still tended to decline more than expected on the basis of fishing mortality when they had high ages at maturity ($F_{1,6} = 4.31$, $p=0.08$), large maximum size ($F_{1,6} = 5.19$, $p=0.06$) and high potential rates of population increase ($F_{1,4} = 5.31$, $p=0.10$). This analysis confirms that growth rate ($F_{1,6} = 0.39$, $p=0.56$) and fecundity ($F_{1,4} = 0.49$, $p=0.52$) do not appear to be important determinants of the response to exploitation.

We also did an alternative analysis of the same data which did not account for the phylogenetic relatedness between stocks. In this traditional cross-species analysis, residuals from the relation between abundance trend and fishing mortality were calculated by treating each stock as an independent data point and these were plotted against the corresponding life history variables (figure 2). The cross-species analysis did not reveal significant relationships between abundance trends and age at maturity (figure 2a, $F_{1,16} = 0.59$, $p=0.46$), growth rate (figure 2b, $F_{1,16} = 2.66$, $p=0.12$), maximum size (figure 2c, $F_{1,16} = 2.19$, $p=0.16$) or the potential rate of population increase (figure 2d, $F_{1,13} = 0$, $p=0.95$).

4. DISCUSSION

Our results provide the first phylogenetically independent evidence to show that larger and later maturing species are less able to withstand a given rate of fishing mortality than their smaller earlier maturing counterparts. Whereas declines in the abundance of large fishes with delayed maturity have been widely reported (Holden 1978; Brander 1981; Greenstreet & Hall 1996; Hudson & Mace 1996), it has not been clear whether this was due solely to characteristics of their life history or to the fact that larger species suffer higher fishing mortality.

The analysis also demonstrates the strength of the phylogenetic comparative method, as conventional cross-species comparisons did not reveal relationships between trends in abundance and life history variables. This underscores our assertion that it is inappropriate to compare the responses of stocks to fishing mortality without first accounting for phylogenetic relationships among taxa. For example, many skate and ray (*Raja*) species have decreased in abundance following fishing (Brander 1981;

Table 1. *Population trends, fishing mortality and life history parameters for the exploited fish stocks*

(Trend: slope of linear relationship between stock abundance and time. F : fishing mortality. T_m : age at maturity. K : growth rate. L_∞ : asymptotic (maximum) length. L_m : length at maturity. eggs: fecundity at L_m . r' : potential rate of population increase. The calculation of these parameters is described in the text.)

species	stock	trend	mean $F \pm \text{s.e.}$	T_m (y)	K (y^{-1})	L_∞ (cm)	L_m (cm)	eggs ($\times 10^{-3}$)	r'	period	references
<i>Melanogrammus aeglefinus</i>	North Sea haddock	-0.008	0.79 ± 0.024	2.5	0.19	68.3	33.5	160.8	2.08	75-94	14, 23
<i>Melanogrammus aeglefinus</i>	West Scotland haddock	-0.003	0.62 ± 0.026	2.0	0.16	67.9	30.6	no data	—	75-94	9
<i>Pollachius virens</i>	North Sea saithe	-0.007	0.61 ± 0.034	4.6	0.07	177.1	55.4	no data	—	75-94	14
<i>Pollachius virens</i>	Arctic saithe	0.001	0.52 ± 0.023	4.9	0.07	157.7	54.6	no data	—	75-94	11
<i>Gadus morhua</i>	North Sea cod	-0.027	0.83 ± 0.020	3.8	0.23	123.1	69.7	1643.1	1.66	75-94	14, 29
<i>Gadus morhua</i>	Irish Sea cod	-0.009	0.86 ± 0.054	2.5	0.39	98.5	60.9	3193.7	2.60	75-94	6, 12, 17
<i>Clupea harengus</i>	Irish Sea herring	0.001	0.44 ± 0.070	1.6	0.66	29.0	22.6	25.8	2.76	75-94	5, 10, 19
<i>Clupea harengus</i>	Celtic Sea herring	0.031	0.62 ± 0.043	1.0	0.44	30.3	22.1	1.8	3.25	75-94	5, 10, 27
<i>Pleuronectes platessa</i>	North Sea plaice	0.003	0.40 ± 0.009	2.5	0.11	54.4	26.6	69.7	1.94	75-94	2, 3, 4, 8, 14, 26
<i>Pleuronectes platessa</i>	Celtic Sea plaice	0.014	0.65 ± 0.032	3.0	0.11	59.4	28.8	41.6	1.54	75-94	1, 15, 25
<i>Merlangius merlangus</i>	West Scotland whiting	-0.018	0.68 ± 0.041	1.5	0.11	56.3	28.4	258.4	3.61	75-94	7, 12, 22
<i>Merlangius merlangus</i>	North Sea whiting	-0.016	0.62 ± 0.028	1.5	0.32	42.4	20.2	83.9	3.28	75-94	14, 22
<i>Solea solea</i>	Celtic Sea sole	-0.002	0.41 ± 0.027	2.5	0.13	49.8	24.2	44.7	1.86	75-94	15, 24
<i>Solea solea</i>	North Sea sole	0.019	0.46 ± 0.010	2.5	0.28	39.2	24.8	88.7	1.98	75-94	2, 3, 4, 8, 14, 30
<i>Micromesistius poutassou</i>	Northern blue whiting	-0.022	0.33 ± 0.030	2.3	0.23	37.1	25.1	24.4	1.95	83-94	13, 18
<i>Trisopterus esmarkii</i>	North Sea Norway pout	0.046	0.76 ± 0.070	2.3	0.52	22.6	18.6	33.8	2.01	83-94	14, 28
<i>Trachurus trachurus</i>	Western horse mackerel	-0.041	0.09 ± 0.013	2.5	0.19	34.1	18.9	19.7	1.72	82-94	16, 20
<i>Scomber scombrus</i>	Western mackerel	-0.010	0.20 ± 0.013	1.8	0.36	39.9	26.2	104.3	2.79	82-94	16, 21

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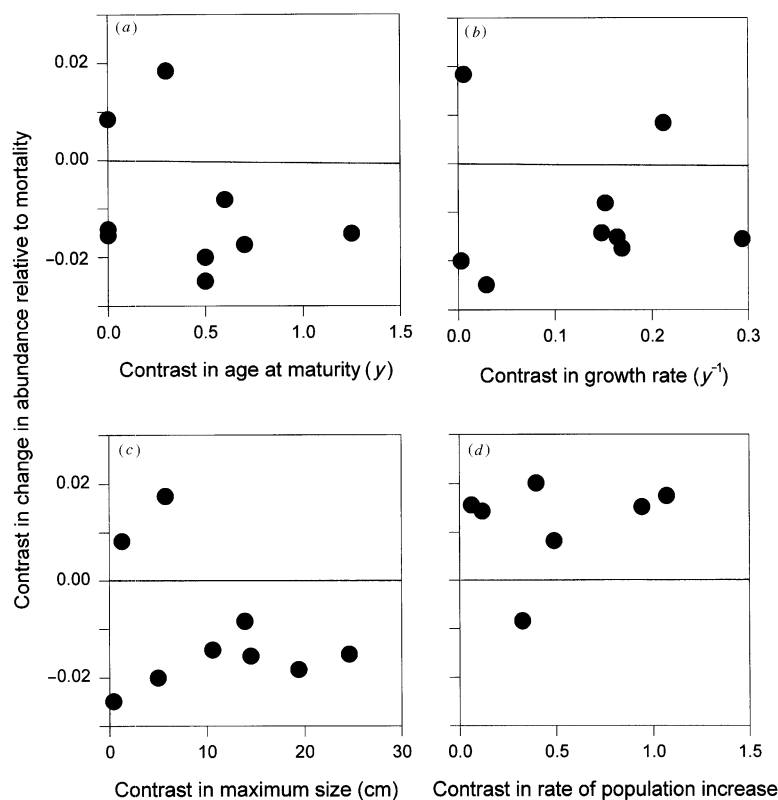


Figure 1. Relations between contrasts in changes in abundance (controlled for fishing mortality) and contrasts in life history variables: (a) age at maturity; (b) growth rate; (c) maximum size; and (d) potential rate of population increase. Explanations of life history variables are provided in the text.

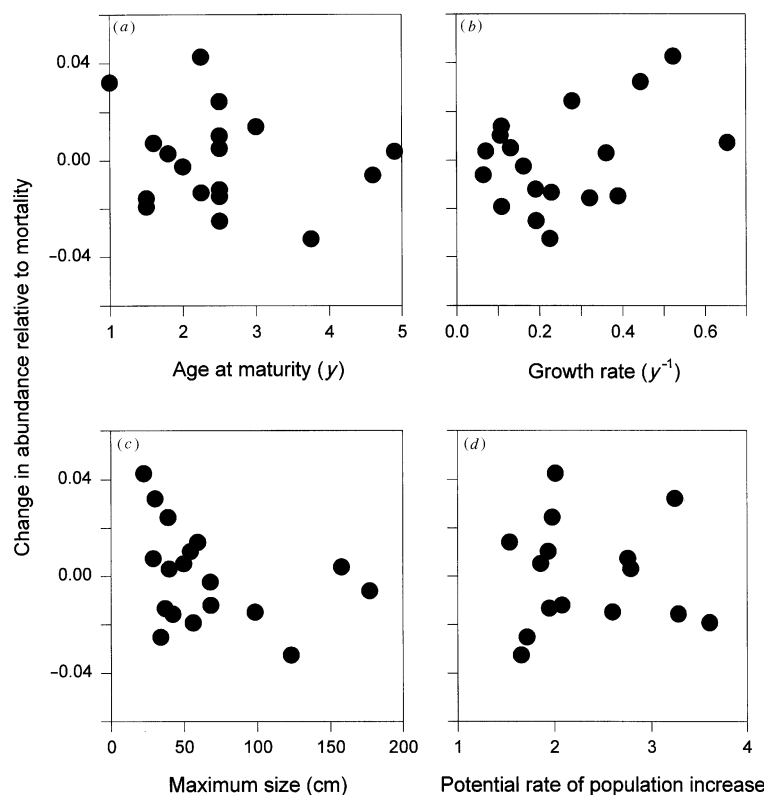


Figure 2. Cross-species relations between changes in abundance (controlled for fishing mortality) and life history variables: (a) age at maturity; (b) growth rate; (c) maximum size; and (d) potential rate of population increase.

Walker & Heessen 1996), a response which has been attributed to their advanced ages at maturity and low fecundity. However, members of this genus share many other characteristics such as broad body shape and the laying of egg cases on the seabed which could also be responsible for their susceptibility to fishing. A comparison between members of this genus, or between stocks of one species, would eliminate these other variables that they have in common (Harvey & Pagel 1991; Martins 1996).

Most fisheries are relatively unselective and many species experience high levels of mortality as bycatch even if they are not the primary targets of the fishery (Alverson 1994). In accordance with empirical observation (Koslow 1988; Russ 1991; Greenstreet & Hall 1996; Jennings & Kaiser 1998), the trends documented here suggest small and early maturing species would increase in relative abundance in an intensively exploited multispecies fishery. The shorter reproductive lifespans of these species may, however, lead to greater instability in population size (Beverton & Holt 1959; Beverton 1990; Charnov 1993). As most fishery management strategies rely upon regulation of catches or fishing effort to synchronize variable fish production processes with fishing effort, we expect that intensively fished systems will be more difficult to manage effectively.

Maturation and growth parameters of fishes are closely interrelated (Alm 1959; Beverton 1963; Leggett & Carscadden 1978; Jennings & Beverton 1991) because of trade-offs among life history allocations (Stearns 1976; Beverton 1987; Charnov 1993), and thus it is not surprising that our analyses indicate that a suite of traits determine the response to exploitation. As our analyses are based on life history, fishing mortality and abundance data from the same time period, they are unlikely to be confounded by evolutionary and phenotypic changes in response to fishing (Stokes *et al.* 1993; Rijnsdorp 1993). However, it would still be instructive to measure life history traits, including a true measure of the intrinsic rate of natural increase, in a series of unexploited populations, and then relate abundance trends under exploitation to differences in life histories.

With increasing concern for the conservation status of many bycatch or non-target stocks (Hudson & Mace 1996; Walker & Heessen 1996), it is important to assess their vulnerability to fishing (Hudson & Mace 1996). Unfortunately, rigorous assessments of vulnerability are rarely possible, because reliable mortality and life history data are usually not available. However, the comparative approach used here can predict responses to fishing by examining the responses of related stocks or species. Our analyses suggest that examination of a relatively simple component of life history, such as the theoretical maximum size, L_{∞} (which is closely correlated with observed maximum size), can indicate the response to fishing. Thus, an *a priori* prediction of the susceptibility of exploited stocks can be made using data that are widely available and without recourse to complex studies of population dynamics. This approach should have general applicability to other taxa.

We thank Trevor Boon, John Hislop, Mike Pawson, Stuart Rogers and Peter Witthames for assistance with obtaining data, Isabelle Côté, Nick Dulvy and the referees for useful comments on the

manuscript and John Cotter for his support. This study was funded by the European Community.

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