

Short-term effects of fishing on life history traits of fishes

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An important aspect of species susceptibility to fishing are the changes in demographic characteristics of populations that fishing might induce. The purpose of this study is to show the short-term effects of fishing on growth and reproduction patterns. This assessment is made through a comparative study of key parameters (mortality, size, age and size at maturity, fecundity) among stocks subject to various levels of exploitation. Data have been assembled for 77 separate (primarily commercial) fish stocks.

Trait variation is partitioned into effects attributable to size, phylogeny, and population. High adult mortality appears to lead to short-term apparently plastic changes in age and size at maturity: exploited populations are characterized by earlier age and increased size at maturity. This compensatory response to exploitation may conceal longer term selection effects, and may be worth considering in stock assessments.

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Introduction

Demographic traits of fishes, such as growth and reproduction patterns, may change under fishing pressure. For example, changes in the growth of Pacific Salmon (Ricker, 1981) and of North Sea sole (de Veen, 1976) and plaice (Rijnsdorp and van Leeuwen, 1996) have been documented. Age and size at sexual maturity have changed for Atlantic cod on the Scotian Shelf (Beacham, 1983), for Atlantic Salmon in North America (Schaffer and Elson, 1975), for North-east Arctic cod (Jørgensen, 1990) and for many stocks of cod, haddock and other fish of the North-west Atlantic (Trippel, 1995). Changes in fecundity have been reported for Atlantic Herring in the Western Gulf of Maine (Kelly and Stevenson, 1985) and for North Sea plaice (Horwood *et al.*, 1986; Rijnsdorp, 1991).

These changes in life history may influence population dynamics. In some cases, their importance in stock assessment has been shown by empirical models: density-dependent growth should be taken into account for North Sea plaice and haddock, otherwise the potential increases in yield expected from a reduced fishing intensity or increased mesh size would be overestimated (Beverton and Holt, 1957). An assessment taking into

account the compensatory responses of the North-west Atlantic mackerel stock led to less optimistic yield projections than classical assessment (Overholtz *et al.*, 1991).

It has, however, proven difficult to demonstrate the fishing origin of these changes because of phenotype-environment interactions (Pitt, 1975; Hempel, 1978; Kotilainen and Aro, 1991; Rijnsdorp *et al.*, 1991; Parmanne, 1992; Rijnsdorp and van Leeuwen, 1992). In addition, published analyses may result in conflicting conclusions: for example, under sustained fishing pressure, length at maturity decreased in North Sea cod from 1920 to 1970 (Hempel, 1978) and in Scotian Shelf cod between 1959 and 1979 (Beacham, 1983), but remained stable in Grand Bank American Plaice from 1957 to 1971 (Pitt, 1975), and increased in North Sea sole between 1957 and 1973 (de Veen, 1976).

Some of these difficulties can be overcome by a comparative approach that consists of comparing data from a large number of populations. The effects of fishing are then statistically separated from residual environmental fluctuations.

The purpose of this study is to investigate the short-term effects of fishing on growth and reproduction patterns. Demographic traits (mortality, size, age and

size at maturity, fecundity) of many fish populations subject to various levels of exploitation are collated from the literature. These traits are analysed with methods developed in the field of evolutionary ecology in order to separate the effect of fishing from other effects. Relationships between adult mortality, variation in which is assumed to be mainly due to fishing, and the other traits are then analysed by multivariate analyses.

Materials

Demographic traits

Traits to be included in such a comparative study may be numerous (Stearns, 1992; see e.g. Hutchings and Morris, 1985; Jennings and Beverton, 1991; Beverton, 1992). The main constraint upon trait selection is the need for reliable estimates of the variables, otherwise the conclusion of the comparative analysis may be spurious (Gaillard *et al.*, 1994). We concentrated on female traits and the following are included:

- We define the time-to-5%-survival ($T_{0.05}$) as the time elapsed from sexual maturity until 95% of a cohort is dead. Life span, commonly used as an indicator of survival, is often estimated by maximum observed age (Beverton and Holt, 1959; Murphy, 1968; Mann *et al.*, 1984; Roff, 1984; Hutchings and Morris, 1985; Jennings and Beverton, 1991; Beverton, 1992). However, such estimates may be biased and highly dependent on the size of the sample used. Kremenz *et al.* (1989) demonstrated that annual survival rates are preferable to observed maximum lifespan in comparative life-history studies. However, annual survival rates may vary between age classes for fish. Moreover, in most fish senescence will not occur and the mortality patterns in a population will not be uniform. Therefore time-to-5%-survival is better suited to fish than life expectation (time-to-50%-survival), as it integrates mortality rates over most adult life. Time-to-5%-survival is estimated from an exponential mortality model, on the basis of total mortality coefficients $Z=F+M$ estimated by VPA or catch curves. This overcomes the problem of the natural mortality coefficient M , which is generally poorly estimated, because errors on M are compensated for by errors on the estimated fishing mortality F . This was checked by a sensitivity analysis (Appendix A): VPA-based estimates of Z are most sensitive to errors in M in the young partially recruited age-classes because M/F is high in these age classes relative to older age classes. These young age classes are not included in the computation of time-to-5%-survival. This is valid for exploited stocks with $F>M$ in older age classes. In unexploited or weakly exploited populations, Z is estimated by a catch-curve. Time-to-5%-survival is directly influenced by fishing as it includes fishing mortality.

- Length-at-5%-survival ($L_{0.05}$) is an adult-size parameter, arbitrarily measured at time-to-5%-survival because of the indeterminate growth of fishes. The L_{∞} parameter of the von Bertalanffy (1934) growth model is usually used in comparative studies of growth or size in fishes (Beverton and Holt, 1959; Beverton, 1963, 1992; Adams, 1980; Pauly, 1980; Roff, 1984, 1991; Gunderson and Dygert, 1988; Jennings and Beverton, 1991). Hutchings and Morris (1985) use maximum length, which has the same potential disadvantages as maximum lifespan. Pauly (1980) defines L_{∞} as "the mean size the fish of a given stock would reach if they were to grow indefinitely in the manner described by the [von Bertalanffy] formula". We are mostly interested in exploited stocks, where few, if any, fish have the opportunity to reach that size. Moreover, L_{∞} is generally poorly estimated in stocks for which data are available only for young (and small) age-classes.

- Age and length at sexual maturity (A_m and L_m): we use length and age at which 50% of the individuals reach maturity, as published by the authors.

- Fecundity (F_b): a mean fecundity per female is difficult to estimate and would include the errors on many terms (e.g. size structure and size-specific fecundity). It seems therefore preferable to include in the study the parameters of the fecundity-length relationship: $F=aL^b$. However, the estimate of a is generally biased because of the log-log procedure used. Finally we use only the power b of the relationship, which is the slope of the log-log fecundity-length regression.

The data are collated from published papers and Working Groups Reports (listed in Appendix B). One difficulty is the need for contemporaneous estimates of all traits for a given stock. The purpose of the study is indeed to examine the effects of fishing mortality on life history traits, but we do not know beforehand how rapidly such effects might appear. I compiled life history data on 77 populations from 49 species of primarily commercial teleost fishes; for some of them I have data for different periods of time. The data are available from the author.

Phylogenetic information

Most of the phylogenetic information used to remove the phylogenetic effects (see Methods below) arises from Eschmeyer (1990) and Lecointre (1994). Additional information obtained from Lecointre (pers. comm.) permits construction of the topology of a phylogenetic tree with few unresolved nodes (Fig. 1), based on morpho-anatomical characters. Branch lengths however are not known: DNA sequence data from parts of the genome can provide information for branch length estimation (Nei, 1987; Harvey and Pagel, 1991), but they are not

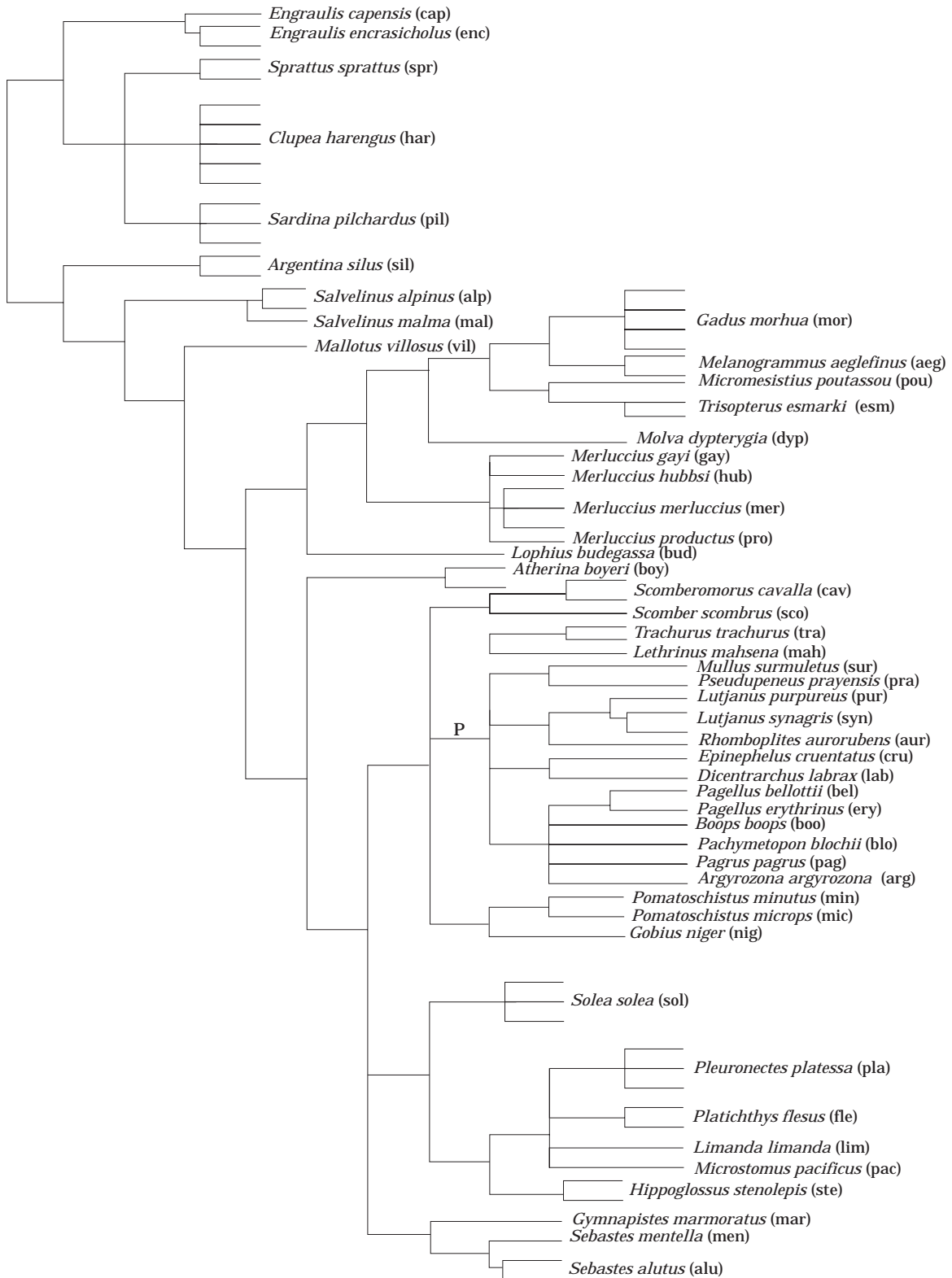


Figure 1. Phylogenetic tree of the sample of teleost fishes analysed. Data from Lecointre (1994, and pers. comm.). The position of taxa along the vertical axis has no phylogenetic meaning. P: Perciforms. In parentheses: species coding for Figure 4.

Table 1. Relationships between the logarithm of demographic trait and the logarithm of length-at-5%-survival ($L_{0.05}$) in 77 populations of fishes: correlation coefficients (r), allometric slopes (β) \pm standard error, and robust allometric slopes (β_r).

Demographic trait	r	β	β_r
Age at maturity A_m	0.73	0.71 ± 0.08	0.72
Length at maturity L_m	0.97	0.93 ± 0.03	0.89
Time-to-5%-survival $T_{0.05}$	0.61	0.60 ± 0.09	0.48

available for all populations of our study. Moreover, branch length estimations depend dramatically on the part of the genome used in the analysis, and the criteria to be used in selecting the part of the genome to be analysed are unclear. Therefore, branch lengths were arbitrarily set as follows: branch length=5 from populations to species, 1 from species to genera, and 4 for all other branches (i.e. the distance between two conspecific populations is 10, between two congeneric populations of different species is 12, between two populations of different genera of the same family is 20, etc). Other combinations of arbitrary distances were used in order to test the sensitivity of the results to branch lengths. The sensitivity of the results to incomplete knowledge of the topology of the phylogeny is also checked by comparing the results of Perciforms considered as monophyletic (Fig. 1) or polyphyletic (Fig. 1 with length of branch "P" set to zero).

Methods

Allometry

Most life history traits change with body size. Size is a major constraint upon metabolic rates and energy assimilation, and thus affects the entire lives of animals, including growth and reproduction (Reiss, 1989) and survival (Calder, 1985). The analysis of the correlations between several of these traits must take into account the fact that size may act as a confounding variable: two traits may be correlated because each is correlated with size. Comparative studies therefore usually remove size-effects (Harvey and Pagel, 1991).

Size-effects are usually described by the power relationship $Y = \alpha L^\beta$, where L is body size, Y is any trait varying with size, α and β are the parameters of the equation. The slope β of the transformed equation $\ln(Y) = \ln(\alpha) + \beta \ln(L)$ was estimated by least-squares regression for each trait (except the parameter b of the fecundity-length relationship, which was already scaled for length), with length-at-5%-survival as the scaling variable. A fair agreement (Table 1) was found between the values of slopes and the expected values of 0.75 generally attributed to time variables (e.g. Platt and Silvert, 1981; Calder, 1985; Brown *et al.*, 1993), and of 1

for length at maturity. The estimated values were then used for removing the part of variation of each trait related to body size: subsequent analyses were performed on size-corrected traits (i.e. on $\ln(A_m) - 0.71 \ln(L_{0.05})$; $\ln(L_m) - 0.93 \ln(L_{0.05})$; $\ln(T_{0.05}) - 0.60 \ln(L_{0.05})$), and results are discussed relative to body size.

Removing phylogenetic correlation

In the framework of evolutionary ecology, many comparative methods have been developed. They allow one to test hypotheses by comparing the attributes of many species. *Ad hoc* methods are needed because species are not statistically independent, but share a common history through their phylogeny: they evolved from common ancestors (e.g. Harvey and Pagel, 1991; Stearns, 1992). I shift this approach by one step and compare populations instead of species. Doing so, I intend to separate phylogenetic and long-term evolved effects from short-term and local effects, which should be influenced by the present environment, especially fishing.

Among the different comparative methods available, we cannot use those derived from Felsenstein's method of pairwise independent comparisons or contrasts (Felsenstein, 1985; Garland *et al.*, 1992; Purvis and Rambaut, 1995) because these methods require the reconstruction of higher node (ancestors) traits, usually by averaging traits of descendants. In the case of exploited fish populations, we know that the influence of fishing on the mortality of populations has increased with time. Therefore we are not allowed to reconstruct past traits on the basis of simple assumptions. For the same reason, we cannot use nested ANOVA or similar methods, which estimate mean traits of higher taxonomic levels (Stearns, 1983; Harvey and Clutton-Brock, 1985; Bell, 1989). We use the so-called phylogenetic autocorrelation method, developed by Cheverud *et al.* (1985) and Gittleman and Kot (1990); the explanations below are mainly based on the latter paper. This method allows one to partition the phenotypic value of a trait into a phylogenetic component (reflecting common evolution) and a population component (environment-dependent). The method is based on phylogenetic distance (in a cladogram or phylogenetic tree) and spatial autocorrelation statistics, which measure effects that vary with distance.

- Moran's I statistic is an autocorrelation coefficient that measures the extent to which each observation resembles that of its neighbours. It is used to answer the question: Are there phylogenetic effects?
- This autocorrelation can be evaluated at different levels and brought together into so-called "phylogenetic correlograms" to determine the taxonomic level at which phylogenetic correlation occurs. Here I computed Moran's I to measure autocorrelation

between populations within species, between species within families, and between families within orders; these levels are dictated by the composition of the data set.

- Finally the method allows one to remove phylogenetic correlation by means of an autoregressive model, which takes the form $Y = \rho WY + \varepsilon$, where Y is a vector of observed trait values, ρ is an autocorrelation coefficient, W is a weighting (neighbouring) matrix, and ε are the residuals. ρWY estimates the phylogenetic part of the trait, and ε the population (environmental) component. The weighting matrix W is derived from a distance matrix D describing the relative positions of the populations on a phylogenetic tree by: $w_{ij} = 1/d_{ij}^\alpha$ (neighbouring between populations i and j). α is a flexibility parameter that accounts for the levels at which autocorrelation occurs. Large α values describe reduced influence of distant populations on the estimated trait – consequently higher influence of close neighbours.

A maximum-likelihood procedure is used to estimate the parameters ρ and α of the autoregressive model. The ability of the model to remove phylogenetic correlation is checked by R^2 , which estimates the proportion of total variance accounted for by phylogeny, and by a phylogenetic correlogram of the residuals (which should not be significant).

Multivariate analysis

Whereas the above fits were performed for each trait separately, we analyse the residuals together by means of a principal component analysis (PCA; Lebart *et al.*, 1984). PCA is performed on the correlation matrix of size-corrected and phylogeny-corrected traits to quantify the residual covariations of life-history traits: the relationships between their environmental component, which variations are assumed to be mainly due to fishing.

Results

Phylogenetic autoregression

All five of the traits in our study show phylogenetic autocorrelation at some level (Table 2). Length-at-5%-survival is the most autocorrelated trait, and also the only one with significant autocorrelation between families within orders. On the other hand, length at maturity is weakly autocorrelated: most of the variance is explained by size (Table 1) and its residual variance may be mostly explained by population factors.

We used autoregressive models to partition each demographic trait into a phylogenetic and a population component (Table 3). α estimates vary from 1.3 to 4.3, reflecting the levels at which most autocorrelation

Table 2. Phylogenetic correlograms, enumerating normalized Moran's I for each trait (to be interpreted as correlation coefficients). *: $0.05 < p < 0.01$; **: $0.01 < p < 0.001$; ***: $p < 0.001$; otherwise $p > 0.05$. A_m : age at maturity; F_b : parameter b of the fecundity-length relationship; L_m : length at maturity; $L_{0.05}$: length-at-5%-survival; $T_{0.05}$: time-to-5%-survival.

Taxonomic rank	A_m	L_m	$L_{0.05}$	F_b	$T_{0.05}$
Species	0.60***	0.05	0.74***	0.33**	0.49***
Family	0.31***	0.11	0.44***	0.27***	0.22**
Order	0.08*	0.03	0.15***	0.03	-0.11

Table 3. Autoregressive model: maximum likelihood estimates of the model's parameters α (distance exponent) and ρ (autocorrelation coefficient), and R^2 -statistic (proportion of total variance accounted for by phylogeny) for each trait.

	A_m	L_m	$L_{0.05}$	F_b	$T_{0.05}$
α	3.1	1.3	4.3	2.1	2.4
ρ	0.965	0.827	0.977	0.980	0.912
R^2	0.36	0.01	0.73	0.09	0.17

occurs. The variance accounted for by phylogeny is quite variable, ranging from less than 10% in length at maturity and the parameter b of fecundity to more than 70% for length-at-5%-survival (Fig. 2). In order to check if the model removes all phylogenetic correlation, we computed the phylogenetic correlograms for the population components of each trait (Table 4). All autocorrelation coefficients become non-significant, demonstrating the ability of the model to remove phylogenetic correlation.

Multivariate analysis

Correlation matrices of size-corrected demographic traits and of their phylogenetic and population parts show different patterns of correlation (Table 5). Spearman's rank correlations were estimated because the distribution of the residuals is unknown: most of the observed correlations are robust, especially the ones discussed below (Table 6). Interestingly, more correlation coefficients are significant in the phylogenetic components matrix than in the size-corrected traits matrix (Table 5: five significant correlation coefficients in phylogenetic components, two in unpartitioned traits). Moreover, two of these correlation coefficients have opposite signs in the phylogenetic and population components (Table 6: $r(L_m, T_{0.05}) > 0$ for the phylogenetic component, < 0 for the population component; $r(F_b, L_{0.05}) < 0$ for the phylogenetic component, > 0 for the population component): in the phylogenetic component

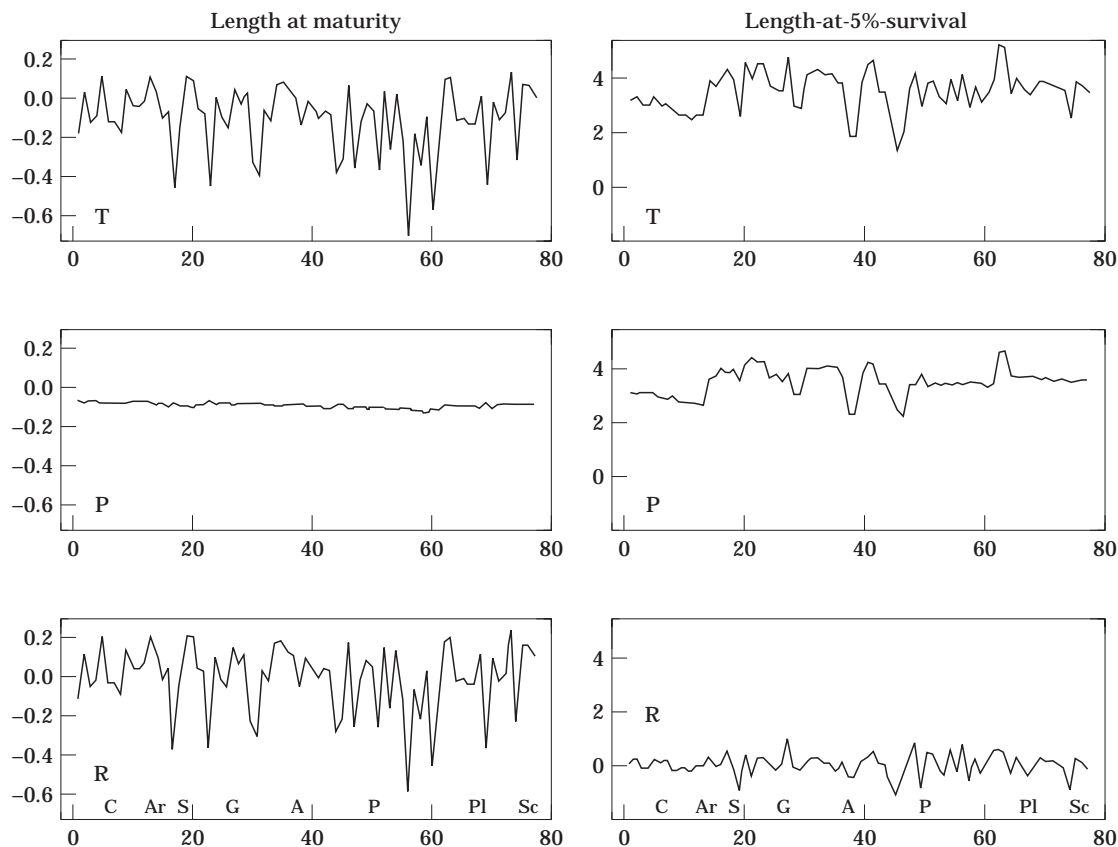


Figure 2. The trait vector (T) and its phylogenetic (P) and residual (R) components. (Left) Plot of size-corrected length at maturity for 77 populations of teleost fishes from the orders Clupeiformes, Argentiniformes, Salmoniformes, Gadiformes, Atheriniformes, Perciformes, Pleuronectiformes, and Scorpaeniformes, and its partition into phylogenetic and population components. (Right) Same decomposition for length-at-5%-survival. The abscissa is ordered from the most ancestral to the most derived taxon used in the analysis.

of the traits, short life is associated with small size and early age at maturity.

Principal component analysis of the population parts of these traits exhibits the positive correlation of time-to-5%-survival with age at maturity, and its negative correlation with length at maturity (1st axis); and a positive link between length at maturity and the parameter b of fecundity (2nd axis; Fig. 3). Time-to-5%-survival is the variable with the highest contribution to

the structure of the analysis (with the highest loading for the first component: 12.7% of total variability). On the other hand, length at maturity and its positive link with F_b appear on the orthogonal second component, although their correlation coefficient is not significant because of non-linearity. This may be interpreted as a phenotypic trade-off between length-at-maturity and the slope of the fecundity-length relationship: individual fecundity in populations with a large size at maturity would potentially increase steeply with length, and conversely; this trade-off seems independent of time-to-5%-survival, and also of fishing.

On the plot of the populations' first two components (Fig. 4a), populations of all taxa appear mingled and not sorted by taxa: as the method removes the phylogenetic part of the variation, the residuals are free of this constraint. In order to display the effect of fishing on the patterns in life history, I plotted the first two components together with an expanding symbol proportional to the ratio of fishing mortality to natural mortality

Table 4. Phylogenetic correlograms, enumerating normalized Moran's I for the population component of each trait. All autocorrelation coefficients are insignificant at the 0.05 level.

Taxonomic rank	A_m	L_m	$L_{0.05}$	F_b	$T_{0.05}$
Species	0.13	0.00	0.08	0.08	0.15
Family	0.03	0.03	0.06	0.12	0.01
Order	0.03	-0.01	-0.05	0.00	-0.06

Table 5. Correlation matrices of (a) size-corrected demographic traits; (b) their phylogenetic components; (c) their population components. Only significant correlation coefficients at the 0.05 level are shown.

(a) Demographic traits	A _m	L _m	L _{0.05}	F _b
L _m		1		
L _{0.05}			1	
F _b				1
T _{0.05}	0.51	-0.24		

(b) Phylogenetic components	A _m	L _m	L _{0.05}	F _b
L _m		1		
L _{0.05}			1	
F _b	0.21		-0.32	1
T _{0.05}	0.67		-0.34	0.25

(c) Population components	A _m	L _m	L _{0.05}	F _b
L _m		1		
L _{0.05}			1	
F _b			0.24	1
T _{0.05}	0.36	-0.31		

Table 6. Spearman's rank correlation matrices of (a) size-corrected demographic traits; (b) their phylogenetic components; (c) their population components. Only significant correlation coefficients at the 0.05 level are shown.

(a) Demographic traits	A _m	L _m	L _{0.05}	F _b
L _m		1		
L _{0.05}			1	
F _b				1
T _{0.05}	0.54			

(b) Phylogenetic components	A _m	L _m	L _{0.05}	F _b
L _m	0.22	1		
L _{0.05}			1	
F _b			-0.42	1
T _{0.05}	0.66	0.28	-0.30	

(c) Population components	A _m	L _m	L _{0.05}	F _b
L _m		1		
L _{0.05}			1	
F _b			0.23	1
T _{0.05}	0.38	-0.29		

(Fig. 4b). As fishing and natural mortality are difficult to estimate, the ratio was converted into four categories. Although most of these figures are not perfectly reliable, their overall distribution is consistent with the assumption that variation in the population component of

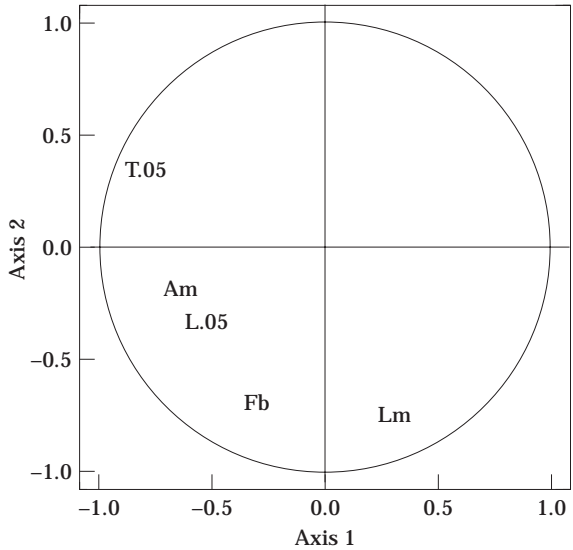


Figure 3. Scaled principal component analysis of the population parts of five demographic traits: plot of the original variables on the first two principal axes. The first two axes account for 56% of total variance: A_m: age at maturity; F_b: parameter b of the fecundity-length relationship; L_m: length at maturity; L_{0.05}: length-at-5%-survival; T_{0.05}: time-to-5%-survival.

time-to-5%-survival is mainly due to fishing. The first component shows a gradient from unexploited stocks with delayed maturity at a small size (e.g. unexploited char of Baffin Island alpO7 and South African Sparidae argA6 and bloA6, left) to short-lived stocks with precocious maturity at a large size (e.g. Mediterranean goby minM8, West African red mullet praA7, Cuban snapper synO7, right). The case of North Sea plaice is of special interest: in the forties, after fishing was interrupted during Second World War, the population has the mortality and maturity traits of an unexploited population (plaN4). In the 1970s, the population is among other exploited populations (plaN7).

Sensitivity analyses

Autoregressive models were fit to the data with different branch lengths: (i) as described previously; (ii) all branches=1; (iii) branch length=1 from populations to species and from species to genera, and 4 for all other branches. Estimates of α consistently increase as the species-population distance increases, whereas ρ estimates and the proportion of total variance accounted for by phylogeny remain constant. The ability of the model to remove phylogenetic correlation is slightly better with set (i): all autocorrelation coefficients become non-significant, whereas L_{0.05} autocorrelation remains significant at the family level with sets (ii) and (iii). As the results of the subsequent multivariate analysis

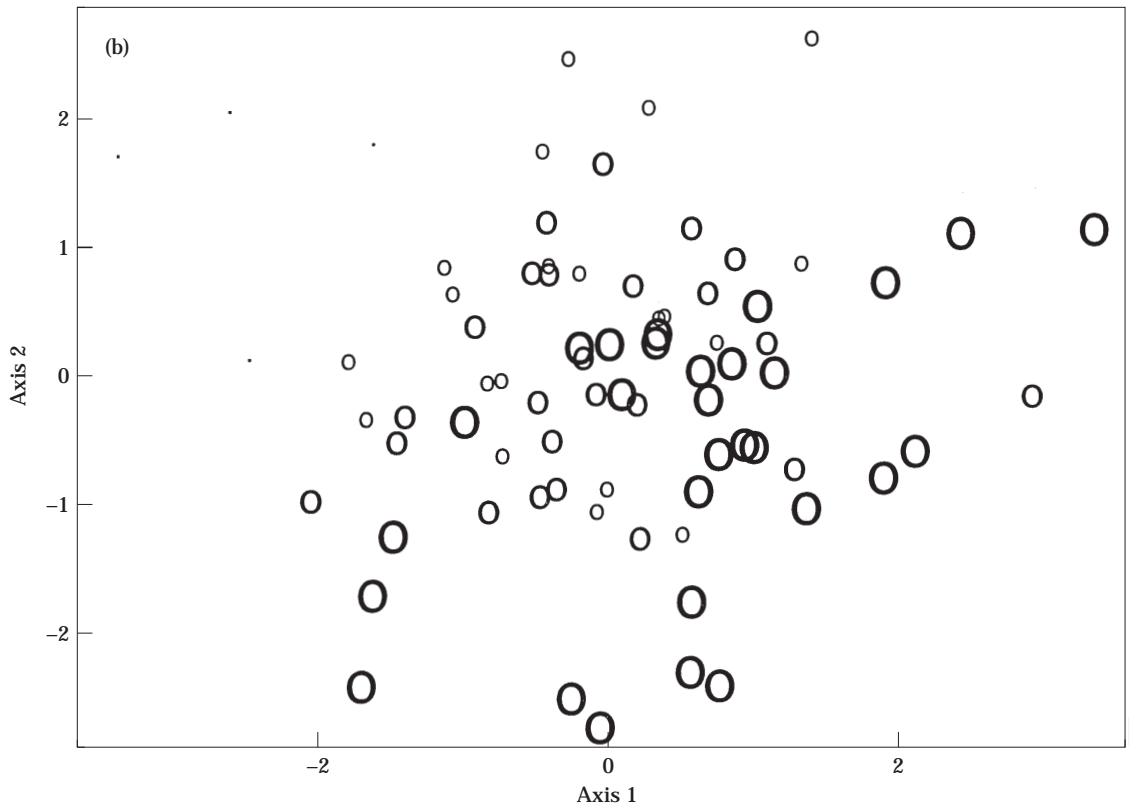
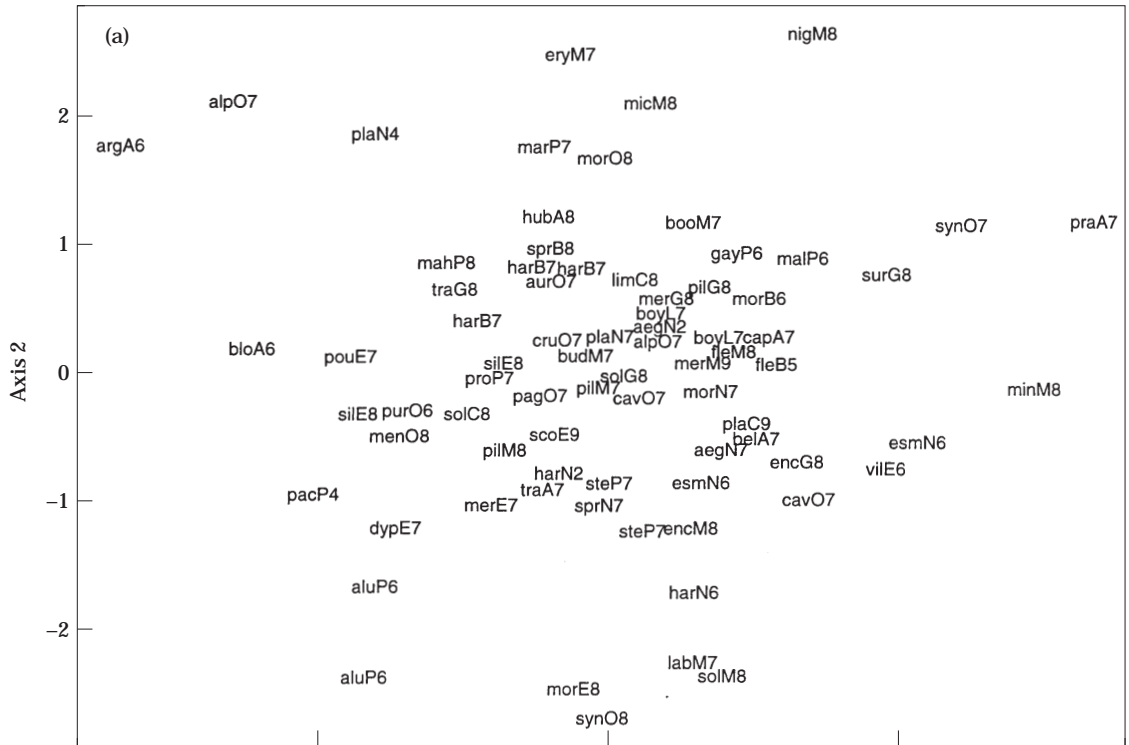


Figure 4.

did not differ significantly, set (i) was used in further computations.

A bias may arise in the results because cod populations used in the study are all under high fishing pressure. Because of the difficulty of finding data on weakly exploited stocks of cod, the influence of the species on final results was checked by comparing the results with and without cod. Autocorrelation and autoregression coefficients are similar; some correlation coefficients of the model and residual matrices become insignificant, but the ones discussed here are robust. The same kind of result is obtained when removing all Gadidae with a short time-to-5%-survival.

Comparing the results of considering Perciforms as polyphyletic or monophyletic shows that the results of the analysis are not sensitive to this uncertainty in the topology of the phylogenetic tree.

Discussion

Autoregressive method

The autoregression method proves able to remove most of phylogenetic autocorrelation. Whereas the partition into phylogenetic and population components was performed on each trait independently, there remains significant correlations in the population components matrix (Table 5). This argues for the ability of the model to separate components which reflect actual parts of the variability. Moreover, more correlation coefficients are significant in the phylogenetic and population components than in the original size-corrected traits: the method seems able to make visible patterns that were concealed in the original data.

I used Gittleman and Kot's method (1990) as suggested in their conclusion: I correlated the residual components of several traits together, and tested these correlations independently of confounding phylogenetic correlations. As these authors have pointed out, their method is appropriate only if there is sufficient genetic variation in the traits. Although life history traits have lower heritabilities than morphological or behavioural traits, their heritabilities are significantly greater than zero (Stearns, 1992). Moreover, there is plenty of genetic variation for life-history traits in natural populations. Therefore it seemed appropriate to apply the autoregression method at the population level, in order to

take into account intraspecific variation in interspecific comparisons.

Phylogenetic information and sampling

Phylogenetic information to be used in comparative studies should be as complete and accurate as possible (Harvey and Pagel, 1991). The phylogenetic autocorrelation method may result in type I errors when the topology of the phylogeny is known very incompletely (Purvis *et al.*, 1994). In the case of teleost fishes, the topology of the tree is well known, except the Perciform branch (Lecointre, 1994), but the results of our study are not sensitive to this uncertainty.

A good knowledge of branch lengths is also required but seldom available (Harvey and Pagel, 1991). Branch lengths elaborated on a common basis are unavailable for the sample of populations used here. But the phylogenetic autoregression method is not the most sensitive to incorrect branch lengths (Purvis *et al.*, 1994) because the parameter α introduces flexibility with regard to distances. The study is representative only of the mostly commercial stocks used in the sample and not of all teleost fishes. This is because sampling was constrained by the availability of data, and it was not possible to obtain a good sampling across phylogeny: many taxa are lacking and represented taxa are not given an equal weight.

Another sampling difficulty arises from the fact that different populations of one species are often exploited with a similar intensity; an extreme case is cod, which has only highly exploited populations. Ideally the study should involve together exploited and unexploited populations of each species, because the autocorrelation method will ascribe to phylogeny the common features of conspecifics. Nevertheless, the low α value estimated for time-to-5%-survival (2.4) indicates that distant populations still have some weight in predicting this trait: conspecifics are not the only populations taken into account in estimating time-to-5%-survival of a given population.

The population component

With regard to the population component, long-lived populations appear to have a small size at maturity at a late age, whereas high adult mortality is associated with

Figure 4. (a) Scaled principal component analysis of the population parts of five demographic traits: the first two principal components of populations. Coding of the populations: first three letters=species name (see Fig. 1); capital letter=location (A: South Atlantic. B: Baltic Sea. C: Channel and Celtic Sea. E: North East Atlantic. G: Bay of Biscay. I: Indian Ocean. M: Mediterranean. N: North Sea. O: West Atlantic. P: Pacific Ocean); number=decade of the XXth century (e.g. 6 means during the sixties). (b) Same figure with an expanding symbol proportional to the ratio of fishing mortality to natural mortality for each population (dots: no fishing mortality. Small circles: $0 < F/M \leq 1$. Intermediate circles: $1 < F/M \leq 2$. Large circles: $F/M > 2$).

Table 7. Changes in size at maturity in various exploited populations (length at which 50% of the individuals reach maturity).

Reference	Species	Location	Period	Sex	Size at maturity (cm) at beginning and end of period	Change in size at age
Pitt (1975)	American plaice	ICNAF Div. 3L	1961–1972	F	41.5–41.1	Increased
		ICNAF Div. 3N	1957–1971	M	25.5–26.0	Increased
de Veen (1976)	Sole	North Sea	1957–1973	F	43.7–42.8	Increased
				M	25.5–25.3	Increased
Bowering (1989)	Witch flounder	Newfoundland	1950–1986	F	27.5–30.0	Increased
Rijnsdorp (1989)	North Sea plaice	Dogger	1904–1986	F	46.0–43.0	Increased
				M	41.0–35.0	Increased
Beacham (1983)	Cod	Southern Bight	1959–1979	F	35.0–24.0	Increased
		Scotian Shelf		F	34.0–30.0	Increased
Hempel (1978)	Cod	North Sea	1920–1970	F	64.0–43.0	No change
				M	61.0–44.0	No change
Rowell (1993)	Cod	North Sea	1893–1974	F	75.0–60.0	No change
				M	65.0–50.0	No change
Clark and Tracey (1994)	Orange roughy	New Zealand	1984–1990	F	75.0–61.0	No change
				M	73.0–54.0	No change
				F	27.1–22.3	Not available
				M	25.7–24.5	Not available

early maturity at a large size. The shift of North Sea plaice in this trade-off when exploited or not, is an argument for an environmental component of the variability of these traits. Time-to-5%-survival is the most contributing variable to the structure of this environmental component; the exploitation level is associated with this structure (Fig. 4b). Both arguments indicate that fishing would be an important aspect of this environment. These short-term environmental effects are of larger magnitude than phylogenetic components, as evidenced by the proportion of total variance accounted for by phylogeny for age and size at maturity and time-to-5%-survival (Table 3). I interpret these short-term environmental effects as the expression of the phenotypic plasticity of growth and maturation in fishes. Phenotypic plasticity was defined by Schmaulhausen (1949) as the ability of a genotype to express various phenotypes across an environmental gradient. Although phenotypic plasticity of growth has been commonly observed, especially density-dependent growth (e.g. Beverton and Holt, 1957; Hubold, 1978; Ross and Almeida, 1986; Overholtz, 1989), in my results it appears mainly in the variations of size and age at maturity, because I worked relative to size by removing size effects.

These results show a good agreement with available experimental evidence. Alm (1959) reports that in some experiments with brook trout, size at maturity increases and age at maturity decreases as growth rate increases. Reznick (1993) showed by a series of experiments on guppies that increased resource availability (which may be *in natura* a consequence of fishing, which reduces population densities) causes an increase in the size at maturity and a decrease in the age at maturity. Another

experiment by Belk (1995) on bluegill sunfish shows that the variance in growth patterns and age and size at maturity observed between populations apparently resulted mostly from environmental differences, not from genetic variation; and that observed patterns of variation between populations are best explained by effects of differences in predator populations.

Many observations of maturity changes under fishing pressure in natural populations have been reported. Age at maturity has been observed to decrease under exploitation in Grand Bank American plaice (Pitt, 1975), in Scotian Shelf cod (Beacham, 1983), in halibut caught in Northern Norway (Haug and Tjemsland, 1986), in North-east Arctic cod (Jørgensen, 1990) and in North Sea plaice (Rijnsdorp, 1989). Trippel (1995) compiled data for 8 cod stocks and 4 haddock stocks of the North-west Atlantic, and 11 other fish populations: in all but one age at maturity of both males and females declined under exploitation, as much as 1 to 3 years or more. Age at maturity was much higher in the unexploited cod of Ogac Lake than in any of the neighbouring exploited stocks (Patriquin, 1967). Also age at maturity decreased as stock biomass decreased (indirect effect of fishing) in North Sea herring (Hubold, 1978), North Sea cod (Hempel, 1978) and Grand Bank cod (Xu *et al.*, 1993).

The negative association between longevity and size at maturity is more unexpected. This finding is in accordance with experimental evidence (Alm, 1959; Reznick, 1993) and with theoretical predictions (Stearns and Koella, 1986; Hutchings, 1993). However, most of the published studies based on field data conclude that length at maturity decreases or remains stable under fishing pressure (Table 7). Most of these changes are of

low magnitude. Still we have to explain this discrepancy. Comparing results on size at maturity is difficult for two reasons. (i) I corrected size at maturity by adult size, whereas other studies did not. Exploitation removes large individuals and hence reduces the mean size of fish in the population. As $L_{0.05}$ decreases, $\ln(L_m) - 0.93 \ln(L_{0.05})$ may increase if the variation in L_m is low. However, correction by size is necessary because otherwise size would act as a confounding variable, and in order to take into account, when comparing size at maturity, the concomitant changes in length at age and in the mean size of the population. Moreover, from a theoretical point of view, the dimensionless number L_m/L_∞ was considered useful in looking for life history generalization (Charnov and Berrigan, 1991). Beverton (1963) and Beverton (1992) used this number in comparative studies and concluded that it tends to be constant within taxa. I also find that adult size explains the most part of length at maturity (94%: Table 1), but I seek to interpret the remaining variation. (ii) The second difficulty arises from the fact that most of published studies of Table 7 consider relatively long series (20 years or more): in these observations long-term effects of fishing may be entangled with short-term plasticity we are dealing with. For age at maturity long-term and short-term effects act in the same direction, but this is not the case for length at maturity (Table 6; Reznick, 1993). This is an advantage of large comparative studies such as ours, which allow one to disentangle long-term and short-term effects.

Another interesting observation, although not directly related to fishing effect, is the positive correlation between the slope of the fecundity-length relationship and $L_{0.05}$: populations with a larger size have a higher fecundity-length slope than populations with a smaller size (Tables 5 and 6). This pattern is not apparent on Figure 3 but on the fourth axis of the PCA (not shown). The slope of the fecundity-length relationship is also positively associated with size at maturity (Fig. 3). These patterns may be interpreted in terms of phenotypic trade-offs. In fish the widespread trade-off between current and future reproduction (Stearns, 1992) appears in the strong negative correlation between the parameters a and b of the fecundity-length relationship $F = aL^b$ (from my data set: $r(a,b) = -0.85$, and -0.88 when corrected for size effects): the lower fecundity is at maturity, the steeper it can increase later. After maturity the surplus power, i.e. the fraction of ingested energy remaining after an individual has paid metabolic costs, is to be shared between growth and reproduction (Ware, 1984). We may hypothesize that if fecundity is high at maturity, a lower part of the surplus power remains for growth, and that consequently fish reach a smaller size. This phenotypic trade-off would be consistent with the one observed by Jennings and Beverton (1991) in a comparative study of life history traits of nine stocks of

Atlantic herring: a low annual reproductive output is associated with late maturity and slow post-maturational growth towards a large maximum size (and vice versa).

Theoretical aspects and mechanisms of the plasticity of size and age at maturity

Several theoretical models have been developed to predict the reaction-norm of size and age at maturity in fishes, with different assumptions on the constraints that will act on the reaction-norm (Stearns and Crandall, 1984; Stearns and Koella, 1986; Perrin and Rubin, 1990; Roff, 1992). These models may not be suitable for exploited populations, because they assume a stable age distribution (Stearns and Crandall, 1984). Some of these models predict dome-shaped norms of reaction for size-to-age at maturity in fishes, which fit Alm's (1959) observations. Stearns and Crandall (1984) show that other shapes of these norms of reaction are plausible under different assumptions. The difficulty in interpreting these conclusions is that a high adult mortality is usually not taken into account as a constraint that may act directly or indirectly on this reaction-norm. Hutchings (1993) constructed reaction-norms by determining how optimal age and size at first reproduction varied with growth rate in two unexploited brook trout populations. Harvesting might result in decreased juvenile density and in increased growth rate; optimal size at maturity increases with growth rate in one population and varies little in the other population, whereas optimal age at maturity declines as growth rate increases in both cases. Moreover, size selective mortality might change the slope of the reaction norm.

How adult mortality due to fishing may act on growth and maturation processes is not clear. The main hypothesis is that fishing decreases the population's density, that growth would be density-dependent, and that the norm of reaction for size-to-age at maturity would be constrained by growth. Evidence of density-dependent growth is abundant in various populations of distantly related taxa (e.g. Beverton and Holt, 1957; Hubold, 1978; Ross and Almeida, 1986; Overholtz, 1989). Growth-dependent plasticity of size and age at maturity was also demonstrated by experimental evidence (Alm, 1959; Reznick, 1993; Belk, 1995) and by field data on lake whitefish (Jensen, 1981). However, other mechanisms may act, for example Rijnsdorp *et al.* (1991), in an extensive study of the variations of growth, maturation and fecundity in several North Sea stocks, suggested that the observed compensation in total egg production may be due to effects of reproductive variability related to the age composition of the spawning population, rather than to density-dependent effects.

Other possible phenotypic effects of high adult mortality may be mediated by maternal effects, defined by

Bernardo (1996) as direct effects of a parent's phenotype on the phenotype of its offspring. Maternal effects appear as a kind of cross-generation phenotypic plasticity, and may affect many demographic traits, including offspring growth and recruitment. Maternal effects are largely documented in mammals, birds, salamanders, lizards, and plants (Bernardo, 1996). Reznick *et al.* (1996) demonstrated experimentally that food availability to mother Poeciliid fishes affects the size of young. Chambers and Leggett (1996) use comparative methods to show that egg size is likely to be significantly modulated by the maternal environment during oogenesis in marine teleost populations; differences in egg size may be propagated through growth into variation in sizes of larvae, juveniles and even adult fishes. Investigating the timing of short-term fishing effects would allow to assess the importance of maternal effects in the observed phenotypic plasticity.

Phylogeny of phenotypic plasticity

This paper concentrates on the population component of teleost life history traits, and investigates fishing effects on life history tactics. The complementary component of these traits, namely the phylogenetic component, is worth investigating in detail. This would give more basic insights into teleost demographic strategies, which are the range of flexible tactics a species may deploy, depending on the environment (Wootton, 1984). This would allow a re-examination of the conclusions of pioneering works about this subject by Beverton and Holt (1959), Beverton (1963), Adams (1980) and Roff (1984), who did not address the problem of separating long-term evolved effects from environmental effects.

This study is based on the hypothesis that the phenotypic part of the answer to fishing would be the same in all taxa of teleost fishes: this phenotypic answer is indeed the residual variation of traits, once the resemblance of phylogenetically close populations has been removed. Hence this work will only reveal the general features of this plasticity throughout our sample of teleost fishes. But it seems plausible that different taxa would have evolved different plasticity patterns in response to a given stress. Table 7 suggests that average size at age increases under fishing pressure in Pleuronectiformes, but remains unchanged in cod. Also Rijnsdorp *et al.* (1991) show that compensation for fishing by enhanced reproductive output appears in three North Sea stocks by three different mechanisms (earlier maturation in plaice, enhanced growth in sole and increased fecundity in cod). Their study has the disadvantage of long-term and short-term effects being entangled (30 years series analysed), and this is a common feature to most studies of fishing effects. There is a need for investigating the differences in short-term responses to fishing in different teleost taxa.

Another criticism that may be addressed to this study is that life-history traits are co-evolved: there are linkages between traits, that constrain the simultaneous evolution of two or more traits (Stearns, 1992). Here we investigate phylogenetic autocorrelation trait by trait, and hence leave co-evolution out of account. This is a general gap in comparative methods, most of which consider the variations of no more than two traits (Harvey and Pagel, 1991); for example, Gittleman (1986) and Read and Harvey (1989) successively investigated the covariations of many pairs of life history traits. A multivariate method that would test for differences in the relationships between several traits, independently of phylogenetic correlation, would be an important advance in this field.

The effects of fishing and fisheries management

Fishing has three types of effects on fish population dynamics: direct effects on population density and on the mean size of individuals; short-term environmental effects on growth and reproduction, mediated by phenotypic plasticity and density-dependent mechanisms; and long-term effects due to the selective pressure imposed by harvesting. Whereas the problems raised by the first type of effects are commonly addressed by fisheries assessment models and management policies, the other two types of effects are seldom considered.

This is partly because these effects are difficult to separate, and may be contradictory. In the phylogenetic component of our traits, short life is associated with a small size and an early age at maturity; this result is in agreement with Reznick (1993) who showed experimentally that, in the longer term, increased adult mortality selects for earlier maturity at a smaller size. Hence we support the conclusion of this author, that compensatory responses of populations to fishing may conceal longer-term selection effects.

Moreover, Nelson (1993) emphasizes that the evolutionary response to selection and its detection depend upon the joint reaction norms of growth and reproduction to changes in density and environmental factors; only when these joint reaction norms have been identified can their evolutionary change be detected. This work is a first step towards this aim: in a rather large sample of teleosts, we document evidence that fishing imposes a phenotypic response in growth and reproduction. It would be worth investigating the shape and genetic variation in the reaction norm. Its influence on exploited population dynamics should be checked: the empirical works of Beverton and Holt (1957) and Overholtz *et al.* (1991) may be given a more basic support in order to develop general models, suitable to various populations.

On the other hand, fishing applies a selective pressure that may shift the long-term selective advantage from a

reproductive pattern to another (Ware, 1984). Further work should use our first results on short-term effects to investigate these changes.

Summary

This work demonstrates a general trend of the short-term effects of fishing on demographic traits in a large sample of teleost fishes: populations develop compensatory responses to fishing by decreasing their age at maturity and increasing their size at maturity. These effects are of large magnitude and may conceal longer-term selection effects.

These effects should be better analysed and quantified and, if necessary, taken into account in stock assessment and management.

A first consequence of this result is the recommendation that maturity ogives used in stock assessment and projections should be regularly updated.

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Appendix A: Sensitivity analysis of total mortality to errors in natural mortality in VPA

The linear sensitivity coefficient of total mortality at age a Z_a to natural mortality at age i M_i , F_a being fishing mortality at age a , is defined as:

$$S\left(\frac{Z_a}{M_i}\right) = \frac{\partial Z_a}{\partial M_i} \frac{M_i}{Z_a} = \frac{\partial Z_a}{\partial M_i} \frac{M_i}{Z_a} = \left(\frac{\partial F_a}{\partial M_i} + \frac{\partial M_a}{\partial M_i} \right) \frac{M_i}{Z_a}$$

(Pelletier, 1990)

Which means that, the higher the fishing mortality, the lower the ratio M/Z and hence the sensitivity.

$$\text{If } i < a, \quad \frac{\partial Z_a}{\partial M_i} = \frac{\partial F_a}{\partial M_i} = 0$$

$$\text{If } i = a, \quad \frac{\partial Z_a}{\partial M_a} = \frac{Z_a(1 - e^{-Z_a})}{M_a(1 - e^{-Z_a}) + Z_a(Z_a - M_a)}$$

$$\text{If } i > a \quad \frac{\partial Z_a}{\partial M_i} = - \frac{1}{1 - \left(\frac{1}{F_a} - \frac{1}{Z_a} + \frac{1}{1 - e^{-Z_a}} \right)} \frac{\partial \ln(N_a)}{\partial M_i},$$

$$\text{with } \frac{\partial \ln(N_a)}{\partial M_i} = \left(1 - \frac{1}{\frac{1}{F_a} - \frac{1}{Z_a} + \frac{1}{1 - e^{-Z_a}}} \right) \frac{\partial \ln(N_{a+1})}{\partial M_i}$$

On can easily show that $\frac{\partial Z_a}{\partial M_{a+j}} < \frac{\partial Z_{a+j}}{\partial M_{a+j}}$ for $j = 1, 2, 3 \dots$

Which means that total mortality at age a is most sensitive to natural mortality at age a , relative to natural mortality at other ages.

An example of $S(Z_a/M_a)$ for haddock in division VIa (West of Scotland), 1983–1992 (data from ICES, 1993) is provided in Table 8.

Appendix B: References of the data

Clupeiformes

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Bay of Biscay *Engraulis encrasicolus* encG8

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Table 8. Sensitivity of total mortality at age *a* to natural mortality at age *a* for West Scotland haddock.

Age	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	Mean
0	0.973	0.982	0.986	0.944	0.721	0.343	0.829	0.973	0.726	0.725	0.82025
1	0.251	0.31	0.251	0.473	0.227	0.17	0.274	0.186	0.154	0.305	0.26006
2	0.201	0.218	0.219	0.271	0.153	0.184	0.181	0.082	0.118	0.221	0.1847
3	0.288	0.123	0.192	0.177	0.137	0.134	0.159	0.125	0.11	0.15	0.13952
4	0.226	0.125	0.136	0.234	0.13	0.136	0.124	0.123	0.071	0.143	0.14485
5	0.242	0.165	0.172	0.274	0.118	0.114	0.109	0.143	0.075	0.105	0.15174
6	0.197	0.153	0.124	0.322	0.073	0.22	0.068	0.252	0.092	0.107	0.16084
7	0.161	0.123	0.156	0.224	0.089	0.14	0.103	0.151	0.087	0.147	0.13807
8	0.225	0.186	0.22	0.286	0.15	0.204	0.165	0.214	0.148	0.211	0.2009

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Gulf of Lions *Engraulis encrasicolus* encM8

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