

A comparative approach to life-history strategies and tactics among four orders of teleost fish

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Whereas a life-history strategy is defined as a complex pattern of co-evolved life-history traits designed for a particular environment, a tactic is the plasticity of these traits that allows populations to cope with environmental variability. Strategies and tactics are sought by comparing traits from a large number of populations of different species. An autoregressive method allows partitioning the variability of demographic traits into two parts: a phylogenetic part (broad strategies inherited from the past) and a population part (the remaining variability, including tactics). The following traits are analysed: adult size as a scaling parameter because life-history traits are known to change with body size; survival, which accounts for fishing and natural mortality; age and size at maturity, and total reproductive output for an individual life-time. Data have been assembled for 67 stocks of four orders: Clupeiformes, Gadiformes, Perciformes, and Pleuronectiformes. It is concluded that these four orders have different life-history strategies, and that tactics are different among strategies. At low abundance, the compensations allowed by these tactics are much less efficient in Clupeiformes than in the other orders considered.

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Introduction

Fish encounter a variable and unpredictable environment during their larval life. Each year adults produce a large number of offspring whose survival is variable. The strategy of spreading a maximum number of offspring to cope with environmental variability would yield highly variable recruitment, unless density-dependence occurs during the early life stages (Beyer, 1989). Stock-recruitment theory has been based on this strong assumption (Ricker, 1954; Beverton and Holt, 1957), and subsequent developments have focused on density-dependent regulation during the period between hatching and recruitment (e.g. Cushing and Harris, 1973; Jones, 1973; Cushing, 1977; Lorda and Clecco, 1987; Beyer, 1989; Fogarty *et al.*, 1991).

However, if regulation processes take place only during early life stages, over-reproduction will occur: there will be a large reproductive effort spent in excess of the required amount (Ware, 1982). The energy spent in over-reproduction may be better used for further growth, that would result in higher future reproduction

and survival. Hence it seems reasonable to assume that regulation processes may act also during the adult stage to stabilize recruitment. This was first evidenced by Bagenal (1973), who reported that fluctuations in recruitment are partially damped by annual variations in size-specific fecundity, related to changes in stock size. Rochet (1998) showed that, as a general rule, teleost fish compensate for the high adult mortality due to fishing by decreasing their age at maturity.

But fish exhibit a wide diversity of life-history strategies (Roff, 1992). Life-history strategies are complex patterns of life-history traits, and refer to the coordinated evolution of these traits together (Stearns, 1992). In a fluctuating environment, fish have to adjust details of their strategy for that strategy to be successful. Hence Wootton (1984) defined reproductive tactics as “those variations in the typical pattern which fish make in response to fluctuations in the environment”. Tactics are permitted by phenotypic plasticity, the ability of a genotype to vary in response to the environment, which is the focus of increasing concern (Stearns, 1989). A strategy may be viewed as an assembly of rules which

specifies how an organism should respond to its own state and its environment (McNamara and Houston, 1996). These rules, which include regulation and compensation processes, we name tactics.

There is no reason to believe that the tactics are the same in species that differ in their life-history strategies (Rijnsdorp *et al.*, 1991; Frank and Leggett, 1994). This study focuses on demographic strategies of fish, and on the different tactics that they might involve. Because fishing mortality is a major factor for many species, an important aspect of these tactics that can be evidenced is the compensation for high adult mortality. Because we are able to measure variations in reproduction more easily than in natural mortality, compensation in reproduction is the most accessible. The compensation in egg production for high adult mortality is the main component of tactics examined here.

Life-history strategies as well as tactics can be described as sets of trade-offs, the linkages between traits that constrain their simultaneous evolution (Stearns, 1992). Classically, trade-offs are measured by the correlation between two traits (Stearns, 1992), but they may involve more than two characters, and these must all be considered when examining the trade-off (Pease and Bull, 1988; Southwood, 1988; Endler, 1995). Here strategies and tactics are sought as multivariate trade-offs.

The comparative approach is used to reveal patterns in spite of measurement errors and environmental fluctuations, which inevitably obscure single stock studies, either for explanatory studies of the variability of demographic traits (Murphy, 1977; Hempel, 1978; Rijnsdorp, 1993; Powell, 1994) or for the study of stock-recruitment relationships (Walters and Ludwig, 1981; Goodyear and Christensen, 1984; Walters and Collie, 1988). The purpose of this study is to examine life-history strategies and tactics in four commercially important orders of teleosts by a comparative analysis of demographic traits. The comparison of populations belonging to different species allows the analysis of trait variability both within and between species. An autoregressive method is used to decompose the variations of traits into a phylogenetic effect (strategy) and a population component (variability of traits within strategies: tactics). These components of various traits (age and size at maturity, adult size, life span, fecundity) are combined together in multivariate analyses. A first multivariate analysis of the phylogenetic components of the traits allows definition of broad strategies. Then a series of multivariate analyses of the population components of the traits describes tactics within each strategy.

Materials

Demographic traits

The main constraint upon trait selection is the need for reliable estimates of the variables, otherwise the

conclusions of the comparative analysis may be spurious (Gaillard *et al.*, 1994). I concentrated on female traits and included the following (for further details on trait selection and estimation, refer to Rochet, 1998).

- Time-to-5%-survival ($T_{0.05}$) is the time elapsed from sexual maturity until 95% of a cohort is dead. This index of survival integrates mortality rates over most adult life (Gunderson and Dygert, 1988). Time-to-5%-survival is estimated from an exponential mortality model, on the basis of total mortality coefficients $Z=F+M$ estimated by Virtual Population Analysis or catch curves. Total mortality estimates are usually more reliable than F and M estimates, because errors on M are compensated for by errors on the estimated fishing mortality F .
- 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 fish.
- Age and length at which 50% of the individuals reach sexual maturity (A_m and L_m) are commonly available in the literature.
- Slope of the fecundity-length relationship (F_b): fecundity, defined as the number of eggs present in the ovaries immediately before spawning, is known to increase with the size of fish within species (Fulton, 1891). This increase is properly described by a power-law $F=aL^b$ (Raitt, 1932). The exponent of this relationship b (or slope of the log-log fecundity-length regression) accounts for the increase in fecundity with size, and hence for the increase in reproductive investment during adult life.
- Total reproductive output (TRO), or life-time fecundity, is estimated as the sum over time-to-5%-survival of annual fecundity, as used by Jennings and Beverton (1991). Annual fecundity is estimated from length-at-age and fecundity-length relationship, and from the mean number of spawning bouts per year in the case of batch-spawners. This compound variable describes the individual contribution to egg production.

The data were collated from published papers and working group reports (listed in Rochet, 1998). As one purpose of the study is to describe environmental influences on life-history trait variations, contemporaneous estimates of all traits for a given stock were sought. Life-history data on 67 populations from 40 teleost species were compiled. The data are available from the author.

Phylogenetic information

Phylogenetic relationships (Fig. 1) were constructed based on the most recent information available for

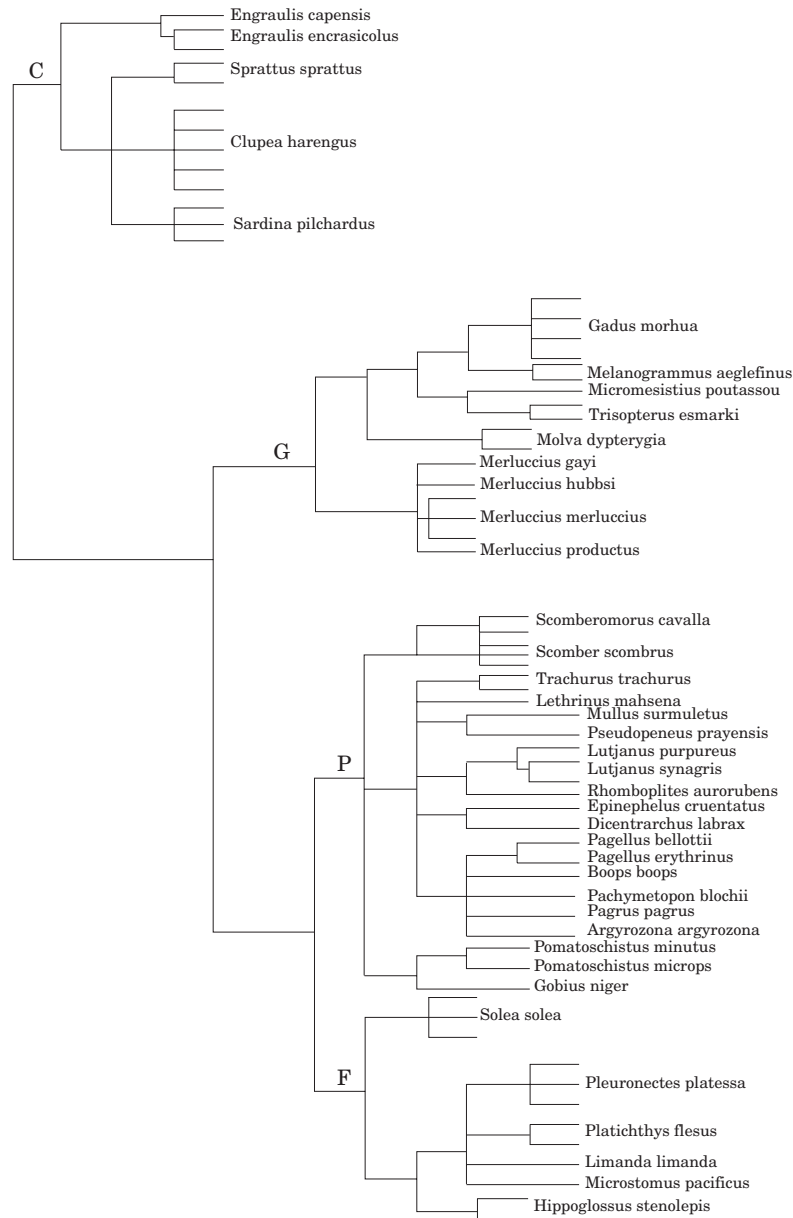


Figure 1. Phylogenetic tree of the sample of teleost species analysed. The position of taxa along the vertical axis has no phylogenetic meaning. C: Clupeiformes; G: Gadiformes; P: Perciformes; Pl: Pleuronectiformes.

teleost species (Eschmeyer, 1990; Lecointre, 1994; Nelson, 1994; Johnson and Patterson, 1996). The phylogenetic tree used is based mainly on morpho-anatomical characters and on molecular traits. Consistent estimates of branch lengths are not available because data came from different studies using different methods, and data are lacking for many branches. Moreover, evolution rates are known to vary among traits (Brower *et al.*, 1996), and for a given trait, between branches of a phylogenetic tree (Mindell and Thacker, 1996) and

along them (Svensson, 1997). The use of either fossil data for dating higher nodes or of molecular data to construct distances between taxa relies on the hypothesis that all traits evolve at the same rate along all branches. For these reasons we considered only the topology of the phylogenetic tree. 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 . . .). It has been shown elsewhere by testing different branch length assignments that the results are not sensitive to branch lengths (Rochet, 1998).

Methods

Decomposition of trait variability

Life-history traits are analysed here under the hypothesis that they are mainly determined by (i) body size, (ii) long-term evolutionary constraints, and (iii) short-term environmental influences. The methods used are an attempt to decompose trait variability between these three sources. Body size is a major constraint upon energy assimilation and metabolic rates, and hence upon the entire life of animals, including growth, reproduction, and survival (Calder, 1985; Reiss, 1989). Size effects are usually described by the allometric relationship $Y = \alpha L^{\beta}$. On the other hand, evolutionary constraints must somehow be reflected in the kinship bonds between populations or species that are described by the phylogenetic tree. It is assumed here that evolutionary constraints can be detected by tracking the resemblance between species that are phylogenetically related. Environmental influence is assumed to act on residual variability, the part of the variability which is not explained by size or by phylogeny.

Many comparative methods have been developed in the framework of evolutionary ecology, because species are not statistically independent, but share a common history through their phylogeny (e.g. Harvey and Pagel, 1991; Stearns, 1992). Some of these methods allow separation of phylogenetic effects from population effects; for example, quantitative genetics methods (Lynch, 1991) and the autoregressive method (Cheverud *et al.*, 1985; Gittleman and Kot, 1990). The latter allows partition of the phenotypic value of a trait into an autoregressive phylogenetic component (reflecting common evolution) and a residual population component (environment-dependent). The method is based on phylogenetic distance (in a phylogenetic tree) and autoregressive models, which describe effects that vary with distance.

The slope β of the log-transformed allometric equation was first estimated by least-squares regression for each trait (except the parameter b of the fecundity-length relationship, which is already scaled for length), with length-at-5%-survival as the scaling variable (Table 1). The estimated values were then used for removing the part of variation of each trait related to body size: subsequent analyses were performed on log-transformed, size-corrected traits (i.e. on $\log(A_m) - 0.69 \log(L_{0.05})$; $\log(L_m) - 0.94 \log(L_{0.05})$; $\log(L_{0.05})$; F_b ; $\log(T_{0.05}) - 0.58 \log(L_{0.05})$; $\log(\text{TRO}) - 1.93 \log(L_{0.05})$).

Table 1. Relationships between the logarithm of demographic trait and the logarithm of length-at-5%-survival ($L_{0.05}$) in 67 populations of fishes: correlation coefficients (r) and allometric slopes (β) \pm standard error.

Demographic trait	r	β
Age at maturity (A_m)	0.77	0.69 ± 0.07
Length at maturity (L_m)	0.97	0.94 ± 0.03
Time-to-5%-survival ($T_{0.05}$)	0.61	0.58 ± 0.09
Total reproductive output (TRO)	0.70	1.93 ± 0.24

Then trait variability was further decomposed by means of an autoregressive model: the phylogenetic component of a population i was estimated as a weighted mean of the observations y_j , for $j \neq i$

$$y_i = \sum_j \rho W_{ij} y_j + \varepsilon_i$$

where y_i are the observed trait values, ρ is an autocorrelation coefficient, W a weighting (neighbouring) matrix, and ε_i are the residuals. 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 which accounts for the levels at which phylogenetic constraint has occurred. Large α values describe reduced influence of distant populations on the estimated trait – consequently higher influence of close neighbours. A maximum-likelihood procedure was used to estimate the parameters ρ and α of the autoregressive model. The proportion of total variance accounted for by phylogeny is estimated by R^2 .

Strategies and tactics

The above fits were performed for each trait separately. Strategies and tactics, as complex combinations of traits, were sought by a multivariate approach. The phylogenetic components of the traits obtained from the autoregressive model were analysed by Principal Component Analysis (PCA; Lebart *et al.*, 1984) to quantify their covariations and show broad strategies. As TRO is estimated from the other traits, this parameter was not included in the PCA.

The patterns of variability within these strategies were then examined by the analysis of the population components of the traits (residuals of the autoregressive model). The difference in trade-offs between the population components within each strategy was tested by analyses of covariance: if the tactics differ among strategies, the covariance between traits should differ between groups of similar strategies. Analyses of covariance were performed on each pair of traits. The

Table 2. Autoregressive model: maximum likelihood estimates of the model's parameters α (distance exponent) and ρ (auto-correlation 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	$T_{0.05}$	TRO
α	2	1.2	4.3	0.6	2.1	1.7
ρ	0.97	0.87	0.98	0.97	0.91	0.97
R^2	0.09	0.04	0.78	0.01	0.14	0.03

tactics were then examined in each group by analysing the correlation matrices of the population components of the traits.

Results

Autoregressive models were fit to partition each demographic trait into a phylogenetic and a population component (Table 2). The variance accounted for by phylogeny is variable, ranging from less than 5% in length at maturity and fecundity traits to more than 70% for length-at-5%-survival. The fit was performed for all traits, regardless of the proportion of variance explained by phylogeny, in order for all traits to receive the same treatment. α estimates vary from 0.6 to 4.3, reflecting the levels at which most phylogenetic influence occurs.

Size-corrected demographic traits and their phylogenetic and population parts show different patterns of correlation. Spearman's rank correlations were estimated because the distribution of the components is unknown (Table 3). Many more correlation coefficients are significant in the phylogenetic components matrix than in the size-corrected traits matrix (seven significant correlation coefficients in phylogenetic components, three in unpartitioned traits). Moreover, two of these correlation coefficients have opposite signs in the phylogenetic and population components ($r(L_m, T_{0.05})$ and $r(F_b, L_{0.05})$).

Principal component analysis of the phylogenetic part of the traits exhibits the positive correlations of age at maturity with size at maturity, time-to-5%-survival, and the slope of the fecundity-length relationship, all of which are negatively correlated with adult size (1st axis); and the negative correlation between length at maturity and F_b (2nd axis; Fig. 2A). On the plot of the populations' first two components (Fig. 2B), populations are perfectly sorted by order. Clupeiformes have a small size and a long lifetime relative to that size, and a late maturity at a large size relative to adult size. To sum up, relative to other fish they first grow then reproduce. On the other extreme of the gradient, Gadiformes have a large size and a short lifespan relative to their size, and they mature early at a small size. Their fecundity increases less steeply with size. In this order, reproduction starts well before the end of growth. Perciformes have the same kind of strategy, with a smaller size at maturity relative to adult size. Pleuronectiformes have intermediate strategies between these extremes.

Table 3. Spearman's rank correlation matrices of (a) size-corrected demographic traits; (b) their phylogenetic components; and (c) their population components. Only significant correlation coefficients at the 0.05 level are shown.

	A_m	L_m	$L_{0.05}$	F_b	$T_{0.05}$
(a) Demographic traits					
L_m		1			
$L_{0.05}$			1		
F_b				1	
$T_{0.05}$	0.49	-0.26			1
TRO	-0.25				
(b) Phylogenetic components					
L_m	0.35	1			
$L_{0.05}$			1		
F_b			-0.48	1	
$T_{0.05}$	0.56	0.26	-0.36	0.33	1
TRO	-0.35				
(c) Population components					
L_m		1			
$L_{0.05}$			1		
F_b			0.29	1	
$T_{0.05}$	0.41	-0.32			1
TRO					

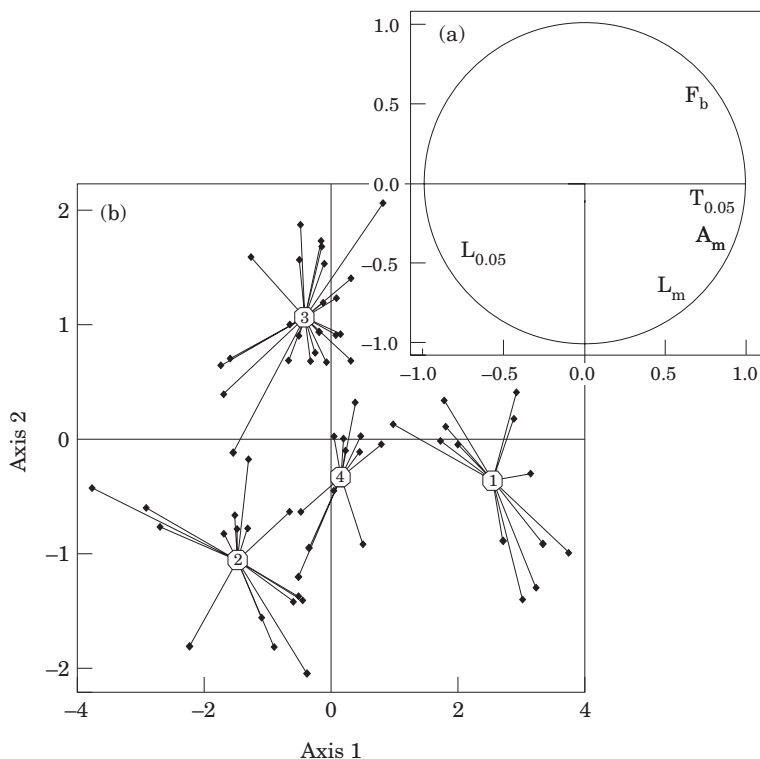


Figure 2. Scaled principal component analysis of the phylogenetic parts of five life-history traits. (a) Plot of the original variables on the first two principal axes. The first two axes account for 49% and 21%, respectively, of total variance. Loadings of the variables on the first axis: $T_{0.05}$ (time-to-5%-survival): 0.536; A_m (age of maturity): 0.497; F_b (exponent of the fecundity-length relationship): 0.428; $L_{0.05}$ (length-at-5%-survival): -0.420; L_m (length at maturity): 0.324. On the second axis: L_m : -0.657; F_b : 0.523; $L_{0.05}$: -0.413; A_m : -0.354. (b) The first two principal components of populations. Each population is connected to the mean value of its order. 1: Clupeiformes; 2: Gadiformes; 3: Perciformes; 4: Pleuronectiformes.

There remain correlations between the population parts of the traits (Table 3), which might be interpreted as phenotypic trade-offs between the traits. As the four orders considered are characterized by different strategies, analyses of covariances of pairs of traits were performed to test whether these trade-offs differ between orders. Among the 10 possible pairs, three are significantly different among the orders at the 0.1 level, and they involve all of the five traits of the analysis (Table 4): it is concluded that the covariances between the population components of traits differ between orders. Hence these components were examined by order. The correlation patterns of the population components differ among orders, as shown by correlation matrices (Table 5): life-history tactics differ among strategies. Their largest components all involve $T_{0.05}$, probably because fishing is the most contrasting variable among environments. $T_{0.05}$ is negatively correlated with F_b in Clupeiformes, positively with A_m in Perciformes, and negatively with L_m in Pleuronectiformes.

Discussion

Life-history strategies

There is a negative link between adult size, on the one hand, and lifespan and age at maturity, on the other

Table 4. Analyses of covariance of pairs of the population components of traits. F statistic (7, 59 degrees of freedom; top) and p-value (bottom) for the model: $Y = \mu_0 + \mu_i + \beta_i X$, i indexing for orders.

Y/X	$T_{0.05}$	A_m	L_m	$L_{0.05}$
A_m	2.39 0.03			
L_m	2.79 0.01	1.40 0.23		
$L_{0.05}$	0.42 0.89	0.42 0.89	0.25 0.97	
F_b	0.71 0.66	0.47 0.86	0.64 0.72	2.03 0.07

Table 5. Correlation matrices of the population components of life-history traits in three orders of teleosts. Only significant correlation coefficients at the 0.05 level (one-tailed test) are shown. No correlation coefficient was significant in Gadiformes ($n=17$).

	A_m	L_m	$L_{0.05}$	F_b	$T_{0.05}$
Clupeiformes ($n=13$)					
L_m		1			
$L_{0.05}$			1		
F_b				1	
$T_{0.05}$				-0.47	1
TRO					0.47
Perciformes ($n=25$)					
L_m		1			
$L_{0.05}$			1		
F_b			0.49	1	
$T_{0.05}$	0.60	-0.43			1
TRO	-0.39	0.42			
Pleuronectiformes ($n=12$)					
L_m		1			
$L_{0.05}$	0.57		1		
F_b				1	
$T_{0.05}$		-0.75			1
TRO					

(Fig. 2). This pattern may be interpreted as follows: reaching a large size may be costly in terms of survival; a longer growth phase and increased mortality would require earlier maturity, well before the end of growth, in order for sufficient offspring to be produced. The contrast between Clupeiformes, on the one hand, and Gadiformes and Perciformes, on the other, illustrates this trade-off and is in agreement with previous descriptions of life-history strategies in Clupeiformes (Blaxter and Hunter, 1982) and Gadiformes (Hislop, 1984). It is also in accordance with the large comparative study of life-history traits among North American fishes by Winnemiller and Rose (1992), who concluded that a positive link exists between longevity and age at maturity; in marine fishes they found a gradient from rapid maturation at small sizes in some Clupeiformes to a large clutch, episodic spawning strategy in a phylogenetically diverse mixture of fishes. However, this finding is not in accordance with the results of Adams (1980), who predicted from the r-K selection theory that adult size, maximum age, and age at maturity should all be positively correlated. The observed patterns fit the prediction in the five groups of teleosts examined by Adams. This may be due to the confounding effect of body size. The r and K-selection hypothesis ignored size effects, as well as the fluctuations in mortality and fecundity schedules (Stearns, 1976), and important assumptions such as the age structure of most population processes (Stearns, 1992).

Size at maturity is negatively correlated with the slope of the fecundity-length relationship. This pattern is less strong and involves traits with a lesser part explained by

phylogeny. However, the pattern is in accordance with previous studies. A comparative study of spawning between various herring and cod populations concluded that steep slopes of fecundity are linked with reduced growth rate after maturation (Schopka and Hempel, 1973). Wootton (1979), too, concluded that short-lived species tend to have lower values of b than longer-lived species from a set of 124 observations on 62 species. We hypothesize that the more growth takes place after maturity, the less energy is available for reproduction, resulting in a slower increase of fecundity with size.

A common criticism of correlation studies is that phenotypic covariance between two traits is not free of environmental effects: the differences in the amplitude and shape of reaction norms of each trait may cause spurious phenotypic correlations (Pease and Bull, 1988; Stearns, 1992; Frank and Leggett, 1994). The decomposition of traits into phylogenetic and population components used here is an attempt to address this problem. Phylogenetic autoregression is purely empirical and extracts the similarities between neighbours from the traits, without any assumption on the way these similarities arose (Gittleman and Luh, 1992). On the one hand, we lack evolutionary models and knowledge to make these assumptions properly, hence a purely statistical approach seems reasonable. On the other hand, we cannot exclude that part of the plasticity of the traits is similar between neighbours and will be assigned to the phylogenetic component of the trait. This is especially true when the environments of the populations considered do not contrast much. For this reason, the study ideally should involve exploited and unexploited

populations of each species, because the autocorrelation method will ascribe to phylogeny the common features of conspecifics. But appropriate data are scarce because of the need for reliable estimates of many traits from the same period. The present sample size is barely sufficient and the results would probably be reinforced by increased sampling. Moreover, the study is representative only of the stocks used in the sample and not of all species of the four orders examined. This is because it was not possible to obtain a good sampling across phylogeny: many taxa are lacking and the represented taxa are not given equal weight.

Life-history tactics

In Clupeiformes, the observed pattern might be interpreted as follows: increased adult mortality may induce a steeper increase of fecundity with size, but this increase in fecundity is not sufficient to compensate for reduced lifespan. Therefore, increased adult mortality results in decreased lifetime fecundity. This scenario is in agreement with much published evidence from single populations, where egg production is density-dependent, as in Gulf of Maine herring (Kelly and Stevenson, 1985), South African *Sardinops ocellatus* (Armstrong *et al.*, 1989), and Japanese *Sardinops sagax* (Kawasaki and Omori, 1995). But in many cases increased fecundity compensates only partially for the reduction in stock caused by fishing: e.g. North Sea Downs herring (Bridge, 1961), various populations of herring (Schopka and Hempel, 1973; Ware, 1985), northern anchovy off California (Fiedler *et al.*, 1986), and Atlantic menhaden (*Brevoortia tyrannus*) (Powell, 1994).

Compensation seems to act mainly on fecundity in Clupeiformes. Density-dependent growth is frequent in herring populations (e.g. Anthony, 1971; Iles, 1971; Hubold, 1978; Toresen, 1990); changes in growth are often associated with changes in age at maturity (e.g. Bridge, 1961; Murphy, 1977; Hubold, 1978). In other Clupeoids, these density-dependent responses in growth and maturity are less clear (Murphy, 1977), although Armstrong *et al.* (1989) report a decrease in length at maturity in exploited South African pilchard. This kind of response may occur in some species but not in all Clupeiformes.

In Gadiformes, this study does not reveal any trend in the population component of life-history traits. This may be due to the weak contrasts of the main environmental variables acting on the populations of the sample. Of 17 Gadiformes populations, 14 are from temperate climates and 10 are heavily exploited (with fishing mortality greater than twice the natural mortality) and none is unexploited. As no positive link appears between total reproductive output and adult lifespan, we may argue that Gadiformes compensate for increased mortality, but this study does not tell us by

which mechanisms. From numerous field observations we know that age at maturity decreases as stock biomass decreases in cod and haddock (Hempel, 1978; Xu *et al.*, 1993; Trippel, 1995). This pattern would probably appear in this study if more unexploited or weakly exploited stocks were included. On the other hand, Rijnsdorp *et al.* (1991) report that in North Sea cod 1963–1989, reproductive output was significantly enhanced in compensation for losses due to exploitation, entirely due to increased fecundity. Increased fecundity at all ages should theoretically result from increased mortality (Gadgil and Bossert, 1970). This would translate to an increase of the constant a of the fecundity–length relationship. This parameter was not included in the study because it is statistically correlated with the slope b . However, it increases with increasing fishing pressure (mean $\ln(a)$ for $F/M < 1$: -1.89 ; for $1 \leq F/M < 2$: -0.90 ; for $2 \leq F/M$: -0.55).

In Perciformes, the analysis shows evidence of effective compensations: a shorter lifespan is associated with earlier maturity at a larger size, probably as a result of increased growth. Early maturity or large size at maturity results in a high lifetime fecundity. As a result, there is no link between lifespan and lifetime fecundity. This is in agreement with field evidence: density-dependent growth and age at maturity are known in many Percids (Spangler *et al.*, 1977; Jensen, 1989) and in mackerel from different stocks (Hempel, 1978; Overholtz *et al.*, 1991). Belk (1995) reports a decreased age and size at maturity in bluegill sunfish (*Lepomis macrochirus*) (Centrarchidae) experiencing high fishing pressure, relative to populations with no fishing but heavier juvenile predation. In a population of perch (*Perca fluviatilis*), a higher temperature due to a nuclear power plant resulted in earlier maturity at a smaller size, increased adult mortality, and reduced fecundity (Sandström *et al.*, 1995). These last two studies conclude that size at maturity would decrease with increased adult mortality, as opposed to the present results. This may be due to concomitant changes in juvenile mortality in both studies. In addition, the increase of size at maturity observed here is relative to adult size, which may decrease under high adult mortality.

A large adult size in Perciformes is associated with a high slope of the fecundity–length relationship. This trend is difficult to interpret in the present study, because of the lack of data on proximal factors that may cause these traits to vary together. For example, high resource availability may favour both growth to a large size and a steep increase of fecundity with size.

In Pleuronectiformes, a large size is associated with late maturity, whereas a long lifespan is associated with a small size at maturity. For flatfish, much has been published on changes of traits under fishing pressure (Table 6). The increase in size at maturity under fishing pressure in North Sea sole is consistent with the present

Table 6. Published changes in various female traits (L_a : length-at-age; L_m : length-at-maturity; A_m : age-at-maturity; L_∞ : asymptotic length; F_a : fecundity-at-age) of exploited flatfish populations (I: increased; D: decreased; N: no change).

Reference	Species	Location	Period	L_a	L_m	A_m	L_∞	F_a
de Veen (1976)	Sole	North Sea	1957–1973	I	I		I	I
Pitt (1975)	American plaice	Grand Bank (3L, 3N)	1961–1972	I	N	D	I	
Trippel (1995)		Grand Bank (3Ps)	1973–1988			D		
Bowering (1989)	Witch flounder	Newfoundland	1950–1986	I	N	D	I	
Trippel (1995)		Grand Bank (2J, 3KL)	1970–1983			D		
Haug and Tjemsland (1986)	Atlantic halibut	North Norway	1956–1985	I	N	D		
Rijnsdorp (1989, 1991); Rijnsdorp and van Leeuwen (1992)	Plaice	North Sea	1904–1986	I	D	D		I
Horwood <i>et al.</i> (1986)	Plaice	North Sea	1947–1980					I

Table 7. Summary of strategies and tactics among four orders of teleost species.

Strategies	Tactics: compensation in reproduction for high adult mortality	
	Mechanisms	Effective*
Clupeiformes	First grow, then reproduce Steep increase of fecundity with size Small size	Steeper increase of fecundity with size No
Gadiformes	Large size Early maturity at small size relative to adult size	Increase of fecundity at all ages, mature at larger size Yes
Perciformes	Early maturity at small size relative to adult size	Earlier maturity at larger size relative to adult size Yes
Pleuronectiformes	Intermediate strategy	Mature at a larger size or earlier maturity Yes

*For an individual life time in the range of mortalities analysed.

study. In apparent disagreement is the increase of L_∞ in exploited flatfish stocks. This is easily explained by the use of $L_{0.05}$ instead of L_∞ in the present study: length-at-5%-survival will tend to decrease in exploited populations due to a decrease in the mean age of fish, even if individual size is larger in old fish. The present study does not evidence any decrease of age at maturity in exploited stocks: in flatfish there may be two groups of populations, one with maturity governed by size, the other one where age is more important than size (Roff, 1982, 1991). Plasticity versus age or size thresholds for maturity is a timely question in animal ecology (Bernardo, 1993), not only in flatfish. According to Kisdi and Meszena (1993), for populations regulated by density dependence in variable environments, even the concept of optimal strategy is meaningless, and multiple evolutionary stable strategies may exist: there may be more than one solution to a given problem.

The analysis of tactics within orders rather than any other taxonomic level was guided both by the good segregation of strategies at this level, and by the necessity of having enough populations in each sample. But, as

discussed above for Clupeiformes and flatfish, different tactics may exist in each other. Although the tactics have common features within orders (summarized in Table 7, together with strategies), there is a need for more detailed investigations at lower taxonomic levels.

Tactics, strategies, and stock–recruitment relationships

Population regulation may involve two components: processes which increase death rates and decrease recruitment when abundance is high, and processes which decrease death rates and increase recruitment when abundance is low. This analysis deals mainly with the latter processes, as most of the populations examined are exploited stocks at low abundance. The tactics evidenced in each strategy relate to those processes which act during the adult phase, i.e., those which shape the left limb of the stock–egg production relationships.

Among the four orders examined, three exhibit compensation processes that keep the individual life-time fecundity at least at a constant level when adult

mortality increases. In Clupeiformes, however, a high adult mortality decreases the individual life-time fecundity. In the absence of stronger compensation in the early life-history stages, this would result in a lesser resilience to exploitation, relative to other orders. At the population level, I predict that the left limb of the stock–egg production relationship in this order will be beneath that of the other orders, and probably less convex. This is in accordance with Myers *et al.* (1995), who sought depensation at low population levels by testing for the shape of this left limb in 128 stock–recruitment relationships: they found significant depensation effects (inflection) in three cases, one herring and two Pacific salmon stocks. Three other stocks show evidence of depensatory dynamics, although not significant: Pacific sardine, Georges Bank herring, and Peruvian anchoveta. Among the orders examined in the present study, only Clupeiformes show evidence of depensation. I suggest that compensation–depensation phenomena at low density may act partially in the egg production phase and not just in young stages survival.

From a model of energy allocation to growth and reproduction, Ware (1980) predicts that herring-like species, which have a steeper increase of energy allocation to reproduction as surplus production increases, should have a smaller adult size, a higher size at maturity relative to adult size, and a less convex stock–egg production curve than gadoids. The results of the present study fit this prediction and appeal for a more detailed prediction of the shapes of the egg production curves at low abundances.

We may hypothesize that Clupeiformes populations are less resilient than other teleosts to overexploitation, not only because of their short lifespan and aggregating behaviour, but also because their strategy involves fewer flexible tactics. Other short-lived species with more efficient compensatory effects may be more resilient, e.g. guppies (*Atheriniformes*), which are known for high plasticity of growth and maturity (Reznick, 1993). The strategy of Clupeiformes (“first grow, then reproduce”) may be associated with a less flexible allocation of energy to growth and reproduction than strategies with maturation much before the end of growth.

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