

Life-history correlates of maximum population growth rates in marine fishes

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Theory predicts that populations of animals with late maturity, low fecundity, large body size and low body growth rates will have low potential rates of population increase at low abundance. If this is true, then these traits may be used to predict the intrinsic rate of increase for species or populations, as well as extinction risks. We used life-history and population data for 63 stocks of commercially exploited fish species from the northeast Atlantic to test relationships between life-history parameters and the rate of population increase at low abundance. We used cross-taxonomic analyses among stocks and among species, and analyses that accounted for phylogenetic relationships. These analyses confirmed that large-bodied, slow-growing stocks and species had significantly lower rates of recruitment and adult production per spawning adult at low abundance. Furthermore, high ages at maturity were significantly correlated with low maximum recruit production. Contrary to expectation, fecundity was significantly *negatively* related to recruit production, due to its positive relationship with maximum body size. Our results support theoretical predictions, and suggest that a simply measured life-history parameter can provide a useful tool for predicting rates of recovery from low population abundance.

Keywords: conservation; comparative study; Ricker; stock-recruitment; population growth rate; fisheries

1. INTRODUCTION

Life histories are constrained by trade-offs between survival and reproduction yielding combinations that should maximize lifetime reproductive output (Roff 1992; Stearns 1992; Charnov 1993). One result of these trade-offs is that animals with 'faster' life histories (e.g. early maturity, high body growth rate, small body size) tend to devote proportionally more of their resources to annual reproductive output than those with 'slower' life histories (Read & Harvey 1989; Gunderson 1997).

While relationships among life-history components are well established, there have been few studies linking these to population dynamics of wild animals. A key population parameter is the intrinsic rate of increase, r . This parameter should indicate the replacement rate of the population at low density (Hoening & Gruber 1990; Myers *et al.* 1999), the time required for recovery (Hutchings 1999) and the ability of a population to persist in the face of demographic stochasticity (Lande 1993). Measuring r in wild populations is very difficult, because empirical estimates may be compromised by density dependence. However, a useful index of r is the standardized slope at the origin of a plot of numbers of recruits versus adult population size (Myers *et al.* 1997, 1999). This reflects the maximum number of individuals produced per adult at low population sizes.

Simple correlates of r could be useful for estimating the recovery potential of severely depleted populations and assessment of the extent to which trends in abundance reflect natural variability or population declines due to exploitation (Jennings 2001; Reynolds *et al.* 2001). The

need to identify such links is pressing for many taxa. For example, many fish species that are not the subjects of detailed population assessment have suffered dramatic declines in abundance due to fishing and are now a subject of conservation concern (Dulvy *et al.* 2000; Frisk *et al.* 2001; Reynolds *et al.* 2002). This particularly applies to many species of reef fishes in tropical waters and temperate bycatch species for which almost no information, apart from knowledge of maximum body size and distribution, is available to set conservation priorities (Johannes 1998; Jennings *et al.* 1999a,b).

Declines in population sizes of some commercially exploited fish species have led to concerns about threats of extinction (COSEWIC 2000; Hilton-Taylor 2000). However, the extent to which marine fishes are threatened by extinction is debatable, as it is often assumed that they are naturally resilient to extinction due to high fecundity, wide distribution and high natural variability in abundance (Matsuda *et al.* 1997; Musick 1999; Butterworth 2000). Some conservation agencies, notably the American Fisheries Society, have argued that risk criteria should reflect the potential productivity of the species, on the basis that more productive species should have more capacity to recover from population declines (Musick 1999; Musick *et al.* 2000). However, due to the considerable difficulty in measuring r , in particular for exploited marine populations, it has been suggested that life-history parameters (notably age at maturity, fecundity and body growth rate) may be used as surrogates for the intrinsic rate of increase (Musick 1999; Reynolds *et al.* 2001).

The aim of this study is to determine whether life-history traits are correlated with a simple index of the intrinsic rate of natural increase in marine fishes, using both cross-species and comparative approaches that take into account the evolutionary relatedness of species (Harvey & Pagel

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1991). Our analyses are based on stocks for which population dynamics and life histories are well known. By using fish populations, which are among the best studied exploited populations, we hope both to test general theories for links between life histories and population dynamics, and to derive general relationships that should be applicable to other taxa (Owens & Bennett 2000; Purvis 2001).

2. METHODS

We collated population and life-history data for 63 commercially exploited stocks of marine fishes in the northeast Atlantic (see Appendix A, table A1). These data were compiled by the International Council for the Exploration of the Sea (ICES) for fisheries stock assessments (www.ices.dk), and provided data on age-specific length and maturity, and adult and recruit abundances. Our analyses were restricted to stocks assessed by ICES in order to ensure that the methods of stock assessment and data reporting were comparable.

(a) Indices of the intrinsic rate of increase

We used the slope at the origin of the Ricker spawner–recruit relationship as an index of the intrinsic rate of population increase (Myers *et al.* 1997, 1999). This relationship has the form

$$R = \alpha S e^{-\beta S},$$

where R is recruit abundance, S is spawner abundance, α is recruits per spawner at low population size, and β is the density-dependent parameter controlling the rate at which recruitment drops as spawner abundance increases (Ricker 1954). We chose this model as it usually gave a much better fit to the data than a Beverton–Holt model. A potential problem is that the data (or lack of data) at high spawner abundance may influence the slope at the origin (α) (Myers *et al.* 1997). We therefore calculated (and report) α using just the 10 observations with the lowest spawner biomass. This is a reasonable approach as the stocks we used had been depleted to low spawner biomass by exploitation. We also calculated α using the entire dataset, and found that this did not significantly alter relationships between life-history parameters and α or estimates of adult production. The Allee effect (depensation) may affect the growth of populations at low population size, resulting in lower than predicted recruitment for a given spawner biomass (Liermann & Hilborn 1997). We tested for gross effects of depensation by deriving α from all data except the 5 years with the lowest spawner abundance, and found that this did not significantly alter relationships between α or adult production and life-history parameters.

We also converted α into estimates of adult spawners produced annually per spawner at low population size following the derivation of Myers *et al.* (1997):

$$S/S = (R/S) \times SpR_{F=0}(1 - p_s),$$

where p_s is adult survival in the absence of fishing (described as e^{-M} , where M is the natural mortality rate) and $SpR_{F=0}$ is the cumulative spawning stock biomass produced per recruit in the absence of fishing. Mean $SpR_{F=0}$ and M values were taken from ICES fisheries management reports (Anon. 1981–1999). We found that North Sea haddock had an extremely high adult production of 139 adults per adult at low population levels. The mean of the other populations (excluding haddock) was 5.8

adults produced per adult, with a standard deviation (s.d.) of 6.6. The value for haddock seems artificially high (more than 20 s.d. from the mean of the rest of the populations), perhaps due to errors in other parameters used to calculate it. Although the significance of the relationship between body size and adult production is not significantly altered when haddock is included in the data, it was felt that the datum was unrealistic and it was excluded from the analyses (see Myers *et al.* 1999).

(b) Life-history parameters

Life-history parameters were calculated using age-specific data on body size and maturity for each stock over the previous 20 years. The time range was limited to reduce the effects of temporal changes in life-history parameters, which can show strong responses to fishing mortality (Rijnsdorp 1993; Rochet 1998). The age at which 50% of the stock attain sexual maturity (T_{mat}) was estimated from logistic curves fitted to the relationship between the proportion of mature individuals and age. Estimates of fecundity (annual egg production) at the age or size at maturity were taken from Rickman *et al.* (2000).

Asymptotic length L_{inf} and body growth rate k were estimated from the von Bertalanffy growth equation,

$$L_{inf} = L_t [1 - e^{-k(t-t_0)}],$$

where L_t is the length at age t , and t_0 is the time at which length is theoretically zero on the modelled growth trajectory (Beverton & Holt 1957). The equation was fitted to length at age data using an iterative technique. Fish weights in the assessment data were transformed to length using relationships from Bedford *et al.* (1986) and Coull *et al.* (1989). For 26 of the 63 stocks, it was not possible to discern an asymptote in the length at age data. Therefore, we also collated estimates of maximum observed body size of the oldest age class (L_{max}). Previous studies indicate that L_{max} is closely correlated with L_{inf} (Froese & Binohlan 2000), and we tested this.

(c) Phylogenetic comparative analyses

Phylogenetically independent analyses were used to correct for spurious correlations that may stem from common ancestry rather than resulting from independent evolutionary events (Harvey & Pagel 1991). Because there is considerable uncertainty in the distinctness of and relationships among stock complexes (Smith *et al.* 1989; Arnason *et al.* 1992), we contrasted mean values of traits by species rather than attempting to describe relationships between stocks within species. Our phylogenetic pairings were determined from relationships described in Nolf & Steurbaut (1980); Nelson (1994); Cooper & Chapleau (1998); Rochet (1998) and Rickman *et al.* (2000).

Phylogenetically independent differences ('contrasts') were calculated by subtracting the smaller value of the life-history trait from the larger one, setting all contrasts to positive (Harvey & Pagel 1991; Reynolds *et al.* 2001). Contrasts in potential rates of population increase (α and adults per adult) were calculated for the same species pair in the same sequence. Contrasts in the potential rate of population growth (γ) were plotted against contrasts in life-history trait (x). The null expectation is that contrasts in population growth will be distributed randomly around zero when all contrasts in life history have been set to positive. We tested this with a binomial test.

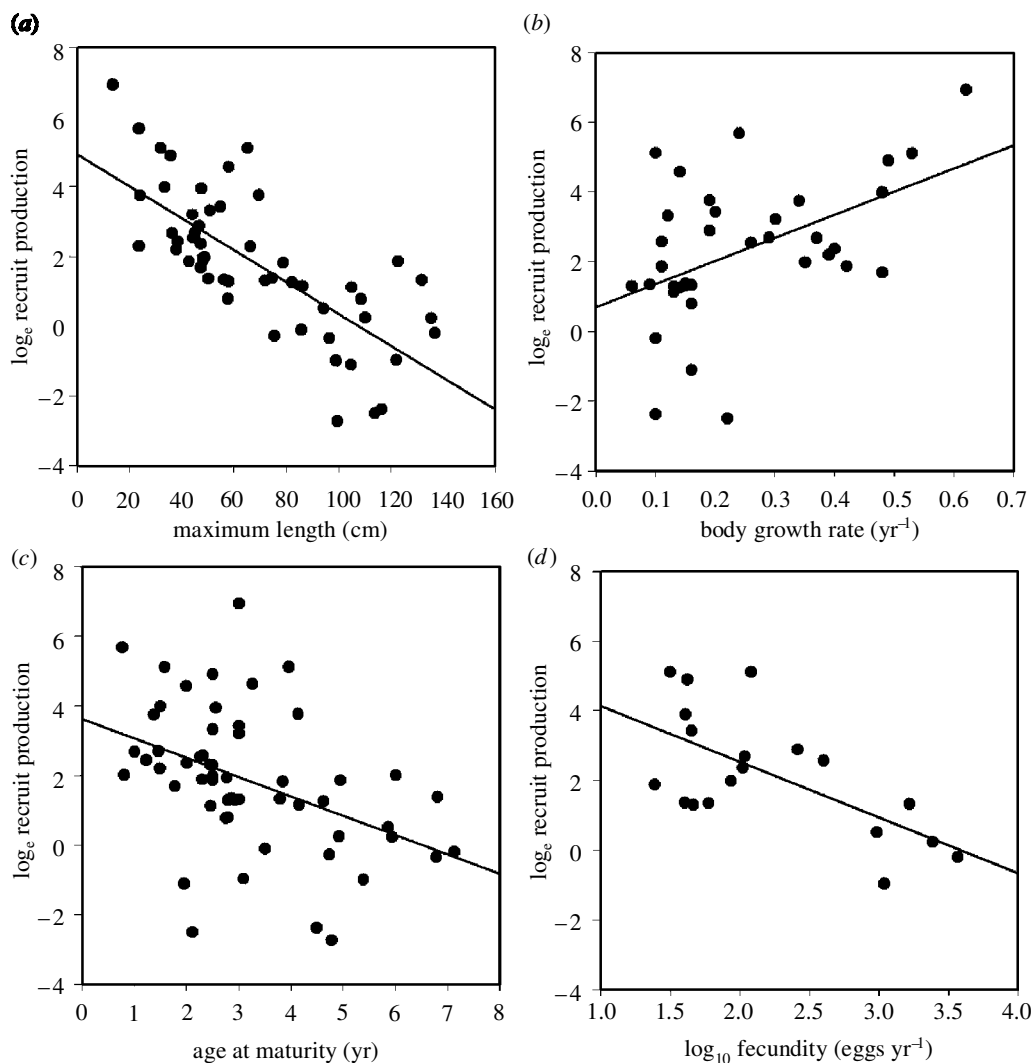


Figure 1. Relationships among stocks between \log_e recruit production (α) and (a) maximum length, (b) body growth rate, (c) age at maturity, and (d) \log_{10} fecundity.

3. RESULTS

(a) Cross-taxonomic analyses

(i) Among stocks

Our two measures of maximum body size, maximum observed length, L_{max} , and asymptotic length, L_{inf} were closely correlated with each other ($r = 0.96$, $n = 37$ stocks, $p < 0.001$). Therefore, given the lack of L_{inf} for 26 stocks (see § 2), L_{max} was used as our measure of body size in the analyses. In all analyses, any relationship between the variable of interest and L_{max} was stronger than any relationship with L_{inf} .

High rates of recruitment per adult (α) were significantly associated with small body size (L_{max} : $r^2 = 0.544$, $F_{(1,54)} = 63.23$, $p < 0.001$; figure 1a), high body growth rates ($r^2 = 0.235$, $F_{(1,35)} = 10.47$, $p = 0.003$; figure 1b) and early maturity ($r^2 = 0.189$, $F_{(1,56)} = 12.78$, $p = 0.001$; figure 1c). Contrary to expectations, high recruitment was correlated with low fecundity ($r^2 = 0.37$, $F_{(1,18)} = 10.005$, $p = 0.006$; figure 1d). Furthermore, the relationship between body size and fecundity was positive and highly significant (L_{max} : $r^2 = 0.80$, $F_{(1,15)} = 60.023$, $p < 0.001$). When we controlled for body size, the relationship between recruitment and fecundity became non-signifi-

Table 1. Partial correlations between life-history characteristics of stocks and \log_e recruit production (α) while controlling for age at recruitment.

	correlation coefficient	<i>n</i>	<i>p</i>
maximum length	-0.669	52	<0.001
body growth rate	0.358	33	0.035
age at maturity	-0.237	54	0.079
fecundity	-0.465	16	0.052

cant ($r = 0.097$, $n = 14$ stocks, $p = 0.721$). Production of recruits to the fishery per adult, although likely to be a good measure of the intrinsic rate of increase, may be biased by the age at which recruitment is measured. We therefore carried out partial correlations between the life-history traits and recruit production while controlling for age at recruitment to the fishery (table 1). These results broadly supported previous results, although age at maturity became non-significant ($p = 0.079$).

High rates of replacement adults produced per adult were also associated with small body size (L_{max} : $r^2 = 0.156$, $F_{(1,44)} = 7.92$, $p = 0.007$; figure 2a) and high body growth

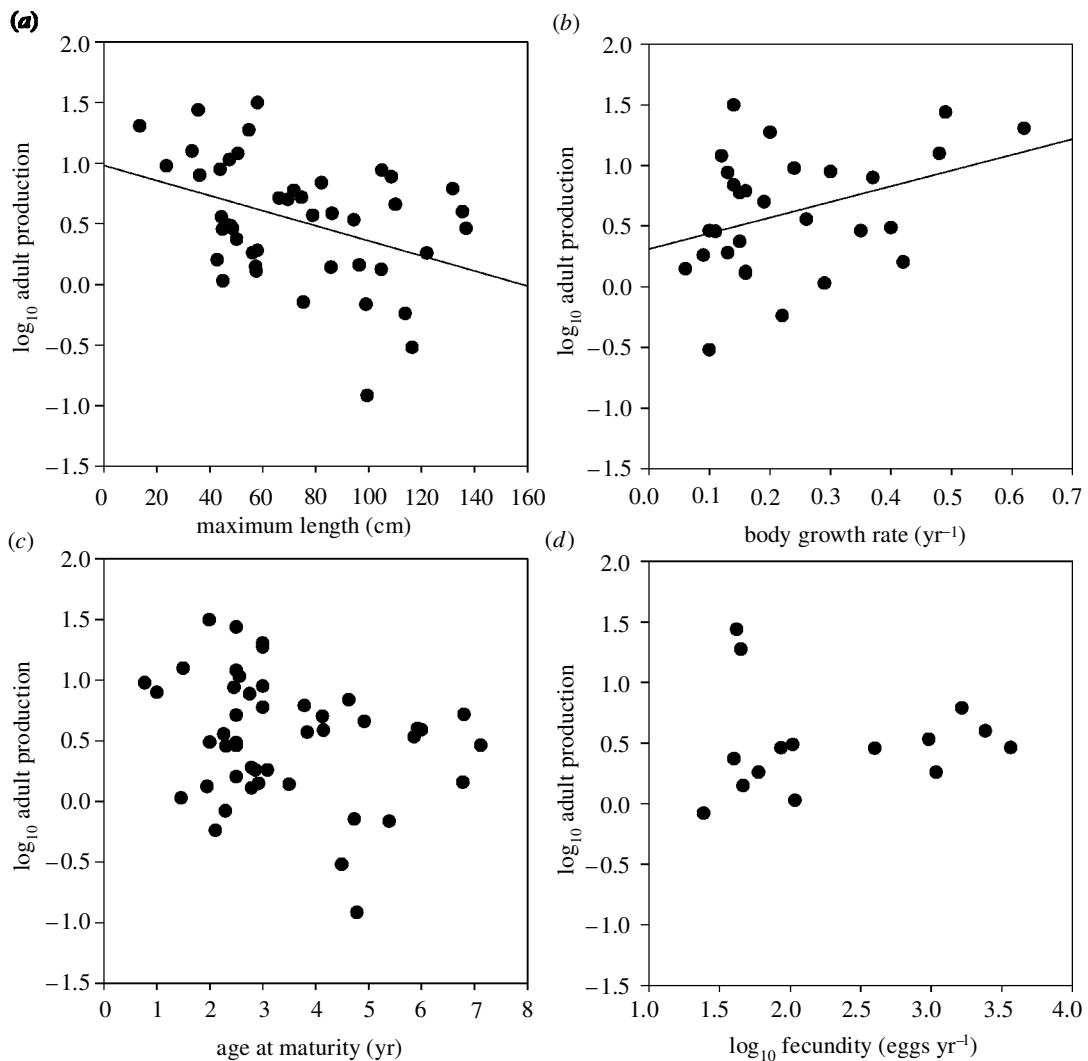


Figure 2. Relationships among stocks between \log_{10} adult production and (a) maximum length, (b) body growth rate, (c) age at maturity, and (d) \log_{10} fecundity.

Table 2. Results of regressions between mean traits for species and mean \log_e recruit production (α) and \log_{10} mean adult production.

	\log_e recruit production				\log_{10} adult production			
	r^2	F	d.f.	p	r^2	F	d.f.	p
maximum length	0.74	41.61	1,15	<0.001	0.44	10.02	1,14	0.007
body growth rate	0.41	7.08	1,11	0.024	0.40	6.54	1,11	0.027
age at maturity	0.34	8.22	1,17	0.011	0.07	1.07	1,15	0.319
fecundity	0.00	0.10	1,7	0.764	0.08	0.61	1,7	0.460

rates ($r^2 = 0.135$, $F_{(1,28)} = 4.226$, $p = 0.05$; figure 2b). However, there was no significant relationship with age of maturity ($r^2 = 0.05$, $F_{(1,45)} = 2.65$, $p = 0.111$; figure 2c), nor fecundity ($r^2 = 0.001$, $F_{(1,14)} = 0.012$, $p = 0.916$; figure 2d).

(ii) Among species

When using mean values for traits within species, we found that high rates of recruit production were again associated with small body size, high body growth rates and early maturity, while the association with fecundity was not significant (table 2). We also found that high rates of adult production were associated with small body size

and high body growth rates, but not with the other traits (table 2).

(b) Phylogenetic comparative analyses

The phylogenetic comparative analyses confirmed that maximum body size is negatively related to recruit and adult production. In six of the seven comparisons between related species that were possible, the species that had the larger maximum length had both a lower recruitment production and a lower adult production (one-tailed sign test, $p = 0.068$). Increase in age of maturity was also accompanied by a decrease in recruit production in seven out of nine cases (one-tailed sign test, $p = 0.090$), but there

was no relationship with adult production (three out of seven cases). We could not test the relationships between adult and recruit production and body growth rate or fecundity due to insufficient data.

4. DISCUSSION

This study has revealed significant relationships between life-history traits of fish species and maximum rates of recruit and adult production per adult at low population sizes. These results were true for comparisons among stocks, among species, and to a limited extent in analyses that accounted for phylogenetic relationships among taxa. These findings thus support predictions of links between key life-history traits and potential population growth rates, with implications for predicting vulnerability to exploitation (Jennings *et al.* 1998) and recovery (Hutchings 2001).

While estimates of the intrinsic rate of natural increase (r) provide the basis for predicting recovery rate, direct use of the Euler–Lotka equation to estimate r (e.g. Hutchings & Myers 1994) is data intensive and is only appropriate for the commercially important stocks where age-specific survival and fecundity schedules are available. Our index of recruit production will be influenced by the age at which recruitment is measured, and this varies for the different stocks included in the analysis. However, analyses controlling for age at recruitment indicate that the relationships were not significantly biased. The calculation of adult production as adults per adult standardizes for differences in age at recruitment, but relies on estimates of natural mortality, which are very difficult to obtain. Moreover, the estimates of spawning stock biomass are not based on consistent age structure (Marshall *et al.* 1999). However, despite the very variable estimates of adult production for individual stocks, the cross-stock and species relationships between adult production and maximum length and body growth rate remain significant.

These results have practical implications for conservation and management. Foremost, they show that of the available life-history data, indices of body length and body

growth rates were consistently the strongest predictors of all indices of the intrinsic rate of increase. From a practical perspective, maximum observed size (L_{\max}) can be used as a surrogate for asymptotic body size (L_{∞}), which is useful when growth data are not available, or species do not grow according to the von Bertalanffy model. Other life-history variables that are more difficult to measure (age at maturity and fecundity), while significantly associated with recruit production, were not significantly related to adult production. This loss of significance should not detract from the strength of the relationships between life-history traits and recruit production, as the conversion of recruit to adult production is greatly hampered by the unreliability of natural mortality estimates.

Our results show that highly fecund species tend to have lower intrinsic rates of increase than those that are less fecund. This is because large body size is a very strong correlate of the intrinsic rate of increase and of absolute fecundity (Sadovy 2001). Among the highly fecund teleosts, there appears to be no empirical basis for assuming that high fecundity confers high resilience to exploitation.

We conclude that body size is a useful index of the intrinsic rate of increase that can be applied to populations and species for which only the most simplistic biological data are available. For example, only a small percentage of the world's marine fish populations are being studied closely enough to enable detailed stock assessments, yet some less-well-studied populations have collapsed as a result of direct targeting by commercial and artisanal fisheries, or as a result of being taken as bycatch (Kaiser & de Groot 2000; Reynolds *et al.* 2002). For these little-studied populations, our results indicate that knowledge of body size may help to predict the relative rates at which they would recover when released from fishing pressure.

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APPENDIX A

Table A1. Data used in the analysis. (Recruit production is in numbers of individuals per kilogram of spawning biomass per year; age of recruits is the age at which individuals recruit to the fishery; M is the instantaneous rate of natural mortality; $S_p R_{E=0}$ is the total spawning biomass produced in a lifetime per recruit in the absence of fishing mortality; adult production is per adult per year; L_{max} is maximum body length; k is body growth rate; T_{mat} is the age at which 50% of individuals become mature; fecundity is in thousands of eggs per year at mean age at maturity (Rickman *et al.* 2000). See § 2 for further descriptions of parameters.)

species	stock	recruit production	age of recruits (years)	M	$S_p R_{E=0}$ (kg)	adult production	L_{max} (cm)	k	T_{mat} (years)	fecundity
anchovy (<i>Engraulis encrasicolus</i>)	Bay of Biscay	5.37	2	0.20	0.70	0.83	136.9	0.10	2.30	24.4
blue whiting (<i>Micromesistius poutassou</i>)	northern ICES	6.53	0	0.20	19.41	2.90	85.7		7.12	3660
cod (<i>Gadus morhua</i>)	Arctic	0.82	3	0.20	8.39	1.38	113.9	0.22	3.50	
	Baltic	0.91	2	0.20	38.60	0.58	108.6		2.11	
	Celtic	0.08	1	0.20	19.60	7.72	135.5		2.75	
	Faroe	2.17	2	0.20	17.50	3.99	122.0		5.93	2418
	Icelandic	1.26	3	0.20	26.30	1.81	105.0		3.09	1081
	Irish Sea	3.07	0	0.20	15.70	8.73	131.8	0.13	2.46	
	Kattegat	3.78	1	0.20	9.00	6.17	122.8	0.16	3.79	1642
	North Sea	6.41	2	0.20	6.75	3.86	86.2	0.11	4.94	
	Norway Coastal	3.16	1	0.20	22.20	1.33	104.8		4.15	
	western Baltic	0.33	1	0.20	1.20	2.86	44.7	0.16	1.95	
	west Scotland	13.14	2	0.20				0.11	2.31	397
flounder (<i>Platichthys flesus</i>)	Baltic									
Greenland halibut (<i>Reinhardtius hippoglossoides</i>)	Arctic	0.71	5	0.15	14.67	1.44	96.5		6.78	
haddock (<i>Melanogrammus aeglefinus</i>)	Arctic	1.67	3	0.20	11.27	2.62	94.4		5.86	960
	Faroe	3.72	2	0.20	8.85	5.97	71.8	0.15	3.00	
	Icelandic	3.51	2	0.20	10.86	6.90	82.2	0.14	4.63	
	North Sea	167.34	0	0.20			65.2	0.10	3.96	120
	Rockall	27.67	1	0.20		12.04	50.7	0.12	2.50	
	west Scotland	96.12	1	0.20	1.80	31.36	58.1	0.14	1.99	
hake (<i>Merluccius merluccius</i>)	northern ICES	0.60	0	0.20	5.20	0.72	75.4		4.73	
	southern ICES	6.23	1	0.20	3.30	3.73	78.9		3.84	
herring (<i>Clupea harengus</i>)	Celtic	14.59	0	0.30	2.10	5.55	36.2	0.37	1.00	
	eastern Baltic	42.20	1	0.25			23.9	0.34	1.37	
	north Gulf Bothnia	101.84	0						3.26	
	south Gulf Bothnia	10.03	1				23.5		2.45	
	Icelandic	9.00	1	0.10	2.13		37.9	0.39	1.49	
	north Ireland	164.78	1	0.25			31.9	0.53	1.58	31.5
	North Sea	134.09	0				35.7	0.49	2.50	41.7
	Norwegian	49.43	1							40.7
	west Ireland	53.96	0	0.30	0.90	6.77	33.3	0.48	1.50	

(Continued.)

Table A1. Continued.

species	stock	recruit production	age of recruits (years)	M	$SpR_{E=0}$ (kg)	adult production	L_{max} (cm)	k	T_{mat} (years)	fecundity
horse mackerel (<i>Trachurus trachurus</i>)	southern ICES	42.95	0	0.15	0.84	5.03	69.5	0.19	4.13	
mackerel (<i>Scomber scombrus</i>)	Arctic	5.41	0	0.15			47.3	0.48	1.78	
	western	10.62	0	0.15	2.08	3.08	47.2	0.40	2.00	104.3
four-spotted megrim (<i>Lepidorhombus boscii</i>)	Iberia	7.49	1	0.15	0.70				0.80	
megrim (<i>Lepidorhombus whiffiagonis</i>)	Celtic	6.97	1	0.15			48.0		2.77	
	Iberia	11.44	1	0.15	1.03		38.4		1.23	
black angler (<i>Lophius budegassa</i>)	Celtic	7.43	2	0.20	2.90	3.91			6.00	
monkfish (<i>Lophius piscatorius</i>)	Celtic	3.98	1	0.20	7.25	5.23	74.6		6.80	
plaice (<i>Pleuronectes platessa</i>)	Celtic	3.86	1	0.20	2.60	1.82	56.2	0.09	2.86	59.6
	eastern English Channel	3.63	1	0.10	5.50	1.90	58.0	0.13	2.79	
	Irish Sea	3.65	1	0.12	3.40	1.41	57.4	0.06	2.92	46.3
	Kattegat	6.59	2	0.10	4.85	3.04	48.0		2.50	
	North Sea	3.93	1	0.10	6.30	2.36	50.1	0.15		
	western English Channel	2.20	1	0.12	5.17	1.29	57.6	0.16	2.79	
saithe (<i>Pollachius virens</i>)	Arctic	0.37	2	0.20	10.06	0.43	99.0		5.39	
	Faroe	1.27	3	0.20	19.75	2.85	110.2		4.92	
	Icelandic	0.09	3	0.20	18.00	0.19	116.4	0.10	4.49	
	North Sea	0.07	1	0.20	10.20	0.12	99.5		4.78	
sardine (<i>Sardina pilchardus</i>)	southern ICES	291.41	0	0.33	0.12	9.50	23.6	0.24	0.77	
sole (<i>Solea solea</i>)	Bay of Biscay	9.22	1	0.10	4.30	3.78			3.00	44.7
	Celtic	30.76	1	0.12	5.40	15.81	54.8	0.20		
	eastern English Channel	23.83	1	0.12	3.15	7.14				
	Irish Sea	12.65	2	0.10	2.99	3.60	44.4	0.26	2.26	
	Kattegat	6.46	2	0.10	2.60	1.60	42.8	0.42	2.50	
	North Sea	7.24	1	0.10	4.20	2.89	48.7	0.35	2.50	86.1
	western English Channel	24.67	1	0.10	3.80	8.92	44.0	0.30	3.00	
sprat (<i>Sprattus sprattus</i>)	Baltic	1020.71	1	0.64	0.04	20.26	13.6	0.62	1.92	
whiting (<i>Merlangius merlangus</i>)	Celtic	9.90	0	0.20	2.88	5.16	66.2		2.50	
	Irish Sea	51.56	0	0.20	1.15	10.75	47.5		2.56	
	North Sea	13.05	1	0.20			44.9	0.29	1.46	107.7
	west Scotland	17.88	1		1.41		46.6	0.19		259

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As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.