

Life history correlates of density-dependent recruitment in marine fishes

Nicholas B. Goodwin, Alastair Grant, Allison L. Perry, Nicholas K. Dulvy, and John D. Reynolds

Abstract: Understanding the relationships among life history traits, density dependence, and population dynamics is a central goal in ecology. It is also vital if we are to predict how populations respond to and recover from exploitation. We used data for 54 stocks of commercially exploited fish species to examine relationships between maximum annual recruitment at low stock size and the density dependence of recruitment at high stock size. We then related these recruitment measures to life history. At low stock sizes, stocks with high maximum recruitment (maximum spawners per spawner) showed the weakest density dependence of recruitment at high stock sizes. Spawning biomass per recruit in the absence of fishing ($SPR_{F=0}$) showed a strong positive correlation with both maximum spawners per spawner and the strength of density dependence. Stocks with high $SPR_{F=0}$ were typically large-bodied, slow-growing, late-maturing, and highly fecund with long generation times. These stocks produced low numbers of recruits each year, but survived to breed repeatedly and had strong density dependence of recruitment. In contrast, small-bodied, early-maturing fish had high annual recruitment and weak density dependence. These results place species on a continuum from “highly reproductive” to “survivors”. But we also demonstrate that density dependence is an important feature of the population biology of survivors.

Résumé : La compréhension des relations entre les caractéristiques démographiques, la dépendance de la densité et la dynamique de population est un des principaux objectifs de l'écologie. Elle est aussi essentielle pour la prédiction des réactions des populations à l'exploitation et de leur récupération subséquente. Nous utilisons des données provenant de 54 stocks de poissons exploités commercialement afin d'examiner les relations entre le recrutement maximum annuel lorsque les stocks sont bas et la dépendance du recrutement de la densité lorsque les stocks sont élevés. Nous relierons ensuite ces estimations du recrutement à la démographie. Lorsque les stocks sont bas, les stocks qui ont un fort recrutement maximum (nombre maximum de reproducteurs par reproducteur) montrent la dépendance de la densité de leur recrutement la plus faible lorsque les stocks sont élevés. La biomasse des reproducteurs par recrue en absence de pêche ($SPR_{F=0}$) est en forte corrélation positive à la fois avec le nombre maximum de reproducteurs par reproducteur et avec l'importance de la dépendance de la densité. Les stocks avec un $SPR_{F=0}$ élevé ont typiquement un grand corps, une croissance lente, une maturation tardive, une forte fécondité et une durée de génération importante. Ces stocks produisent un petit nombre de recrues chaque année, mais ils survivent assez longtemps pour se reproduire plusieurs fois et leur recrutement montre une forte dépendance de la densité. En revanche, les poissons à corps plus petit et à maturation précoce ont un recrutement annuel élevé et une faible dépendance de la densité. Ces résultats permettent de placer les espèces le long d'un continuum allant des « reproducteurs prolifiques » aux « survivants ». Nous démontrons aussi, cependant, que la dépendance de la densité est une caractéristique importante de la biologie de population des survivants.

[Traduit par la Rédaction]

Introduction

Life histories and density dependence are pivotal to our understanding of population dynamics (Roff 1992; Stearns 1992; Tuljapurkar and Caswell 1997). Species with high in-

trinsic rates of population increase (r) are expected to have a high capacity to recover from overexploitation or from an environmental shock that reduces the population (Myers et al. 1997; Hutchings and Reynolds 2004). However, population growth rates are also determined by density dependence

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and environmental stochasticity. We need to understand the interplay among these processes to predict the ability of populations to withstand human impacts, such as fishing. Unfortunately, both r and the strength of density dependence are difficult to measure in wild populations. This has led to a search for simple aspects of the biology of species that can be used to predict these key parameters, and hence population dynamics, at both low and high population sizes.

Life history theory offers a promising framework for building bridges between demography and fundamental aspects of species biology. There is now a large body of empirical evidence supporting predictions of trade-offs between life history components that underpin adaptations for maximizing individual fitness (reviewed in Stearns 1992; Charnov 1993; Roff 2002). For example, previous studies of commercially exploited marine fishes have identified life history traits, such as body size and age at maturity, that predict maximum recruitment at low population size (Denney et al. 2002) and abundance trends in exploited species (Jennings et al. 1998; Reynolds et al. 2005; Hutchings and Reynolds 2004). To date, no study has examined whether such life history traits are correlated with reductions in recruit survival with increasing population size, otherwise known as density-dependent recruitment or compensation.

At high population sizes, density-dependent processes that reduce the number of recruits produced per spawner are thought to result from competition for habitats and food, leading to limits on population sizes (Rose et al. 2001; Myers 2002). This density dependence results in a less than proportional increase in recruitment with population size, giving a population some capacity to compensate for the effects of exploitation (Cushing 1975) and also giving it some assimilative capacity to resist the effects of pollution, poor environmental conditions, or other environmental shocks (Grant 1998). There is evidence that life history traits may influence the degree of density-dependent mortality because species that reach a stable equilibrium population size tend to be slow growing, late maturing, and have high early survival (Stearns 1992; Roff 2002). However the reasons behind these relationships have been the subject of extensive debate. Pianka (1970) suggested that selection pressures on some species favour rapid population growth, whereas those on other species favour competitive ability. Stearns (1976) presented bet-hedging as an alternative conceptual framework, in which longer-lived adults maximize individual fitness in a variable environment by breeding many times, rather than having one or a few large bursts of reproduction, as is typical of fast-growing or semelparous species (reviewed by Winemiller 2005). Debates of these issues have suffered from a paucity of evidence on the significance of density dependence in wild populations and a failure of a number of studies to find any trade-off between competitive ability at high densities and population growth rate at low densities (e.g., Luckinbill 1978; Velicer and Lenski 1999).

The aim of this study is to establish whether there is a relationship between maximum recruitment at low population sizes and the strength of the density-dependent recruitment (or compensatory reserve), as indicated by a decline in recruits per spawner at high population sizes. We also aim to identify whether any life history traits are correlated with the

strength of density dependence at high population sizes for a wide range of fish stocks. Ultimately, we hope to use life history as an a priori predictor of density-dependent relationships for data-poor populations.

Materials and methods

Data sources

We collated age-structured life history information and time series of adult and recruit abundances for stocks of commercially exploited marine fishes in the northeast Atlantic. These data were published by regional Working Groups, whose assessments are available from the International Council for the Exploration of the Sea (ICES; <http://www.ices.dk/iceswork/workinggroups.asp>). ICES stock assessments use virtual population analysis of commercial catch-at-age data to estimate annual spawning stock biomass and age-specific vital rates and recruit abundance (Pope 1972; Darby and Flatman 1994). We derived life history measures from the most recent 5-year mean values of weight, maturity, and natural mortality at age. Fecundity was derived from published weight–fecundity or length–fecundity relationships. Spawner–recruit relationships were calculated only for stocks with a spawner and recruit abundance time series of at least 15 years and when the range of spawning biomass was at least 50% of the maximum observed spawning biomass. This criterion reduced the data set to 54 stocks from a possible 63. The median length of time series was 29 years, with a range from 15 to 93 years. Typically, the minimum observed spawning stock biomasses were 74% ($\pm 2.2\%$ standard error, SE) lower than the maximum observed biomass.

Life history parameters

Asymptotic weight (W_∞), referred to here as maximum weight, and body growth rate (κ) were estimated from the von Bertalanffy growth equation:

$$(1) \quad W(i) = W_\infty [1 - e^{-\kappa(i-i_0)}]^b$$

where $W(i)$ is weight at age i , κ is body growth rate, i_0 is the age at hatching, and b is the exponent from the length–weight relationship ($W = aL^b$). In the absence of stock assessment values of b (39 of 54 stocks), regional or species means were taken from FishBase (Froese and Pauly 2004). Weight-at-age data were based on a 5-year mean of catch weights from the most recent stock assessment. We only included age classes fully selected by the fishery because mean weights at age for younger age classes could be biased towards the larger individuals more likely to be caught. Although this excludes some age classes, the von Bertalanffy parameters were estimated over a wide range of weights. Typically, the minimum observed body weights were 84% ($\pm 1.5\%$ SE) lower than the maximum body weight. For parameter estimation, a nonlinear least squares technique (see Quinn and Deriso 1999) was used to fit both an additive and a multiplicative error-structured model for eq. 1, for which the multiplicative model was first converted to its natural logarithm. Starting parameters were W_∞ = maximum observed weight, $\kappa = 0.2$, and $i_0 = 0$. We used estimates of W_∞ and κ from the model with the lowest sums of squares and narrowest confidence intervals.

The age at 50% maturity (T_{mat}) was calculated from the logistic function where the rate of change is a parabolic function of age:

$$(2) \quad \text{Mat}(i) = \frac{1}{1 + e^{-\theta(i - T_{\text{mat}})}} \quad (\theta, T_{\text{mat}} > 0)$$

where $\text{Mat}(i)$ is the proportion mature at age i , θ represents the curvature of the logistic curve, and T_{mat} is the age at the inflection point. Parameters were estimated using a nonlinear least squares data fitting by the Gauss–Newton method. The initial starting value for T_{mat} was taken from the first age class in which more than 50% of individuals were observed to be mature.

Fecundity at the age at 50% maturity (Fec_{mat}) was calculated from the linear interpolation of log-transformed mean fecundity at age. Mean fecundity at age was derived from weight-at-age data taken from stock assessments and published weight–fecundity and length–fecundity relationships.

We also used two life history measures that incorporated the combined elements of survival, reproduction, and body growth rate. Generation time (G) is the mean time between reproduction of the parent generation and reproduction of its own offspring and is calculated as

$$(3) \quad G = \frac{\sum x l_x m_x}{\sum l_x m_x}$$

where x is the age class, l_x is the probability of survival, and m_x is the mean fecundity. Spawners per recruit ($\text{SPR}_{F=0}$) is the cumulative spawning biomass (kg) produced by a recruit over the course of its lifetime in the absence of fishing mortality (Gabriel et al. 1989):

$$(4) \quad \text{SPR}_{F=0} = \sum_i^{i_{\text{max}}} N_i e^{-[M_i(i - i_{\text{rec}})]} W_i \text{Mat}_i$$

where $N_i = 1$ is the recruit present in the first age class, W_i is weight (kg) at age i , Mat_i is the proportion mature at age i , M_i is natural mortality at age i , and i_{rec} is the age at recruitment. The term i_{rec} is included to ensure that the calculation of $\text{SPR}_{F=0}$ starts from the same age class for all stocks, otherwise stocks whose recruits are counted in older age classes would have disproportionately high values of $\text{SPR}_{F=0}$. This calculation makes the simplifying assumption that fecundity is proportional to body weight after adjusting for the fraction of fish in each age class that are mature. The same assumption is made in most stock assessments. Life history parameters and measures are summarized for each stock (Appendix Table A1).

Estimating spawner–recruit parameters

Within a fisheries context, recruits are juvenile fish of a given age that become vulnerable to fishing gear used in research surveys. The age of this vulnerability varies among species (Appendix Table A2). Various models can be used to describe the form of the density-dependent relationship between spawner biomass and the numbers of recruits (see Hilborn and Walters 1992; Quinn and Deriso 1999). We used the Ricker (1954) and hockey stick (Barrowman and Myers 2000) models because together they capture a wide

range of spawner–recruit relationships, and their statistical fit was more robust across a range of stocks than for a more complex, three-parameter model (e.g., Shepherd 1982). Both models assume an upper limit to recruitment. The Ricker model has the form

$$(5) \quad R_t = \alpha S_t e^{-\beta S_t + \epsilon_t} \quad (\alpha, \beta > 0, \epsilon)$$

where the number of recruits R_t is a function of S_t , where S is the spawner biomass at time $t - i_{\text{rec}}$, α is the slope at the origin, and β governs the population size at which density dependence occurs. We introduce variation in recruitment after density-dependent regulation, where ϵ_t is a normal recruitment variation with a mean of 0 and variance σ^2 . The parameter α is the maximum annual recruit production, and the product of β and S_t is density-dependent recruit mortality. The hockey stick model has the form

$$(6) \quad R_t = \alpha \min(S, S^*, \epsilon) = \begin{cases} \alpha S_t e^{\epsilon_t} & \text{if } S_t < S^* \\ \alpha S^* e^{\epsilon_t} & \text{if } S_t \geq S^* \end{cases}$$

where α is the linear slope of a bisected line up to the point S^* , which is the spawner biomass beyond which there is a constant number of recruits for further increases in stock size, and ϵ_t is the normal recruitment variation with mean of 0 and variance σ^2 .

Ricker and hockey stick parameters were estimated using maximum likelihood procedures. We used a lognormal error distribution for the likelihood function:

$$(7) \quad \ell(R|\hat{\sigma}) = -\frac{n}{2} \log_e \left\{ \frac{2\pi}{n} \sum [\log_e R_t - \log_e f(S_t)]^2 \right\} - \sum \log_e R_t - \frac{n}{2}$$

where R_t is the number of recruits in each year, the estimated $\hat{\sigma}$ is the standard deviation of recruit variation, n is the length of the time series, and $f(S_t)$ is the number of recruits predicted from spawning stock biomass (SSB) by either the Ricker or hockey stick models above. Starting parameters for the Ricker model were estimated from a least squares regression of the linear form $\log_e(R/S) = \log_e(\text{intercept}) - (\text{slope})S$, where $\alpha = \exp(\text{intercept})$ and $\beta = -\text{slope}$ (Quinn and Deriso 1999). Starting parameters for the hockey stick model were $\alpha = 1$ and $S^* =$ spawning stock biomass at median recruitment. Evaluation of the maximum likelihood values indicated that the Ricker model provided a better fit to the spawner–recruit data than did the hockey stick model in 32 of the 54 stocks. The hockey stick failed when the turning point S^* could not be reconstructed. Spawner–recruit parameters, standard deviations based on bootstrap analysis, and model fits are presented for each stock (Appendix Table A2).

Spawner–recruit parameter estimation may be influenced by serial correlation in the time series, whereby annual spawner–recruit data lack independence because years of strong recruitment may have a positive or negative effect on future spawning biomass and recruitment (Walters 1985). A first-order autoregressive model of recruitment did not improve the model fit (for all 54 stocks: $\chi^2 < 2.06$; $df = 1$; $p > 0.15$). Before including a wide range of potential lagged

effects, further work is required to interpret how serial correlation influences parameter estimates and density-related processes.

Calculation of the equilibrium spawning stock biomass

The mean equilibrium for the unexploited spawning stock biomass ($SSB_{F=0}$) was calculated using an age-structured, stochastic population model without fishing mortality. Annual recruitment variation was lognormally distributed around the fitted spawner–recruit relationship. The numbers in each age class i were calculated as

$$(8) \quad N_{(i+1,t+1)} = N_{(i,t)} e^{-M} \quad \text{for } i = \text{age at recruitment to } i_{\max} - 1$$

$$N_{(i_{\max},t)} = N_{(i_{\max},t)} e^{-M} + N_{(i_{\max}-1,t)} e^{-M}$$

where N_i is the number of individuals in each age class at time t , and M is the instantaneous rate of natural mortality; i_{\max} is the age at which we assume demographic parameters no longer change with age, so the age class i_{\max} denotes all individuals of age i_{\max} and older. The age class aggregation is the plus group described in stock assessments and typically contributed between 2% and 9% of the spawning biomass. In each yearly time step, the total SSB was the summed weight of all reproductive males and females in the stock.

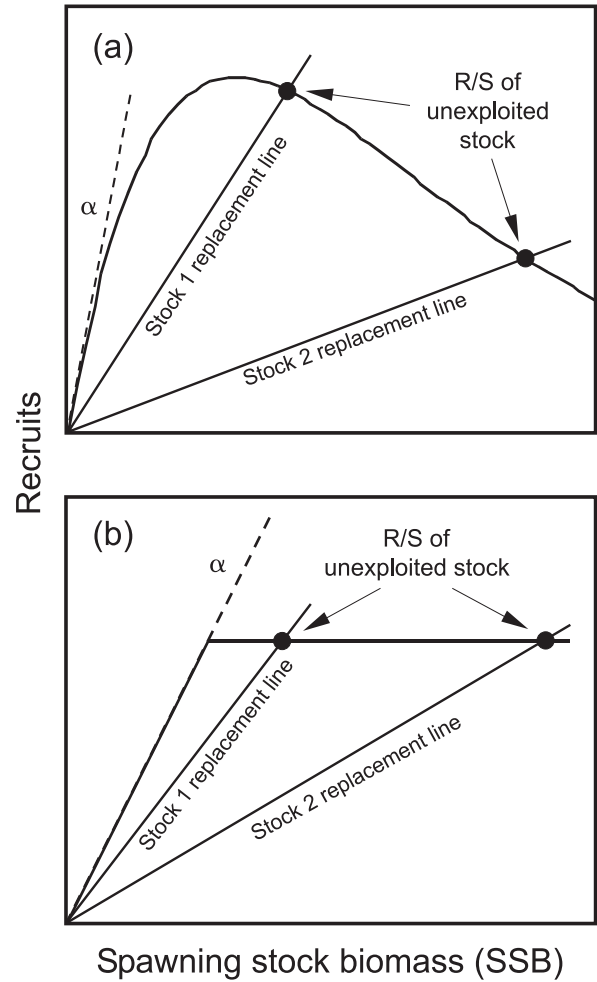
$$(9) \quad SSB = \sum_i^{i_{\max}} N_i W_i Mat_i$$

The number of individuals entering the stock as new recruits is a function of SSB (eq. 9) and either the Ricker or hockey stick models of recruitment (eqs. 5 and 6). $SSB_{F=0}$ was calculated as the mean biomass over 1000 time steps after equilibrium had been reached. We used both models of recruitment to ensure that results were not merely a function of the choice of spawner–recruit relationship.

Standardized measures of density-independent and density-dependent recruitment

Maximum annual recruitment per spawner (α) is described by the slope at the origin from either the Ricker or hockey stick models (eqs. 5 and 6). However, α is not directly comparable across stocks with different life histories. Individuals with short reproductive life spans must have higher annual recruitment to replace themselves, whereas long-lived individuals spawn over many years and can replace themselves at lower levels of annual recruitment. The standardized, density-independent measure of α accounts for differences in an individual’s lifetime recruit production, which is a function of their expected lifetime spawning biomass discounted for repeat spawning over their lifespan (Myers et al. 1997, 1999). We first calculate the maximum recruits per recruit at low spawner abundance ($\hat{\alpha}$; the product of α and $SPR_{F=0}$) (Gabriel et al. 1989; see eq. 4 above). The final standardized unit for comparison across stocks, maximum spawners per spawner ($\tilde{\alpha}$), is defined as the average number of adult spawners that are produced annually per spawner at low spawner abundance. If p_s is the annual adult survival, such that $p_s = e^{-M}$, then $\hat{\alpha} = \sum_{i=0}^{\infty} p_s^i \tilde{\alpha}$. The sum of this geometric

Fig. 1. Graphic representation of the compensation ratio (CR) for (a) Ricker and (b) hockey stick spawner–recruit models. When spawning stock biomass is at unexploited levels ($SSB_{F=0}$), both stock 1 and stock 2 have lower recruit survival per spawner (R/S) compared with their maximum recruit survival at low stock sizes (α ; dashed line). The closer the gradient of the stock replacement line is to the gradient of α , the weaker the effect that density has on R . So stock 2 has a higher CR (eq. 11) and is exposed to stronger density-dependent recruit mortality than stock 1.



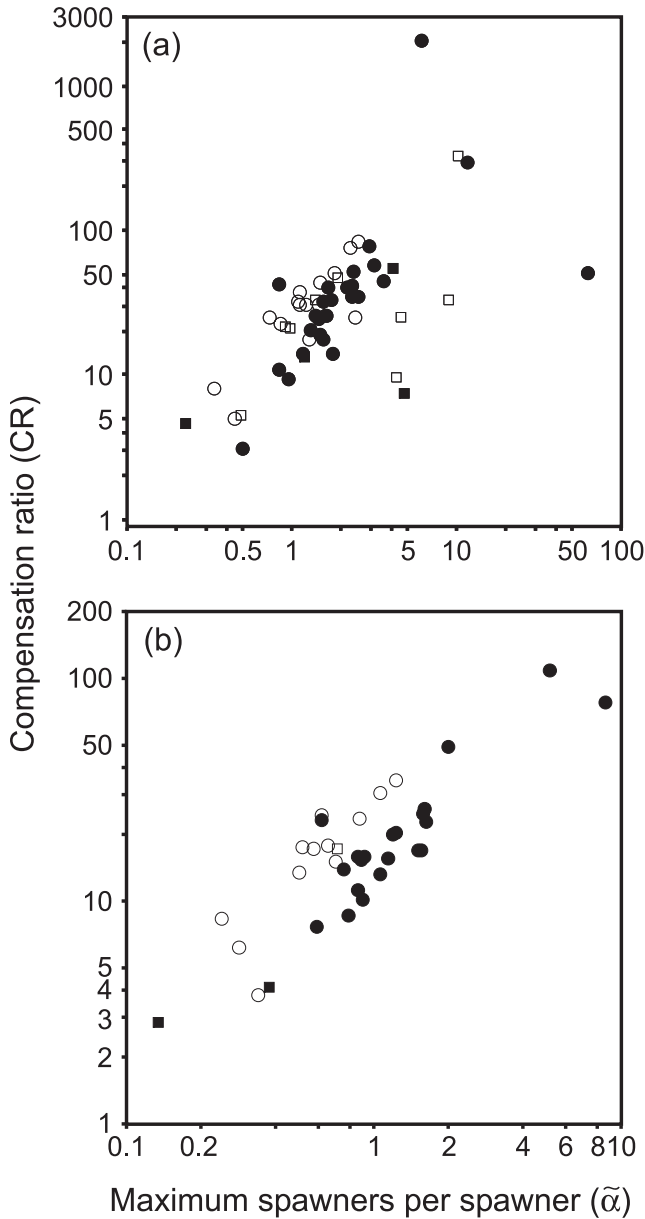
series (eq. 10a) can be rearranged to give $\tilde{\alpha}$ (Myers et al. 1997, 1999).

$$(10a) \quad \hat{\alpha} = \tilde{\alpha} / (1 - p_s)$$

$$(10b) \quad \tilde{\alpha} = \hat{\alpha} (1 - p_s) \quad \text{where } \hat{\alpha} = \alpha SPR_{F=0}$$

A measure of negative density-dependent recruit mortality reveals a less than proportional increase in recruit survival with increasing spawning stock biomass. Stocks that show a strong reduction in recruit survival have the greatest compensatory capacity to buffer against increases in adult mortality. Goodyear (1977) developed an index of this compensatory capacity, the compensation ratio (CR), to illustrate the reduction in compensatory reserve with increased fishing (decreasing spawning biomass). CR is used here as a standardized measure of density-dependent recruitment to compare across stocks and is calculated as the ratio

Fig. 2. Correlation between \log_e maximum spawners per spawner ($\tilde{\alpha}$) and \log_e compensation ratio (CR) derived for stocks based on (a) Ricker, and (b) hockey stick spawner–recruit models. High values of CR indicate strong density-dependent recruitment. \square , Clupeiformes; \bullet , Gadiformes; \blacksquare , Perciformes; \circ , Pleuronectiformes.



of maximum recruit survival, taken as the slope at the origin (α) or a spawner–recruit curve, and $SSB_{F=0}$ (eq. 11) (Fig. 1).

$$(11) \quad CR = \frac{\alpha}{\text{Recruit survival at } SSB_{F=0}}$$

A compensation ratio of one indicates no change in recruit mortality over the whole range of spawning biomass; higher values indicate strong decline in recruit survival. Values for $\tilde{\alpha}$, $SSB_{F=0}$, and CR are presented in Appendix Table A3.

Results

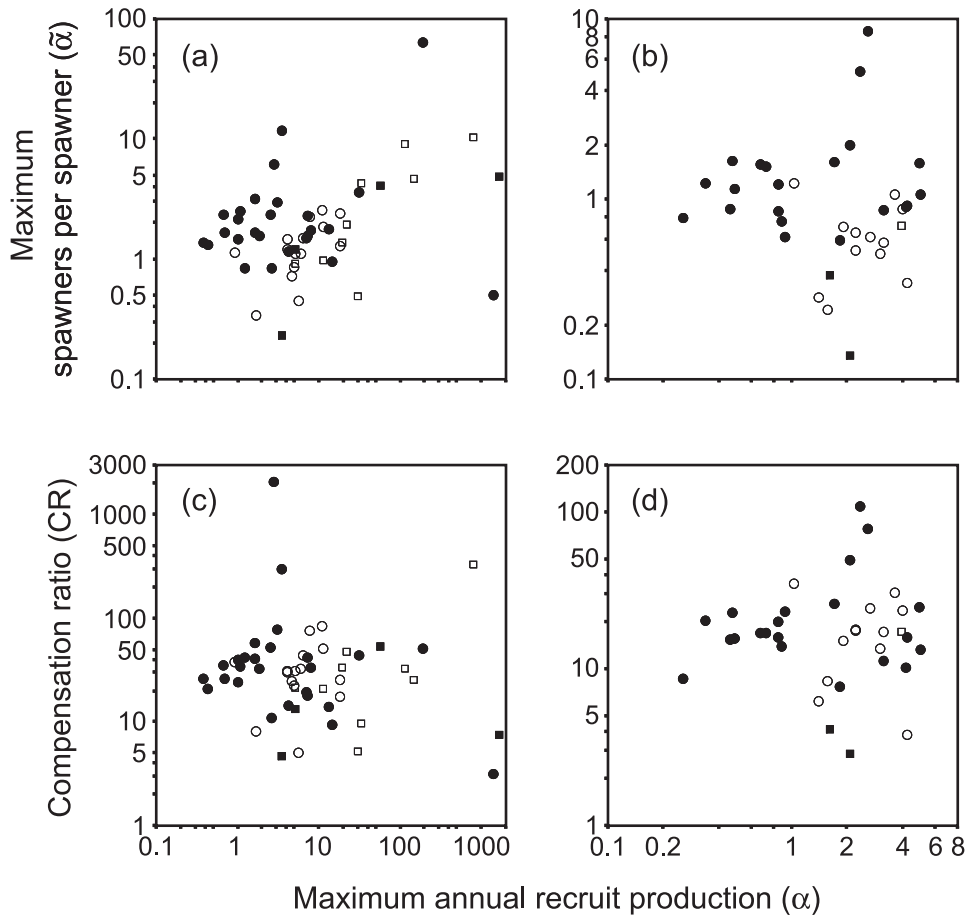
CR was strongest in stocks with high maximum spawners per spawner ($\tilde{\alpha}$) (Ricker: Pearson's $r = 0.62$, $n = 54$, $p < 0.001$; hockey stick: $r = 0.85$, $n = 36$, $p < 0.001$; Fig. 2). This correlation did not depend on the form of the spawner–recruit model, and estimates of $\tilde{\alpha}$ and CR were similar for the dome-shaped Ricker and plateau-shaped hockey stick models ($\tilde{\alpha}$: $r = 0.88$, $n = 36$, $p < 0.001$; CR: $r = 0.88$, $n = 36$, $p < 0.001$). The pattern of $\tilde{\alpha}$ versus CR was also consistent among stocks and species within Gadiformes and Pleuronectiformes, the two orders with sufficient data points for comparison (Fig. 2). The hockey stick correlation between $\tilde{\alpha}$ and CR was stronger than that with the Ricker stick recruitment model. When the 54 stocks were split into two groups (those that did fit a hockey stick model ($n = 36$) and those that did not ($n = 18$)), we found that the hockey stick did not fit stocks characterized by high values of Ricker's α (Ricker mean $\log_e \alpha \pm 1$ SE: hockey stick did fit = 1.04 ± 0.15 ; hockey stick did not fit = 4.00 ± 0.40 ; $t_{52} = 6.86$; $p < 0.001$). Stocks that did not fit the hockey stick model also had low values of $SPR_{F=0}$ (mean $\log_e SPR_{F=0} \pm 1$ SE: hockey stick did fit = 1.28 ± 0.17 ; hockey stick did not fit = -1.20 ± 0.44 ; $t_{52} = -5.29$; $p < 0.001$). However, these same stocks were not characterized by weak density dependence (Ricker mean $\log_e CR \pm 1$ SE: hockey stick did fit = 3.50 ± 0.18 ; hockey stick did not fit = 3.10 ± 0.25 ; $t_{52} = -1.34$; $p = 0.188$).

One explanation for the strong positive correlation between $\tilde{\alpha}$ and CR might be that stocks with high α could achieve maximum recruitment at lower spawning stock sizes, and so for a given mean unexploited SSB they would show a stronger degree of density-dependent recruitment. However, this is not the correct interpretation because, with one exception, α showed weak or no association with $\tilde{\alpha}$ (Ricker: $r = 0.36$, $n = 54$, $p = 0.007$; hockey stick: $r = -0.08$, $n = 36$, $p = 0.625$; Figs. 3a, 3b) or with CR (Ricker: $r = -0.12$, $n = 54$, $p = 0.375$; hockey stick: $r = -0.052$, $n = 36$, $p = 0.907$; Figs. 3c, 3d).

The composite life history measure ($SPR_{F=0}$) proved to be the best single predictor of both α and CR (Fig. 4). Stocks with high $SPR_{F=0}$ had the lowest α (Ricker: $\log_e \alpha = 2.44 - 0.91 \log_e SPR_{F=0}$, $r^2 = 0.76$, $F_{[1,53]} = 166.6$, $p < 0.001$, Fig. 4a; hockey stick: $\log_e \alpha = 1.26 - 0.60 \log_e SPR_{F=0}$, $r^2 = 0.57$, $F_{[1,35]} = 44.9$, $p < 0.001$, Fig. 4b). Stocks with a high $SPR_{F=0}$ also had the strongest compensation ratio (Ricker: $\log_e CR = 3.24 + 0.28 \log_e SPR_{F=0}$, $r^2 = 0.23$, $F_{[1,53]} = 15.35$, $p < 0.001$, Fig. 4c; hockey stick: $\log_e CR = 2.25 + 0.42 \log_e SPR_{F=0}$, $r^2 = 0.34$, $F_{[1,35]} = 17.68$, $p < 0.001$, Fig. 4d).

There are significant correlations between individual life history traits and $\tilde{\alpha}$ and CR (Table 1). Five of the twenty relationships were significant for the two recruitment models (Table 1). By chance alone, we would expect only one to be a false positive. Broadly speaking, large-bodied, late-maturing stocks had stronger density dependence at large stock sizes. However, individual life history traits had little explanatory power (Table 1). This was because individual life history traits could not predict both α and $SPR_{F=0}$, the major components of $\tilde{\alpha}$ (see eq. 10). However, they did provide an indirect estimate of $\tilde{\alpha}$ via their relationships with $SPR_{F=0}$, as well as α (Tables 2 and 3). Stocks with high α were typically

Fig. 3. Relationships between \log_e maximum annual recruit production (α) and \log_e maximum spawners per spawner ($\tilde{\alpha}$) (a, b) and \log_e compensation ratio (CR) (c, d) derived for stocks based on (a, c) Ricker and (b, d) hockey stick spawner–recruit models. □, Clupeiformes; ●, Gadiformes; ■, Perciformes; ○, Pleuronectiformes.



small-bodied, early-maturing, and had low fecundity and a fast generation time (Table 2). Life history traits explained between 8% and 67% of the variation in $SPR_{F=0}$ among stocks, with high $SPR_{F=0}$ among stocks with a heavy maximum body weight, slow growth rate, late age at maturity, high fecundity, and long generation time (Table 3).

Recall that 18 stocks did not fit the hockey stick model of recruitment. On closer inspection, 16 of these stocks had $SPR_{F=0}$ values of less than 1 kg (Figs. 4b and 4d). For stocks ≥ 1 kg $SPR_{F=0}$, a multiple regression based on individual life histories confirmed that the strongest CR was found in large-bodied, late-maturing stocks, with relatively low fecundity at maturity (Table 4).

Discussion

Our results have revealed that strong density-dependent recruit mortality at high spawner abundance occurs in marine fish stocks that produce high maximum numbers of spawners per spawner at low abundance. The correlation between density-related recruitment processes taking place at opposite ends of the spawner abundance spectrum is strongly mediated by life history traits. Stocks with high lifetime $SPR_{F=0}$ had low α and also longer generation times associated with multiple breeding over their lifetime. These results support other studies that link individual life history

traits to rates of annual recruitment (Myers et al. 1997; Hutchings 2001; Denney et al. 2002). They also suggest that fish exhibit a life history continuum that is similar to birds, ranging from “highly reproductive species” to “survivor species” (Sæther and Bakke 2000). More importantly, our work provides the first evidence for a relationship between life history traits and density-dependent recruitment at large population sizes, whereas Sæther and Bakke (2000) did not take density dependence into account.

Stocks with high $SPR_{F=0}$ are composed of individuals that show the expected trade-off between low α and high rates of repeat spawning over a lifetime. This bet-hedging strategy is common among species with a long reproductive lifespan and an extended age structure, which have the opportunity to spread their reproductive effort over a greater number of annual production cycles (Warner and Chesson 1985; Stearns 1992). Weak density-dependent recruit mortality (compensation) among stocks with low $SPR_{F=0}$ reflects the life history strategy of small, fast-growing species that exploit unpredictable productivity. This responsiveness is thought to create population dynamics with a high variance in population numbers. Slow-growing and late-maturing species have more stable populations and constant low annual recruitment at high population sizes.

The similarity of results for Ricker and hockey stick models of recruitment suggests a general pattern of association be-

Fig. 4. Relationship between \log_e maximum spawners per recruit in the absence of fishing ($SPR_{F=0}$) and (a, b) \log_e maximum annual recruit production (α) and the (c, d) \log_e compensation ratio (CR) for (a, c) Ricker and (b, d) hockey stick spawner–recruit models. □, Clupeiformes; ●, Gadiformes; ■, Perciformes; ○, Pleuronectiformes.

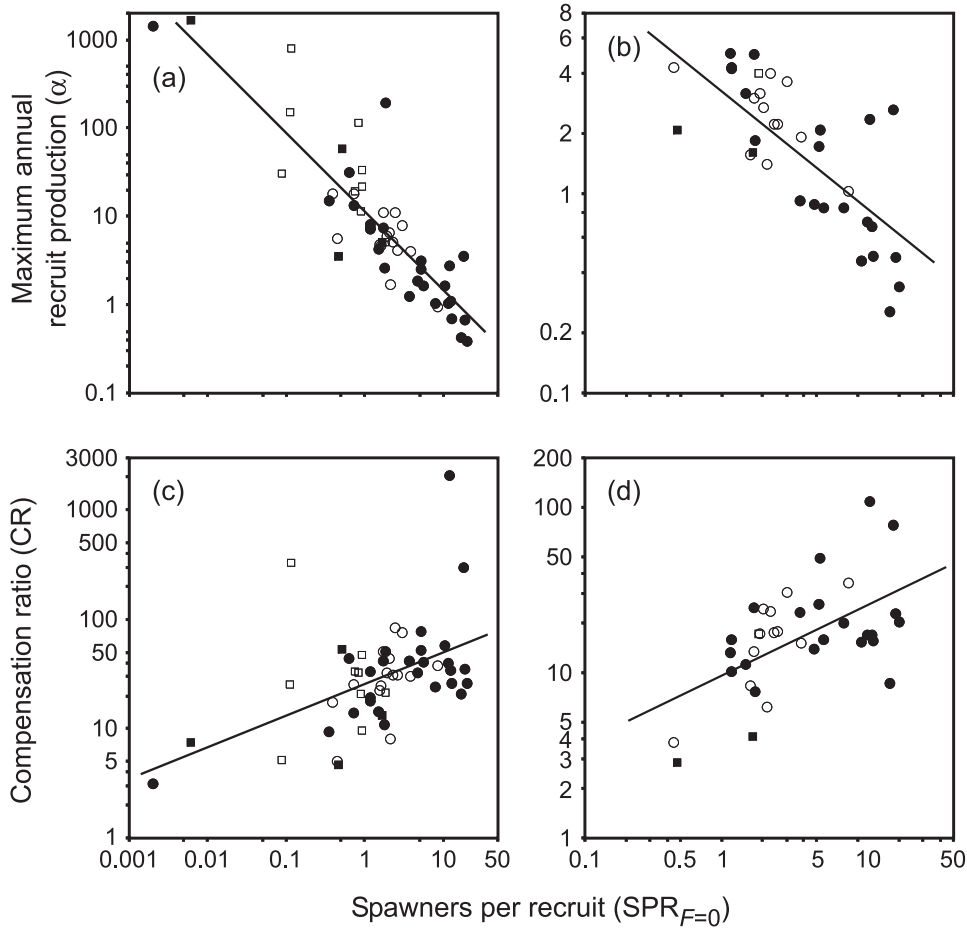


Table 1. Relationships between stock \log_e life histories and (i) \log_e maximum spawners per spawner ($\tilde{\alpha}$) and (ii) \log_e compensation ratio (CR), derived from Ricker and hockey stick spawner–recruit relationships.

| Life history trait | Ricker | | | | Hockey stick | | | |
|---|--------|-------------|-----|-------|--------------|-------------|-----|--------|
| | Slope | Model r^2 | N | P | Slope | Model r^2 | N | P |
| $\log_e \tilde{\alpha}$ | | | | | | | | |
| Maximum weight (W_∞) | -0.01 | <0.01 | 45 | 0.873 | 0.33 | 0.49 | 30 | <0.001 |
| Growth rate (κ) | 0.27 | 0.04 | 45 | 0.181 | -0.10 | 0.01 | 30 | 0.691 |
| Age at maturity (T_{mat}) | -0.08 | <0.01 | 53 | 0.729 | 0.46 | 0.07 | 35 | 0.129 |
| Fecundity (Fec_{mat}) | 0.03 | <0.01 | 43 | 0.721 | 0.28 | 0.20 | 27 | 0.016 |
| Generation time (G) | -0.06 | <0.01 | 43 | 0.899 | 0.19 | <0.01 | 27 | 0.767 |
| $\log_e CR$ | | | | | | | | |
| Maximum weight (W_∞) | 0.14 | 0.08 | 45 | 0.066 | 0.21 | 0.23 | 30 | 0.006 |
| Growth rate (κ) | -0.09 | <0.01 | 45 | 0.700 | -0.07 | <0.01 | 30 | 0.766 |
| Age at maturity (T_{mat}) | 0.46 | 0.05 | 53 | 0.091 | 0.72 | 0.17 | 35 | 0.011 |
| Fecundity (Fec_{mat}) | 0.24 | 0.16 | 43 | 0.007 | 0.13 | 0.05 | 27 | 0.256 |
| Generation time (G) | 0.97 | 0.09 | 43 | 0.048 | 0.77 | 0.07 | 27 | 0.189 |

tween $\tilde{\alpha}$ at low spawner abundance and density dependence at high abundance. The assumed form of density-dependent recruitment, which is rarely clear-cut, may therefore make little difference if we want to establish whether a stock has strong recruit potential at low stock sizes or has the capacity to buffer against the early phases of exploitation at high

stock sizes (high compensatory reserve). This is not to suggest that alternative spawner–recruit functions are redundant, rather that difficulties in identifying their shape or exact parameterisation need not be a fundamental barrier to an assessment of how a stock might respond to exploitation, or indeed how it recovers from it.

Table 2. Partial correlations between stock \log_e life histories and \log_e maximum annual recruit production (α) derived from Ricker and hockey stick spawner–recruit relationships while controlling for age at recruitment.

| Life history trait | Ricker | | | | Hockey stick | | | |
|--------------------------------------|---------------------|-------------|-----|--------|---------------------|-------------|-----|--------|
| | Partial correlation | Model r^2 | N | P | Partial correlation | Model r^2 | N | P |
| Maximum weight (W_∞) | −0.67 | 0.60 | 45 | <0.001 | −0.42 | 0.31 | 30 | 0.021 |
| Growth rate (κ) | 0.27 | 0.33 | 45 | 0.069 | −0.33 | 0.25 | 30 | 0.073 |
| Age at maturity (T_{mat}) | −0.43 | 0.41 | 53 | 0.001 | −0.11 | 0.18 | 35 | 0.522 |
| Fecundity (Fec_{mat}) | −0.64 | 0.53 | 43 | <0.001 | −0.59 | 0.38 | 27 | 0.001 |
| Generation time (G) | −0.50 | 0.41 | 43 | 0.001 | 0.16 | 0.08 | 27 | 0.417 |
| Spawners per recruit ($SPR_{F=0}$) | −0.83 | 0.77 | 53 | <0.001 | −0.70 | 0.57 | 35 | <0.001 |

Table 3. Linear regressions between \log_e life history characteristics of stocks and the \log_e spawners per recruit ($SPR_{F=0}$).

| Life history trait | Constant | Slope | Model r^2 | F | df | P |
|-------------------------------|----------|-------|-------------|------|-----|--------|
| Maximum weight (W_∞) | 0.09 | 0.61 | 0.67 | 88.9 | 144 | <0.001 |
| Growth rate (κ) | −0.5 | −0.59 | 0.08 | 3.7 | 144 | 0.062 |
| Age at maturity (T_{mat}) | −1.37 | 2.01 | 0.36 | 29.6 | 152 | <0.001 |
| Fecundity (Fec_{mat}) | −7.21 | 0.65 | 0.45 | 34.1 | 143 | <0.001 |
| Generation time (G) | −6.43 | 3.67 | 0.49 | 41.0 | 142 | <0.001 |

Table 4. Results of the multiple regression between \log_e life histories and \log_e compensation ratio (CR) for (i) Ricker and (ii) hockey stick recruitment models.

| Ricker ^a | | | | |
|-------------------------------|-------------|-------------------|----------|--------|
| Trait | Coefficient | SE of coefficient | t_{22} | P |
| Constant | 2.13 | 0.49 | 4.31 | <0.001 |
| Maximum weight (W_∞) | 0.18 | 0.10 | 1.76 | 0.090 |
| Age at maturity (T_{mat}) | 1.06 | 0.46 | 2.30 | 0.029 |
| Hockey stick ^b | | | | |
| Trait | Coefficient | SE of coefficient | t_{19} | P |
| Constant | 4.69 | 1.61 | 2.92 | 0.009 |
| Maximum weight (W_∞) | 0.32 | 0.10 | 3.06 | 0.007 |
| Age at maturity (T_{mat}) | 0.72 | 0.33 | 2.17 | 0.043 |
| Fecundity (Fec_{mat}) | −0.25 | 0.14 | −1.80 | 0.088 |

Note: Data were limited to those stocks whose $SPR_{F=0}$ is ≥ 1 kg, which equates to a maximum weight of approximately 1.5 kg or heavier. SE, standard error.

^aMultiple $r^2 = 0.29$; $F_{2,28} = 5.66$; $p = 0.009$.

^bMultiple $r^2 = 0.50$; $F_{3,19} = 6.42$; $p = 0.003$.

Individual life history traits were poor predictors of the two standardized measures of recruitment: $\tilde{\alpha}$ and CR. The positive relationship between maximum weight and $\tilde{\alpha}$ and CR derived from the hockey stick method could be due to a bias against smaller-bodied stocks. These stocks were excluded from the regression because the hockey stick model did not fit (Appendix Table A2). Indeed, we showed that these nonfitting stocks had an average value of α (derived from the Ricker model) that was 26 times greater than those that did fit hockey stick models.

A composite measure of life history traits ($SPR_{F=0}$) summarized the important elements from several traits and was much more informative. Unfortunately, few species have the age-specific life history data and estimates of natural mortality necessary to calculate $SPR_{F=0}$. Natural mortality is particularly difficult to estimate, and stock assessments often resort to giving this parameter a default estimate, such as

0.2. However, a multiple regression using more easily measured traits such as body size and age at maturity provided a reasonable prediction of CR for both Ricker and hockey stick recruitment models. Body size alone was a strong predictor of $SPR_{F=0}$, which would also enable an indirect estimate of the CR. Life history invariants and scaling rules could also be applied where direct measures are missing (Pope et al. 2000; Dulvy et al. 2004).

Iteroparity is thought to have evolved as a bet-hedging strategy to compensate for years of recruitment failure due to adverse environmental conditions (Stearns 1976; Hutchings 2002). This environmental component to recruitment implies a density-independent process. This might appear to contradict our evidence that bet-hedgers, which are typically large, late-maturing, and long-lived, have strong density-dependent recruit mortality. The strong density dependence among these species may be explained by compe-

tion among both recruits and adults, which depresses recruit survival at high densities. We suggest that both the negative intercohort effects on recruit survival and the strategy of producing large numbers of small offspring are not mutually exclusive. The outcome would be that bet-hedging can still exploit favourable environments and show unpredictable recruitment patterns, but individuals at high densities suffer a reduction in $\tilde{\alpha}$.

The environment is also expected to affect the recruit survival of pelagic and demersal fishes in different ways. For example, pelagic fishes are thought to track and exploit environmental conditions and show very little increase in recruit mortality with stock size (weak density dependence or compensation). However, since most pelagic species are small and short-lived, we cannot say whether or not pelagic and demersal fishes have different constraints upon maximizing recruit survival than would be predicted from life histories alone. A more wide-ranging pelagic data set is required to adequately address this question.

This study can be used to predict how stocks will respond to fishing and to assess vulnerability to extinction, particularly in data-poor situations. Stocks with low $SPR_{F=0}$ have weak density dependence and high annual production; at the outset of fishing, even low fishing mortality could rapidly deplete stocks with little compensatory recruitment, but show high resilience to extinction at very low stock sizes (e.g., Atlantic herring, *Clupea harengus*). Conversely stocks with strong density dependence have a greater compensatory reserve that is initially very productive, but then collapse through low resilience at small stock sizes as a result of low annual recruit production (e.g., Atlantic cod, *Gadus morhua*). The power of basic life history traits to predict $SPR_{F=0}$ also facilitates a precautionary approach to fisheries management because $SPR_{F=0}$ is already used to derive the biological reference points that indicate recruitment overfishing (Gabriel et al. 1989; Mace and Sissenwine 1993). For conservation managers, our results offer a further biological basis for developing meaningful vulnerability criteria for fishes that include density dependence (Hutchings 2001; Reynolds et al. 2002; Dulvy et al. 2003).

Future development of this approach could include habitat and environmental variables (such as temperature and productivity) to account for the remaining variance in density dependence. A community approach could also address the potential interactions among recruits of different species competing for similar resources during early life stages. Clearly, the timing and location of reproduction and the early life history combinations of developing offspring will also affect annual recruitment; these have not been considered in this study.

In conclusion, we have shown that a simple composite measure of life history (spawners per recruit) is correlated with density-dependent recruitment in commercially exploited fish populations. The correlation with density dependence remains when $SPR_{F=0}$ are combined with annual recruitment to yield the maximum number of spawners per spawner. We also found that populations that grow slowly from small sizes have the strongest density-dependent recruitment at large population sizes. These results suggest that we can build a framework based on life histories to predict marine fish population dynamics across species and populations.

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Appendix A

Appendix appears on the following pages.

Table A1. Summary of stock maximum weight (W_{∞}), growth rate (κ), age at 50% maturity (T_{mat}), fecundity at maturity (Fec_{mat}), generation time (G), and the maximum age class in the life history model (i_{max}) based on postrecruitment, age-specific values.

| Stock ^a | $\text{SPR}_{F=0}$ (kg) | W_{∞}^b (kg) | κ (year ⁻¹) | T_{mat} (years) | Fec_{mat} | G (years) | i_{max} (years) | M |
|--|----------------------------|------------------------|-----------------------------------|-----------------------------|---------------------------|----------------|-----------------------------|-----------|
| European anchovy (<i>Engraulis encrasicolus</i>) | | | | | | | | |
| BB | 0.115 | 0.07 | 0.25 | 0.50 | 1 52 800 | 3.1 | 5 | 0.12 |
| Atlantic cod (<i>Gadus morhua</i>) | | | | | | | | |
| CS and West Channel | 19.959 | 17.61 | 0.37 | 2.21 | 2 014 900 | 5.1 | 7 | 0.20 |
| Faroe Plateau | 11.577 | 76.13 | 0.07 | 2.97 | — | — | 9 | 0.20 |
| Iceland | 18.851 | 33.61 ^c | 0.12 | 5.06 | 520 460 | 10.2 | 14 | 0.20 |
| Irish Sea | 12.687 | 86.17 | 0.11 | 2.06 | 1 522 700 | 5.0 | 7 | 0.20 |
| Kattegat | 7.864 | 19.89 | 0.23 | 2.24 | — | — | 8 | 0.20 |
| Northeast Arctic | 12.078 | 129.20 | 0.07 | 6.95 | 1 361 800 | 10.4 | 13 | 0.20–0.38 |
| NS, Skagerrak, and East Channel | 18.107 | 18.99 | 0.24 | 3.73 | 806 250 | 7.7 | 11 | 0.20–0.80 |
| West Baltic | 5.264 | — | — | 2.82 | 935 830 | 5.5 | 7 | 0.20–0.24 |
| West Scotland | 12.972 | 28.53 | 0.20 | 2.02 | 917 720 | 5.1 | 7 | 0.20 |
| Blue whiting (<i>Micromesistius poutassou</i>) | | | | | | | | |
| Northern ICES | 0.356 | 0.33 ^c | 0.15 | 2.24 | 19 323 | 6.2 | 10 | 0.20 |
| Fourspotted megrim (<i>Lepidorhombus boscii</i>) | | | | | | | | |
| Iberia | 0.384 | — | — | 0.98 | 27 870 | 4.2 | 7 | 0.20 |
| Greenland halibut (<i>Reinhardtius hippoglossoides</i>) | | | | | | | | |
| Northeast Arctic | 8.568 | — | — | 9.17 | 16 250 | 12.7 | 15 | 0.15 |
| Haddock (<i>Melanogrammus aeglefinus</i>) | | | | | | | | |
| Faroe Plateau | 5.610 | 5.11 | 0.18 | 3.07 | — | — | 8 | 0.20 |
| Iceland | 4.724 | 6.89 | 0.17 | 3.76 | — | — | 9 | 0.20 |
| Northeast Arctic | 3.726 | 3.18 | 0.22 | 5.85 | 939 630 | 8.4 | 11 | 0.20–0.29 |
| NS, Skagerrak, and Kattegat | 1.827 | 3.24 | 0.17 | 2.52 | 125 740 | 7.1 | 10 | 0.20–2.05 |
| Rockall | 1.193 | 0.79 | 0.21 | 2.50 | 122 610 | 4.9 | 7 | 0.20 |
| West Scotland | 1.735 | 1.55 | 0.22 | 1.96 | 41 326 | 5.4 | 8 | 0.20 |
| European hake (<i>Merluccius merluccius</i>) | | | | | | | | |
| Iberia | 1.501 | 5.50 ^c | 0.15 | 3.19 | 165 850 | 6.2 | 8 | 0.20 |
| NS, CS, and Channel | 1.778 | 14.21 ^c | 0.13 | 3.78 | 723 880 | 6.4 | 8 | 0.20 |
| Atlantic herring (<i>Clupea harengus</i>) | | | | | | | | |
| CS and Southwest Ireland | 0.894 | 0.23 ^c | 0.31 | 1.00 | 14 359 | 5.6 | 9 | 0.10–1.00 |
| East Baltic | 0.088 | — | — | 1.83 | 6 988 | 5.0 | 8 | 0.20–0.30 |
| Iceland | 1.885 | 0.41 ^c | 0.29 | 3.40 | 25 393 | 10.0 | 15 | 0.10 |
| Irish Sea | 0.745 | 0.20 ^c | 0.52 | 1.58 | 32 693 | 5.2 | 8 | 0.10–1.00 |
| Norway | 0.922 | 0.43 ^c | 0.23 | 4.28 | 41 177 | 9.3 | 16 | 0.15–0.90 |
| NS | 0.834 | 0.26 ^c | 0.45 | 1.84 | 4 422 | 6.2 | 9 | 0.10–1.00 |
| West Scotland | 0.923 | 0.24 ^c | 0.45 | 1.87 | 42 424 | 5.8 | 9 | 0.10–1.00 |
| Atlantic horse mackerel (<i>Trachurus trachurus</i>) | | | | | | | | |
| Northeast Atlantic | 0.469 | 0.29 | 0.18 | 3.56 | 109 130 | 7.3 | 11 | 0.15 |
| Iberia | 0.513 | 0.31 | 0.22 | 3.75 | 64 468 | 7.9 | 12 | 0.15 |
| Atlantic mackerel (<i>Scomber scombrus</i>) | | | | | | | | |
| West stock | 1.683 | 0.65 | 0.26 | 1.90 | 294 940 | 6.7 | 12 | 0.15 |
| Megrim (<i>Lepidorhombus whiffiagonis</i>) | | | | | | | | |
| CS, West of Ireland, West Channel, and BB | 0.734 | 8.87 | 0.08 | 2.76 | — | — | 10 | 0.20 |
| Iberia | 0.442 | 5.11 | 0.05 | 1.23 | — | — | 7 | 0.20 |
| Norway pout (<i>Trisopterus esmarki</i>) | | | | | | | | |
| NS and Skagerrak | 0.002 | — | — | 1.23 | 15 125 | 2.1 | 4 | 1.60 |
| European plaice (<i>Pleuronectes platessa</i>) | | | | | | | | |
| CS | 2.029 | 1.53 | 0.14 | 2.86 | 67 880 | 6.5 | 9 | 0.12 |
| East Channel | 3.031 | 8.77 | 0.05 | 2.90 | 73 638 | 7.2 | 10 | 0.10 |
| Irish Sea | 1.562 | 6.85 | 0.05 | 2.94 | 63 233 | 6.4 | 9 | 0.12 |
| NS | 3.817 | 1.42 ^c | 0.12 | 2.50 | 52 240 | 9.0 | 15 | 0.10 |

Table A1 (concluded).

| Stock ^a | SPR _{F=0} (kg) | W _∞ ^b (kg) | κ (year ⁻¹) | T _{mat} (years) | Fec _{mat} | G (years) | i _{max} (years) | M |
|--|----------------------------|-------------------------------------|----------------------------|-----------------------------|--------------------|--------------|-----------------------------|-----------|
| Skagerrak and Kattegat | 2.432 | — | — | 2.50 | 49 915 | 7.4 | 11 | 0.10 |
| West Channel | 2.590 | 1.62 ^c | 0.16 | 2.86 | 65 241 | 6.9 | 10 | 0.12 |
| Pollock (<i>Pollachius virens</i>) | | | | | | | | |
| Faroe Plateau | 10.556 | — | — | 5.03 | — | — | 12 | 0.20 |
| Iceland | 17.005 | 21.09 | 0.14 | 4.91 | — | — | 14 | 0.20 |
| NS, Skagerrak, Kattegat, West Scotland, and Rockall | 5.164 | — | — | 4.68 | 1 149 100 | 7.9 | 10 | 0.20 |
| Sandeel (<i>Ammodytoidei</i> spp.) | | | | | | | | |
| NS | 0.006 | 0.03 ^c | 0.36 | 1.50 | 62 | 3.2 | 4 | 0.60–1.20 |
| European pilchard (<i>Sardina pilchardus</i>) | | | | | | | | |
| Iberia | 0.110 | 0.08 | 0.53 | 0.96 | 379 610 | 3.3 | 6 | 0.33 |
| Common sole (<i>Solea solea</i>) | | | | | | | | |
| CS | 1.907 | 0.80 | 0.21 | 3.06 | 100 300 | 7.1 | 10 | 0.10 |
| East Channel | 1.727 | 0.69 | 0.15 | 2.50 | 84 834 | 7.4 | 11 | 0.10 |
| Irish Sea | 1.641 | 0.60 | 0.16 | 2.40 | 83 306 | 6.5 | 10 | 0.10 |
| NS | 2.296 | 18.01 | 0.02 | 2.50 | 130 060 | 9.2 | 15 | 0.10 |
| West Channel | 2.131 | 0.74 | 0.18 | 3.06 | 139 190 | 7.7 | 12 | 0.10 |
| Whiting (<i>Merlangius merlangus</i>) | | | | | | | | |
| CS and West Channel | 1.181 | 8.15 | 0.05 | 1.50 | — | — | 7 | 0.20 |
| Irish Sea | 0.637 | 0.61 | 0.35 | 1.50 | — | — | 6 | 0.20 |
| NS and East Channel | 0.725 | 0.32 ^c | 0.71 | 1.46 | 221 710 | 4.8 | 8 | 0.20–0.95 |
| West Scotland | 1.163 | 2.98 | 0.08 | 1.50 | 312 410 | 4.5 | 7 | 0.20 |

Note: Spawner per recruit (SPR_{F=0}) is a composite measure of an individual's lifetime contribution to spawning biomass (see eq. 4). The instantaneous rate of natural mortality (*M*) shows the range of age-specific values.

^aBB, Bay of Biscay; Channel, English Channel; CS, Celtic Sea; NS, North Sea.

^bParameter *b* in the von Bertalanffy growth equation (eq. 1) was required to calculate W_∞. Values were mostly taken from regional or mean species estimates in FishBase (Froese and Pauly 2004).

^cData was taken from stock assessments.

Table A2 (concluded).

| Stock ^a | Ricker | | | | | Hockey stick | | | | | R _{age} (years) | | | | | |
|---|--------|-------|-----------------------|--|------|--------------|------|------|-------|-----------|-----------------------------|-------|------|------|----|---|
| | α | SD α | β (10 ⁻⁵) | SD β (10 ⁻⁷) ^b | σ̂ | LL | SS | α | SD α | S* | | SD S* | σ̂ | LL | SS | N |
| Atlantic mackerel (<i>Scomber scombrus</i>) | | | | | | | | | | | | | | | | |
| Western stock | 5.11 | <0.01 | 0.04 | < | 0.43 | -469 | 5.5 | 1.60 | <0.01 | 2 508 200 | 0 | 0.43 | -469 | 5.4 | 30 | 0 |
| Megrim (<i>Lepidorhombus whiffiagonis</i>) | | | | | | | | | | | | | | | | |
| CS, West of Ireland, West Channel, and BB | 18.08 | 0.32 | 2.3 | 413.73 | 0.23 | -230 | 1.0 | — | — | — | — | — | — | — | 17 | 1 |
| Iberia | 5.58 | <0.01 | 18.14 | < | 0.50 | -136 | 4.3 | 4.26 | 0.03 | 2 094 | 413 | 0.50 | -136 | 4.5 | 15 | 1 |
| Norway pout (<i>Trisopterus esmarki</i>) | | | | | | | | | | | | | | | | |
| NS and Skagerrak | 1424.3 | <0.01 | 0.43 | < | 0.58 | -523 | 9.5 | — | — | — | — | — | — | — | 28 | 0 |
| European plaice (<i>Pleuronectes platessa</i>) | | | | | | | | | | | | | | | | |
| CS | 6.46 | 0.13 | 47.34 | 149.70 | 0.52 | -201 | 5.7 | 2.68 | 1.23 | 1 983 | 537 | 0.51 | -199 | 5.9 | 23 | 1 |
| East Channel | 7.83 | <0.01 | 11.66 | < | 0.36 | -236 | 2.9 | 3.66 | 0.25 | 6 558 | 3 189 | 0.36 | -236 | 2.9 | 22 | 1 |
| Irish Sea | 4.89 | <0.01 | 12.28 | < | 0.36 | -375 | 5.0 | — | — | — | — | — | — | — | 37 | 1 |
| NS | 4.06 | <0.01 | 0.35 | < | 0.40 | -605 | 7.2 | 1.92 | 0.25 | 219 400 | 23 202 | 0.41 | -603 | 7.3 | 45 | 1 |
| Skagerrak and Kattegat | 11.04 | <0.01 | 5.75 | < | 0.37 | -263 | 5.0 | 2.23 | 0.07 | 22 596 | 685 | 0.45 | -258 | 4.3 | 23 | 2 |
| West Channel | 4.13 | 0.09 | 29.97 | 133.97 | 0.50 | -227 | 7.0 | 2.23 | 0.08 | 2 528 | 179 | 0.50 | -226 | 7.6 | 26 | 1 |
| Pollock (<i>Pollachius virens</i>) | | | | | | | | | | | | | | | | |
| Faroe Plateau | 1.65 | <0.01 | 1.85 | < | 0.46 | -399 | 10.5 | 0.46 | 0.03 | 55 047 | 5 371 | 0.51 | -396 | 9.3 | 38 | 3 |
| Iceland | 0.43 | <0.01 | 0.44 | < | 0.57 | -391 | 12.3 | 0.26 | 0.03 | 132 810 | 134 990 | 0.56 | -391 | 12.1 | 37 | 3 |
| NS, Skagerrak, Kattegat, West Scotland, and Rockall | 2.51 | <0.01 | 0.32 | < | 0.43 | -411 | 6.3 | 1.71 | 0.17 | 157 200 | 15 900 | 0.43 | -411 | 6.2 | 32 | 1 |
| Sandeel (<i>Ammodytoidei</i> spp.) | | | | | | | | | | | | | | | | |
| NS | 1643.3 | 33.84 | 0.09 | 0.28 | 0.57 | -367 | 6.1 | — | — | — | — | — | — | — | 18 | 0 |
| European pilchard (<i>Sardina pilchardus</i>) | | | | | | | | | | | | | | | | |
| Iberia | 149.06 | <0.01 | 0.43 | < | 0.46 | -395 | 6.7 | — | — | — | — | — | — | — | 24 | 0 |
| Common sole (<i>Solea solea</i>) | | | | | | | | | | | | | | | | |
| CS | 6.03 | <0.01 | 43.26 | < | 0.30 | -287 | 2.8 | 3.15 | 0.14 | 1 486 | 63 | 0.30 | -287 | 2.6 | 31 | 1 |
| East Channel | 11.15 | <0.01 | 14.76 | < | 0.38 | -214 | 2.9 | 3.02 | 0.17 | 8 289 | 1 561 | 0.39 | -214 | 2.8 | 20 | 1 |
| Irish Sea | 4.65 | <0.01 | 25.79 | < | 0.58 | -276 | 10.6 | 1.56 | 0.16 | 4 305 | 356 | 0.59 | -275 | 10.6 | 31 | 2 |
| NS | 5.11 | <0.01 | 1.68 | < | 0.78 | -510 | 26.8 | 4.02 | <0.01 | 24 712 | 0 | 0.77 | -511 | 26.1 | 45 | 1 |
| West Channel | 1.68 | 0.02 | 7.28 | 39.82 | 0.27 | -306 | 4.7 | 1.41 | 0.03 | 3 673 | 473 | 0.27 | -305 | 4.8 | 33 | 1 |
| Whiting (<i>Merlangius merlangus</i>) | | | | | | | | | | | | | | | | |
| CS and West Channel | 7.31 | <0.01 | 2.83 | < | 0.54 | -242 | 6.5 | 4.20 | <0.01 | 20 100 | 0 | 0.55 | -242 | 6.2 | 21 | 0 |
| Irish Sea | 31.47 | <0.01 | 9.83 | < | 0.43 | -263 | 5.0 | — | — | — | — | — | — | — | 22 | 0 |
| NS and East Channel | 13.47 | 0.34 | 0.23 | 1.25 | 0.32 | -334 | 2.8 | — | — | — | — | — | — | — | 22 | 1 |
| West Scotland | 7.14 | <0.01 | 2.79 | < | 0.40 | -283 | 5.3 | 5.02 | 0.12 | 17 425 | 852 | 0.41 | -282 | 5.5 | 24 | 1 |

Note: α, maximum annual recruitment per spawner; SD, standard deviation; β governs the population size at which density dependence occurs; σ̂, log error; LL, log-likelihood; SS, sum of squares; S*, spawning stock biomass at median recruitment; N, length of time series; R_{age}^a, age-at-recruitment; —, spawner-recruit data did not fit the hockey stick relationship. Standard deviations are based on bootstrap analysis with 1000 iterations; each iteration included a full spawner-recruit fitting procedure (see Methods for details about fitting methods).
^aBB, Bay of Biscay; Channel, English Channel; CS, Celtic Sea; NS, North Sea.
^bA less than symbol (<) indicates SD β < 0.00000001.

Table A3. Summary of Ricker and hockey stick estimates of maximum spawners per spawner ($\tilde{\alpha}$), mean unexploited spawning stock biomass ($SSB_{F=0}$), and the compensation ratio (CR).

| Stock ^a | Ricker | | | Hockey stick | | |
|--|------------------|-------------|---------|------------------|-------------|--------|
| | $\tilde{\alpha}$ | $SSB_{F=0}$ | CR | $\tilde{\alpha}$ | $SSB_{F=0}$ | CR |
| European anchovy (<i>Engraulis encrasicolus</i>) | | | | | | |
| BB | 10.24 | 314 370 | 330.97 | — | — | — |
| Atlantic cod (<i>Gadus morhua</i>) | | | | | | |
| CS and West Channel | 1.38 | 226 180 | 25.81 | 1.22 | 282 820 | 20.47 |
| Faroe Plateau | 2.16 | 169 190 | 40.07 | 1.51 | 562 700 | 16.98 |
| Iceland | 2.32 | 3 307 300 | 34.83 | 1.63 | 11 397 000 | 22.94 |
| Irish Sea | 2.52 | 59 493 | 34.45 | 1.56 | 201 600 | 17.02 |
| Kattegat | 1.47 | 238 660 | 24.12 | 1.20 | 547 050 | 19.99 |
| Northeast Arctic | 6.09 | 4 699 100 | 2081.28 | 5.14 | 24 524 000 | 109.25 |
| NS, Skagerrak, and East Channel | 11.59 | 1 945 900 | 297.86 | 8.57 | 12 642 000 | 78.78 |
| West Baltic | 2.96 | 333 570 | 77.69 | 1.99 | 1 672 700 | 49.72 |
| West Scotland | 1.64 | 116 380 | 25.81 | 1.14 | 323 900 | 15.61 |
| Blue whiting (<i>Micromesistius poutassou</i>) | | | | | | |
| Northern ICES | 0.96 | 6 308 000 | 9.46 | — | — | — |
| Fourspotted megrim (<i>Lepidorhombus boscii</i>) | | | | | | |
| Iberia | 1.28 | 12 000 | 17.65 | — | — | — |
| Greenland halibut (<i>Reinhardtius hippoglossoides</i>) | | | | | | |
| Northeast Arctic | 1.12 | 273 160 | 37.91 | 1.22 | 796 560 | 34.8 |
| Haddock (<i>Melanogrammus aeglefinus</i>) | | | | | | |
| Faroe Plateau | 1.65 | 133 160 | 40.45 | 0.86 | 387 290 | 15.9 |
| Iceland | 1.57 | 274 450 | 32.17 | 0.76 | 832 930 | 13.95 |
| Northeast Arctic | 0.84 | 1 320 300 | 42.03 | 0.62 | 3 705 000 | 23.34 |
| NS, Skagerrak, and Kattegat | 63.5 | 1 717 700 | 50.63 | — | — | — |
| Rockall | 1.75 | 25 326 | 33.4 | 0.92 | 57 947 | 15.77 |
| West Scotland | 2.31 | 138 050 | 41.91 | 1.57 | 435 790 | 24.7 |
| European hake (<i>Merluccius merluccius</i>) | | | | | | |
| Iberia | 1.16 | 186 260 | 14.17 | 0.86 | 361 320 | 11.26 |
| NS, CS, and Channel | 0.84 | 801 420 | 10.96 | 0.59 | 1 179 900 | 7.71 |
| Atlantic herring (<i>Clupea harengus</i>) | | | | | | |
| Celtic Sea and Southwest Ireland | 0.97 | 378 280 | 20.9 | — | — | — |
| East Baltic | 0.49 | 3 407 500 | 5.2 | — | — | — |
| Iceland | 0.91 | 1 147 400 | 21.36 | 0.71 | 2 737 600 | 17.22 |
| Irish Sea | 1.38 | 150 900 | 32.94 | — | — | — |
| Norway | 4.27 | 19 432 000 | 9.52 | — | — | — |
| NS | 9.04 | 4 251 400 | 32.8 | — | — | — |
| West Scotland | 1.92 | 425 440 | 47.24 | — | — | — |
| Atlantic horse mackerel (<i>Trachurus trachurus</i>) | | | | | | |
| Northeast Atlantic | 0.23 | 3 711 400 | 4.66 | 0.14 | 4 534 800 | 2.86 |
| Iberia | 4.12 | 346 540 | 54 | — | — | — |
| Atlantic mackerel (<i>Scomber scombrus</i>) | | | | | | |
| Western stock | 1.20 | 5 851 600 | 13.27 | 0.38 | 10 410 000 | 4.15 |
| Megrim (<i>Lepidorhombus whiffiagonis</i>) | | | | | | |
| CS, West of Ireland, West Channel, and BB | 2.40 | 139 870 | 25.07 | — | — | — |
| Iberia | 0.45 | 9 374 | 4.99 | 0.34 | 8 749 | 3.82 |
| Norway pout (<i>Trisopterus esmarki</i>) | | | | | | |
| NS and Skagerrak | 0.50 | 264 810 | 3.11 | — | — | — |

Table A3 (concluded).

| Stock ^a | Ricker | | | Hockey stick | | |
|---|------------------|--------------------|-------|------------------|--------------------|-------|
| | $\tilde{\alpha}$ | SSB _{F=0} | CR | $\tilde{\alpha}$ | SSB _{F=0} | CR |
| European plaice (<i>Pleuronectes platessa</i>) | | | | | | |
| CS | 1.48 | 7 973 | 43.41 | 0.61 | 34 707 | 24.25 |
| East Channel | 2.26 | 37 186 | 76.39 | 1.05 | 231 540 | 30.5 |
| Irish Sea | 0.86 | 25 398 | 22.64 | — | — | — |
| NS | 1.47 | 983 620 | 30.46 | 0.70 | 3 148 900 | 15.18 |
| Skagerrak and Kattegat | 2.56 | 76 890 | 83.39 | 0.52 | 390 830 | 17.52 |
| West Channel | 1.21 | 11 466 | 30.87 | 0.65 | 42 400 | 17.81 |
| Pollock (<i>Pollachius virens</i>) | | | | | | |
| Faroe Plateau | 3.15 | 219 630 | 57.56 | 0.88 | 844 890 | 15.35 |
| Iceland | 1.31 | 687 530 | 20.61 | 0.79 | 1 612 500 | 8.69 |
| NS, Skagerrak, Kattegat, West Scotland, and Rockall | 2.35 | 1 243 000 | 52.03 | 1.60 | 3 825 800 | 25.9 |
| Sandeel (<i>Ammodytoidei</i> spp.) | | | | | | |
| NS | 4.82 | 2 229 000 | 7.43 | — | — | — |
| European pilchard (<i>Sardina pilchardus</i>) | | | | | | |
| Iberia | 4.62 | 754 390 | 25.07 | — | — | — |
| Common sole (<i>Solea solea</i>) | | | | | | |
| CS | 1.1 | 8 031 | 32.27 | 0.57 | 25 046 | 17.17 |
| East Channel | 1.83 | 26 551 | 50.29 | 0.50 | 113 890 | 13.36 |
| Irish Sea | 0.73 | 12 458 | 24.86 | 0.24 | 35 165 | 8.36 |
| NS | 1.12 | 204 050 | 30.99 | 0.88 | 580 530 | 23.49 |
| West Channel | 0.34 | 28 768 | 8.06 | 0.29 | 24 954 | 6.18 |
| Whiting (<i>Merlangius merlangus</i>) | | | | | | |
| CS and West Channel | 1.57 | 101 720 | 17.81 | 0.90 | 203 150 | 10.11 |
| Irish Sea | 3.64 | 38 553 | 44.29 | — | — | — |
| NS and East Channel | 1.77 | 1 158 300 | 14.07 | — | — | — |
| West Scotland | 1.50 | 105 760 | 19.13 | 1.06 | 233 930 | 13.31 |

^aBB, Bay of Biscay; Channel, English Channel; CS, Celtic Sea; NS, North Sea.