Coexistence in North Sea fish communities: implications for growth and natural mortality

Henrik Gislason, John G. Pope, Jake C. Rice, and Niels Daan

For a fish community to persist over time, all species must be able on average to replace themselves on a one-for-one basis over their lifetime. We use this principle and a size-based equilibrium model where asymptotic length is used as a functional trait to investigate how natural mortality should scale with size within and across pelagic and demersal species of North Sea teleosts. The model predicts natural mortality to scale with body length raised to a power of -1.66 at current levels of exploitation. Additionally, natural mortality of demersal species should be proportional to asymptotic length raised to a power of 0.80, so generating a higher natural mortality at a given length for large species than for small ones. The model also suggests that the exponent in the scaling of the von Bertalanffy growth parameter K with asymptotic length should be more negative for pelagic than for demersal species. We test our results by analysing independent estimates of predation mortality, the scaling of maximum recruitment per unit of spawning-stock biomass with asymptotic length, and the general relationship between K and asymptotic length for demersal and pelagic families of fish. All tests are consistent with our modelling results.

Keywords: coexistence, fish communities, growth, life history, natural mortality, net reproductive rate, replacement, size-based model, size structure, stock–recruitment.

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H. Gislason: National Institute of Aquatic Resources, Technical University of Denmark, Charlottenlund Slot, DK–2920 Charlottenlund, Denmark. J. G. Pope: Norwegian College of Fishery Science, University of Tromsø, N–9000 Tromsø, Norway. J. C. Rice: DFO Science Advisory Secretariat, Department of Fisheries and Oceans, 200 Kent Street, Ottawa, Ontario, Canada K1A 0E6. N. Daan: Institute for Marine Resources and Ecosystem Studies, PO Box 68, 1970 AB IJmuiden, The Netherlands. Correspondence to H. Gislason: tel: +45 33963361; fax: +45 33963333; e-mail: hg@difres.dk.

Introduction

Modelling exploited fish populations (Quinn and Deriso, 1999) often involves attempts to close the life cycle of the population by functionally linking numbers of recruits to numbers of spawners. This includes examining processes that regulate the number of recruits produced per unit of spawning-stock biomass (R/SSB) and processes regulating the spawning-stock biomass produced per recruit (SSB/R). In both cases, the underlying principle has been that for a population to persist, on average its members will have to replace themselves on a one-for-one basis over their lifetime. Failure to replace at least one-for-one will lead to population declines, which cannot continue indefinitely without extinction. Consistently replacing at a rate greater than one-for-one will produce population growth that cannot continue indefinitely for ecological and energetic reasons.

Approaches for equilibrium and temporary non-equilibrium modelling of single populations are well established (Murdoch, 1994), with density dependence as a routine property of at least some processes, including feeding, growth, and recruitment. However, when such models are placed in a community context, additional considerations emerge. Fish communities do persist over time in the sense that sympatric species coexist over geological timescales (Daan et al., 1990). For this to happen, not only must

individual populations on average maintain replacement, but competitors, predators, and prey on average must coexist. This does not mean that the populations need ever reach a static equilibrium, nor that the dynamics of species need be tightly coupled. However, it does mean that no predator population can consistently prevent its prey populations from being able to replace themselves spawner-for-spawner, or consistently fail to find sufficient prey to support replacement of itself. Density dependence remains a necessary consideration at the community scale, although the ways it is expressed requires more directed study.

How populations solve the challenges of existence are reflected in their life-history strategies (Stearns, 1992), in solutions to the challenges of coexistence and coadaptation in their strategies of predation and predator avoidance (Holt and Polis, 1997), and in trade-offs among life-history processes (Kneitel and Chase, 2004). Many of the more abundant fish species of commercial interest are trophic generalists, occupying broad feeding niches (Garrison and Link, 2000; Trenkel et al., 2005). This raises questions about how multiple populations can coexist without the bulk of the biomass gradually becoming monopolized by a few species characterized by sets of life history, predation, and predator-avoidance strategies and parameters that make them more efficient at replacement, or more effective as a predator or

at avoiding predation. Species coexistence in communities means that just as single-species models must close the loop for replacement from spawner to spawner (or egg to egg), multispecies models must close the life cycles of all populations in a community simultaneously, with spawner-for-spawner (or egg-for-egg) replacement on average. Otherwise, populations will gradually be lost and eventually the community will come to consist of only the few most successful species.

Size has proven a powerful property for understanding and modelling the processes involved in life-history strategies leading to replacement. Basic biological processes, such as metabolism, food intake, growth, reproduction, and mortality, all scale with body size (Kooijman, 2000; Brown *et al.*, 2004; West and Brown, 2005). For fish populations, there have been empirical observations of relationships between von Bertalanffy growth parameters, natural mortality, and size or age at first maturity (Pauly, 1980; Beverton, 1987; Charnov, 1993; Jensen, 1996). These size-based relationships have been found among as well as within species, allowing size-dependent scaling to be combined with the theory of life-history strategies to understand fish community dynamics (Charnov *et al.*, 2001; Denney *et al.*, 2002; Goodwin *et al.*, 2006). Using functional traits such as asymptotic length (L_∞) to provide scaling relationships across species in size-based models offers a promising avenue for identifying the trade-offs involved in the processes important for coexistence (McGill *et al.*, 2006). The size-based multispecies models of Hall *et al.* (2006) and Pope *et al.* (2006) focused primarily on the role that size-based predation plays in fish community regulation. We confront the question of whether recruitment scales with asymptotic length (L_∞) across the species in a given community. This question is fundamental for community persistence, by framing the requirement for, on average, one-for-one replacement in the setting of all the interacting populations in the community.

Two pieces of evidence suggest that strong size-dependent scaling in recruitment is necessary to allow species to coexist. First, empirically there is a large and systematic difference between large and small species in the maximum R/SSB (Denney *et al.*, 2002). Those authors found that large, slow-growing species generated significantly lower maximum R/SSB than did smaller, fast-growing species. Across 54 northeast Atlantic stocks, maximum R/SSB scaled with maximum length raised to a power close to -3, indicating that a species with $L_\infty = 100$ cm produces 1000 times fewer R/SSB than would a species with $L_\infty = 10$ cm (Denney *et al.*, 2002). Second, in developing multispecies size-based predation models for Georges Bank and the North Sea, respectively, Hall *et al.* (2006) and Pope *et al.* (2006) found that for their models to match observed values for abundance, small species needed to consistently generate a higher R/SSB than larger ones. Hall *et al.* (2006) found that the maximum R/SSB estimated from data collected by Myers *et al.* (1995) scaled to asymptotic length raised to a power of -2.3. At low population sizes, a species with $L_\infty = 10$ cm would need to produce $\sim$200 times more R/SSB in their model than a species with $L_\infty = 100$ cm. Likewise, Pope *et al.* (2006) found it impossible to maintain both small and large species in their model simulations unless the R/SSB of the small species was three orders of magnitude higher. If on average R/SSB was constant over all species, over time only the largest species would remain in both model simulations.

These apparent differences in realized R/SSB between small and large teleosts have important implications for replacement of populations in a community. Consider two species for which their L_∞ differs by a factor of 10. If both species have the same SSB, spawn once annually, and produce the same number of eggs per gramme of female body mass, they should both produce approximately the same total number of eggs annually. However, because of the difference in R/SSB, these equal numbers of eggs will result in the smaller species producing $2-3$ orders of magnitude more recruits. Because the biological processes producing this difference are acting on prerecruits that are of the same size, regardless of how big they will eventually grow, this difference begs for a plausible explanation.

To investigate possible causes of the difference in R/SSB, we construct a simple size-based model and use it to explore the conditions required for simultaneous replacement of different sizes of coexisting fish species. Our model uses the scaling of mortality, growth, maturation, and fecundity with L_∞ to calculate the net reproductive rate, R, for fish of different L_∞ in the equilibrium situation. The differences in survivorship may reflect differences in predator-avoidance strategy, so the model considers demersal and pelagic habitats separately, to reflect the different potential strategies for predator avoidance in the two types of habitat. The model is parameterized with data on fishing mortality and scaling factors for growth and reproduction representative for the North Sea fish community. We use the model to estimate how natural mortality should scale with body size and L_∞ to achieve replacement (i.e. $R = 1$) simultaneously for all species, irrespective of their L_∞. We also use the model to explore what aspects of species life histories and behaviours may contribute to the estimated scaling of mortality with size. Winemiller and Rose (1992) classified fish species according to different life-history strategies. McCann (1998) used these strategies in a stage-structured model with density-dependent interactions, and was able to obtain coexistence for only two out of four strategies. Others have used differences in average body size to explain coexistence (e.g. Etienne and Olff, 2004; Scheffer and van Nes, 2006). However, before this study, the scaling of growth and reproduction with L_∞ and length has not been used to explore how natural mortality should scale with body size. Nor have the implications that a large difference in R/SSB for small and large species would have for recruitment and replacement been addressed.

Our model and analyses are limited by incomplete information on the reproduction and early life stages of marine teleosts. Most fish species produce eggs with a median diameter of $\sim$1 mm (Chambers, 1997; Appendix Table A2), and mature gonads account for $\sim$20% of female body weight. Nonetheless, the reproductive potential of stocks may vary systematically as a function of an individual's age and size, and changes in sex ratio, sexual maturity, and condition (Tomkiewicz *et al.*, 2003). Likewise, estimates of the natural mortality of first-feeding post-larvae used as input to our model are uncertain, so we investigate the sensitivity of our results to changes in relative fecundity and to the natural mortality of the post-larvae. We check the model by comparing the output with estimates of natural mortality derived from multispecies virtual population analysis (MSVPA) using comprehensive stomach content data, with growth characteristics of pelagic and demersal families of fish from FishBase (Froese and Pauly, 2006), and with the scaling of maximum recruit production with L_∞ reported by Denney *et al.* (2002). We also investigate the possibilities for coexistence in a simpler model where no distinction is made between pelagic and demersal habitats. Finally, we discuss the implications of our findings in the context of

general differences in life-history characteristics of demersal and pelagic species, and for management.

The model
General description
The model describes a fish community composed of a number of teleost populations in steady state, i.e. where growth, mortality, and recruitment are constant over time. As in the size-based model of Pope *et al.* (2006), where additional justification for many of the formulations that follow are presented, we represent different fish species in the community by their L_∞, with one hypothetical species per 5 cm increment from the smallest to the largest species present, and use information on how growth, mortality, and reproduction scale with L_∞ to model the steady-state populations in each L_∞ group. However, in contrast to Pope *et al.* (2006), we also account for fish <5 cm and include eggs, larvae, and early juveniles. Further, we split the species into demersal and pelagic, to account for possible habitat-related differences in scaling factors.

Briefly, the model calculates the number of individuals for each L_∞ group ("species") in subsequent size classes, and estimates the total number of eggs produced by the mature females. The calculations start with the same number of eggs (E_0) for all species. These eggs and the subsequent yolk-sac larvae suffer from mortality. The yolk-sac larvae become post-larvae when they start feeding at a fixed length, L_0. The post-larvae grow and suffer mortality until they become juveniles at a length, L_{met}. Juvenile demersal species settle and may experience a change in the level of their natural mortality at settling, whereas juvenile pelagic species continue to have a natural mortality determined exclusively by their individual length. Both pelagic and demersal species are subject to fishing mortality. Females mature at a size L_{mat} after which they start to produce eggs. Relative fecundity is used to calculate the total lifetime egg production (E_{1,L_∞}) of a cohort for each L_∞ group. The model is finally used to find the values of natural mortality (M_L) producing a one-for-one replacement of eggs ($R = 1$) across the size range of fish species found in the fish community (i.e. a value of $E_{1,L_\infty}/E_0$ as close as possible to 1 for all L_∞ groups in the range). Length is measured in cm, body weight in g, age in years, and all mortality and growth rates are annual unless otherwise specified.

Egg and yolk-sac larval survival
Of the E_0 eggs spawned, only some will hatch to become yolk-sac larvae, and only a fraction of the yolk-sac larvae will survive to become post-larvae. If the fractions surviving the egg (C_e) and yolk-sac larval stages (C_y) are known, the initial number of post-larvae at length L_0, (N_{L_0}) can be calculated from

$$N_{L_0} = C_e C_y E_0. \tag{1}$$

Growth
Many fish species undergo major ontogenetic changes during their early development (Fuiman and Higgs, 1997), and parameters derived from adult fish often provide a poor description of larval growth. We follow Pepin (1991) and describe post-larval growth as an allometric function of larval length:

$$\frac{dL}{dt} = aL^b, \tag{2}$$

where a and b are constants. The solution to this equation is

$$L = \left(L_0^{(1-b)} + a(1-b)t\right)^{(1/(1-b))}. \tag{3}$$

Rearranging Equation (3) provides the age (t_L) of a post-larva of given length L:

$$t_L = \frac{\left(L^{(1-b)} - L_0^{(1-b)}\right)}{a(1-b)}. \tag{4}$$

For juvenile and adult fish, we follow Pope *et al.* (2006) and use the von Bertalanffy equation

$$L = L_\infty\left(1 - e^{-K(t-t_0)}\right), \tag{5}$$

where t is age and t_0 can be found from

$$t_0 = t_{L_{met}} + \frac{1}{K}\ln\left(\frac{L_{met} - L_\infty}{L_\infty}\right), \tag{6}$$

where $t_{L_{met}}$, the age at the end of the post-larval stage, is estimated by inserting L_{met} in Equation (4).

The growth parameter K is assumed to scale with L_∞. However, the scaling may be habitat-dependent and may hence differ for pelagic and demersal species:

$$K_{dem} = d_{dem}L_\infty^{e_{dem}} \quad \wedge \quad K_{pel} = d_{pel}L_\infty^{e_{pel}}. \tag{7}$$

Mortality
The natural mortality of juvenile and adult fish is difficult to determine empirically (Quinn and Deriso, 1999), and fisheries scientists seem divided into those who consider it to be a species-specific constant depending on life-history parameters such as asymptotic length or K (Pauly, 1980; Jensen, 1996; Griffiths and Harrod, 2007) and those who consider it to be an allometric function of individual body size (McGurk, 1986; Lorenzen, 1996). We assume that natural mortality (M_L) consists of a size-dependent part reflecting predation and a constant size-independent part generated by all other causes of natural death ($M1$), which is identical for all species and sizes. In accord with general size-spectrum theory (Peterson and Wroblewski, 1984; Andersen and Beyer, 2006), predation is assumed to scale with individual body size, using the same exponent (n) for all species and stages. However, to explain the relationship between L_∞, K, and M_L identified by Pauly (1980), we also allow for potential differences in the predation mortality-at-length on different species depending on their asymptotic size.

Conceptually, such a difference seems more likely for demersal species than for pelagic. Many piscivorous fish species are found in association with the seabed, and small demersal fish found at or close to the seabed are likely to run a considerable risk of being eaten (Myers and Cadigan, 1993; Van der Veer *et al.*, 2000; Hixon and Jones, 2005; review by Juanes, 2007). Among the smaller species found on sandy or muddy seabeds, many are characterized by adaptations to reduce predation, such as spines, flattened body size, venom, and cryptic or burying behaviour, but such adaptations are largely lacking in the larger species. Species with these adaptations have been demonstrated to have a low natural mortality (Griffiths and Harrod, 2007). Hence, for demersal species, the assumption that M_L may depend on

asymptotic length once they have settled seems reasonable. We therefore describe their predation mortality as a power function of both individual and asymptotic lengths, with a constant rest mortality ($M1$) added to account for diseases and other non-size-related causes of death:

$$M_L = M1 + h_{\text{dem}} L_\infty^{\ i} L^n. \tag{8}$$

For pelagic species, adaptations to reduce predation seem less likely to differ systematically among small and large species, so we assume that predation mortality depends on individual length, L, only:

$$M_L = M1 + h_{\text{pel}} L^n. \tag{9}$$

This equation is also used to describe mortality in the pelagic post-larval phase of demersal and pelagic fish alike, because empirical investigations have shown natural mortality to be a function of individual size (McGurk, 1986; Bailey and Houde, 1989; Pepin, 1991), whereas dependence on asymptotic length has not been identified so far. Natural mortality is therefore described as being habitat-dependent, using Equation (8) for demersal life stages and Equation (9) for all pelagic stages.

Fishing mortality-at-length (F_L) is modelled by an equation borrowed from Pope *et al.* (2006):

$$F_L = \frac{F(1 + \kappa(L_\infty - \lambda))}{1 + \exp(\gamma(\delta L_\infty - L))}, \tag{10}$$

where δ is the length in proportion of L_∞ at which 50% of the individual fish become selected by the fishery, γ a slope parameter, κ and λ the parameters expressing how fast fishing mortality changes between species in relation to their L_∞, and F is the overall level of fishing mortality acting on all species. The nominator is intended to change species-specific fishing mortality linearly from small to large species, and the denominator ensures that the length at 50% of maximum exploitation of each species is reached when the individual fish have attained a fraction (δ) of their L_∞. Fishing mortality is thus modelled as a function of L_∞, but with the usual sigmoid relationship between exploitation rate and length.

Numbers at length

For each L_∞-group, the population is divided into a number of equally sized length intervals of width ΔL. For post-larvae, the number of survivors at length $L + \Delta L$ is calculated from the numbers surviving to length L:

$$N_{L+\Delta L} = N_L e^{-M_L(t_{L+\Delta L} - t_L)}, \tag{11}$$

where the value of M_L is calculated at the midpoint of the interval, and t_L is the age at length L. For juvenile and adult fish, the number of survivors at the end of each length interval is calculated from the Jones (1974) equation:

$$N_{L+\Delta L} = N_L \left(\frac{L_\infty - (L + \Delta L)}{L_\infty - L} \right)^{Z_L/K}, \tag{12}$$

where Z_L refers to total mortality ($Z_L = F_L + M_L$), estimated at the midpoint of the length interval. To ensure that the steep decline in

natural mortality with size in the smallest size classes can be adequately captured, ΔL was set to 0.25 cm.

Reproduction

To calculate the total lifetime egg production of each L_∞ group, the average number of individuals in each length interval is first calculated from

$$\overline{N}_{L,L+\Delta L} = \frac{N_L - N_{L+\Delta L}}{Z_L}, \tag{13}$$

and the average annual biomass in the length interval is estimated by multiplying the average numbers by their body weight, W_L, which is determined by

$$W_L = 0.01 \left(L + \frac{\Delta L}{2} \right)^3. \tag{14}$$

Survivors recruit to the spawning stock when they reach (knife-edge) maturity-at-length (L_{mat}), determined from

$$L_{\text{mat}} = q L_\infty^{\ s}, \tag{15}$$

after which half of them (the females) start producing eggs; s and q are constants.

Relative fecundity (RE) is expressed as the number of eggs produced per gramme of female, and is assumed to scale with L_∞:

$$\text{RE} = u L_\infty^{\ v}, \tag{16}$$

where u and v are constants. Multiplying RE by $0.5 \times$ SSB provides the total lifetime egg production. Thus, for each L_∞ value, the number of eggs generated can be calculated from

$$E_{1,L_\infty} = \sum_{L=L_{\text{mat}}}^{L_\infty - \Delta L} 0.5 \, \text{RE} \, W_L \overline{N}_{L,L+\Delta L}. \tag{17}$$

The ratio of parent egg production and offspring egg production, the net reproductive rate, can be expressed as

$$R_{L_\infty} = \frac{E_{1,L_\infty}}{E_0}. \tag{18}$$

Parameter estimation

Growth and maturity data are available for many fish species, and have previously been shown to scale with L_∞ (Cury and Pauly, 2000; Froese and Binohlan, 2000), whereas the parameters describing the relationship between M, L_∞, and L are more difficult to estimate and are generally lacking. However, assuming that all species within a given range of L_∞ should be able to replace themselves, the model can estimate the combination of M parameters that would, given empirical estimates of all other parameters and as far possible, produce a one-for-one replacement. We use the model to calculate the net reproductive rate in the equilibrium situation for every 5 cm of asymptotic length, and estimate the missing mortality parameters by minimizing the standard deviation of R over the range of L_∞ values observed to coexist in the North Sea fish community, subject to the constraint that within this range, the net reproductive rate should, on average, equal 1.

Because different calculations are necessary for demersal and pelagic species, the actual minimization is done by minimizing the sum of the standard deviation for demersals and pelagics:

$$
\text{Min} \left[\sqrt{\frac{\sum_{L_\infty = L_{\infty,\text{MIN}}}^{L_{\infty,\text{MAX}}} (R_{L_\infty}^{\text{dem}} - \overline{R_{L_\infty}^{\text{dem}}})^2}{(D-1)}} + \sqrt{\frac{\sum_{L_\infty = L_{\infty,\text{MIN}}}^{L_{\infty,\text{MAX}}} (R_{L_\infty}^{\text{pel}} - \overline{R_{L_\infty}^{\text{pel}}})^2}{(P-1)}} \right], \quad (19)
$$

subject to the constraints

$$
\overline{R_{L_\infty}^{\text{dem}}} = 1.0 \quad \wedge \quad \overline{R_{L_\infty}^{\text{pel}}} = 1.0, \quad (20)
$$

where D is the number of 5 cm L_∞ groups within the size range from the smallest ($L_{\infty,\text{MIN}}$) to the largest ($L_{\infty,\text{MAX}}$) value of L_∞ for demersal species, P the number of L_∞ groups for pelagics, and $\overline{R_{L_\infty}^{\text{dem}}}$ and $\overline{R_{L_\infty}^{\text{pel}}}$ the average net reproductive rates of demersal and pelagic species, respectively, over the size ranges observed.

The model was implemented in Excel, and Solver was used to find the parameters generating the minimum standard deviation of the net reproductive rate for different values of L_∞, so maximizing the possibilities for coexistence of species of different asymptotic lengths. An overview of the variables and constants used is provided in Appendix Table A1.

Parameter values and model setup

Estimates of L_∞, K, L_{mat}, and RE for North Sea teleosts from different sources are given in Appendix Table A2. Usually, the estimates used have been derived from fish sampled in the North Sea proper. When multiple von Bertalanffy growth estimates were available for a single species, we selected those where the value of the age at zero length was <1, and where L_∞ was within ± 33% of the maximum length given in Froese and Pauly (2006), to avoid bias caused by questionable age readings or insufficient coverage of the length range. Overall, 45 pairs of L_∞ and K estimates were available, 35 estimates of L_∞ and L_{mat}, and 16 estimates of L_∞ and RE (Figure 1).

Non-linear regression was then used to estimate the scaling parameters for growth, maturity, and relative fecundity (d, e, q, s, u, and v), and their approximate confidence intervals (Table 1). The relationships for growth and maturity against L_∞ are highly significant for all species combined ($p < 0.0001$; n = 45 and n = 35, respectively), and for demersal species ($p < 0.0001$; n = 41 and n = 31, respectively), but barely significant for pelagic species ($p = 0.03$ and $p = 0.04$, respectively; n = 4 in both cases). The scaling parameters for the pelagic species do not differ significantly from the parameters estimated for demersal species. The relationship between RE and L_∞ is significant for all species combined ($p = 0.0003$, n = 16), but the exponent does not differ significantly from zero. To calculate the total egg production in the model, an average RE of 997 eggs per gramme female (s.d. = 758) is therefore used for all L_∞ groups.

The survival of eggs and early larvae is temperature-dependent (Pepin, 1991). With average surface temperatures in the North Sea of 5°C in March and 6°C in April (ICES, 2006), the fractions surviving the egg and yolk-sac larval stages can be estimated as 0.435 and 0.074, respectively (Pepin, 1991), corresponding to an overall total survival of 3.2% to the post-larval stage. This stage is assumed to start when the larvae commence feeding at an average length of 0.5 cm (Russell, 1976). From then on, the larvae grow in accordance with the empirical model of Pepin (1991), with an exponent b equal to 0.54 and a constant a equal to 0.064 at 10°C, the average North Sea surface temperature in the period from April to July (ICES, 2006). The post-larvae are assumed to metamorphose at a size of 4 cm, corresponding to an age of 114 d, after which their growth starts to follow the von Bertalanffy growth equation, with a growth parameter K determined by their asymptotic length, L_∞.

The estimated empirical relationship between K and L_∞ was kept for demersal species, but for pelagic species the scaling exponent (e_{pel}) was estimated within the model because of the limited number of four observations available from the North Sea. To
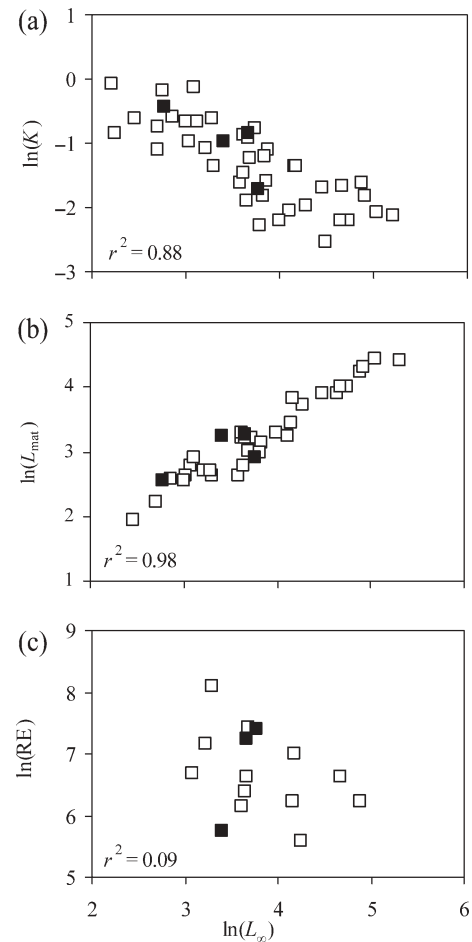
Figure 1. Relationships between three life-history parameters and the natural logarithm of L_∞ (asymptotic length, cm). (a) Natural logarithm of K (growth constant, year^{-1}), (b) natural logarithm of L_{mat} (length at first maturity, cm), and (c) natural logarithm of RE (relative fecundity, number of eggs per gramme female body weight). Open squares, demersal species; filled squares, pelagic species. Data from Appendix Table A2.

Table 1. Estimates of parameters (with 95% CI in parenthesis) from non-linear regressions of K, L_{mat}, and RE against L_∞.

Expression	Parameter	All species combined	Demersal species	Pelagic species
$K = dL_\infty^e$	d	3.15 (1.44, 4.88)	3.07 (1.30, 4.85)	6.48 (−21.1, 34.1)
	e	−0.64 (−0.82, −0.47)	−0.64 (−0.83, −0.45)	−0.83 (−2.18, 0.52)
$L_{mat} = qL_\infty^s$	q	0.72 (0.41, 1.00)	0.64 (0.35, 0.92)	5.10 (−28.9, 39.1)
	s	0.93 (0.85, −1.03)	0.95 (0.86, 1.06)	0.41 (−1.48, 2.30)
$RE = uL_\infty^v$	u	5194 (−11 924, 22 312)	–	–
	v	−0.44 (−1.36, 0.47)	–	–

The data are from Appendix Table A2.

generate values of K for pelagic species in accord with the observations, d_{pel} was adjusted so that the K for a pelagic species with an L_∞ of 32.1 cm (the average value for the pelagic species included in the non-linear regression) remained the same ($K_{32.1}$ = 0.38 year^{-1}), irrespective of changes in e_{pel}:

$$d_{pel} = \frac{K_{32.1}}{(32.1)^{e_{pel}}}. \quad (21)$$

The parameters of Equation (10) describing fishing mortality as a function of individual and asymptotic lengths were taken from Pope *et al.* (2006). Other natural mortality, $M1$, was assumed to be 0.1 year^{-1} for all sizes. This value corresponds to the lowest value of natural mortality used for adult fish in North Sea stock assessments. The L_∞ ranges for demersal and pelagic species were set at 10–180 and 10–50 cm, respectively, in accord with the size range of the species included in Appendix Table A2. All calculations were constrained to produce replacement within these ranges. Hence, solutions were sought where $R_{L_\infty}^{dem} = 1.0 \wedge R_{L_\infty}^{pel} = 1.0$. These criteria were met in all runs.

Initial runs produced unlikely parameter estimates or failed to converge, suggesting that the model was over-parameterized. A constraint on natural mortality was therefore introduced. Newly hatched fish larvae are reported to suffer daily mortalities in the order of 10–50% per day (McGurk, 1986; Bailey and Houde, 1989; Pepin, 1991; Houde and Zastrow, 1993). According to Pepin (1991), the daily mortality of a first-feeding post-larva is some 15.1% d^{-1} at 10°C. Assuming natural mortality to be 15.1% d^{-1} or 59.7 year^{-1} in the first post-larval size class ($\bar{L}$ = 0.625 cm) allowed h_{pel} to be calculated from

$$h_{pel} = \frac{(59.7 - M1)}{0.625^n}, \quad (22)$$

and reduced the number of parameters to be estimated to 4 (n, i, e_{pel}, and h_{dem}; Appendix Table A1).

The sensitivity of the model to changes in input parameters was examined by changing fecundity by a factor 100, 10, and 0.1, by changing M_{L_0} by ±50%, and by halving $M1$. In addition to a key-run where scaling relationships were allowed to differ for the pelagic and the demersal habitats, runs with identical growth and mortality relationships and parameters were used to explore the consequences of simplifying the model. Using the scaling parameters for species combined (shown in the first column of Table 1), natural mortality was assumed to depend only on individual size, L, or to follow the formula of Pauly (1980) and hence to depend only on L_∞.

Results

Key-run

The overall exponent expressing the scaling of M_L with length for both pelagic and demersal species was estimated at $n = -1.66$ (Table 2).

For pelagic species, the minimum standard deviation of the net reproductive rate over the L_∞ interval from 10 to 50 cm was generated with an estimated exponent in the K/L_∞ relationship of e_{pel} = −1.34. The model produced a dome-shaped replacement curve with a maximum in net reproductive rate for species with an asymptotic length of ∼30 cm and a difference of less than a factor of 4 in net reproductive rate within the pelagic L_∞ range of 10–50 cm (Figure 2a). The total natural mortality (M_L) of a 25 cm fish was 0.23 year^{-1} (Figure 2b).

For demersal species, the deviation in net reproductive rate over the L_∞ range 10–180 cm was minimized when M_L after settling was almost proportional to L_∞ ($i = 0.8$). The differences between maximum and minimum replacement within the length range considered were again small. R increased gradually with L_∞ to peak at a value of 85 cm, after which it declined

Table 2. Parameter estimates from the key-run compared with estimates obtained when relative fecundity (RE) is multiplied by 100, 10, and 0.1, and when initial post-larval mortality ($M_{0.625}$) is multiplied by 0.5 and 1.5.

Model version		Key-run	RE changed			Post-larval M changed	
Expression	Parameter		100	10	0.1	0.5	1.5
$K = d_{pel}L_\infty^{e_{pel}}$	e_{pel}	−1.34	−1.17	−1.25	−1.45	−1.23	−1.38
$M_L = M1 + hL_\infty^i L^n$	n	−1.66	−1.24	−1.41	−2.22	−1.11	−2.31
	h_{pel}	27.3	33.3	30.8	21	16.9	31.6
	h_{dem}	1.71	6.01	3.6	0.76	3.33	0.61
	i	0.8	0.46	0.6	1.12	0.46	1.18
M_L for a 50 cm fish	$M_{50,dem}$ (L_∞ = 130 cm)	0.22	0.55	0.39	0.13	0.51	0.12
	$M_{50,pel}$	0.14	0.36	0.23	0.1	0.32	0.1
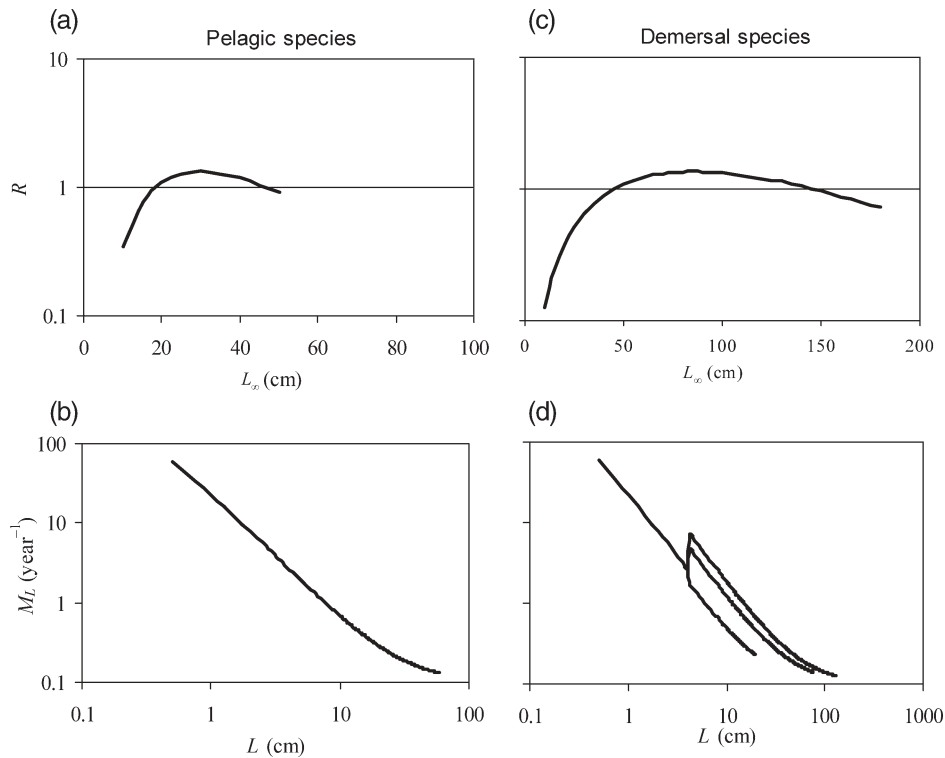
Figure 2. Comparison of the relationship between (a and c) net reproductive rate (R) and asymptotic length (L_∞), and (b and d) natural mortality-at-length (M_L) and length (L) for (a and b) pelagic and (c and d) demersal species. In (d), curves after metamorphosis are presented for three values of L_∞ values (upper curve, 130 cm; intermediate curve, 75 cm; lower curve, 20 cm).

(Figure 2c). A demersal fish with $L_\infty = 85$ cm had an $R \sim 4$ times higher than a 20 cm species, and twice as high as a 180 cm species. The M_L of a 5-cm newly settled fish was in the order of 0.4% d^{-1} (1.33 year^{-1}) for $L_\infty = 20$ cm, but 1.5% d^{-1} (5.54 year^{-1}) for $L_\infty = 130$ cm (Figure 2d). The natural mortality of a 50-cm fish with $L_\infty = 75$ cm was 0.18 year^{-1}, whereas the value for an individual of the same length with $L_\infty = 130$ cm was 0.22 year^{-1}.

Because of the reasonably constant replacement of fish of different size and the realistic values for natural mortality, this run was adopted as the key-run. For both demersal and pelagic species, the value of M/K at half the asymptotic size of a species was virtually independent of L_∞, ranging between 1.1 and 1.5.

Sensitivity

Given the uncertainty in the relationship between SSB and viable egg production, as well as in larval mortality, Table 2 also provides estimates for key parameters under alternative assumptions about these factors. The scaling factors for both growth and mortality were much more sensitive to the value of post-larval mortality than to changes in fecundity: a tenfold change in fecundity produced a similar change in the parameter estimates as a twofold change in the initial natural mortality of the post-larvae. The exponent in the length–mortality relationship (n) changed substantially between the different runs, but remained within the interval -1.11 to -2.31. The exponent in the M_L/L_∞ relationship of demersal species after settling (i) changed from 0.46 to 1.18 when the initial daily post-larval mortality was set at 7.5% and 22.5%, respectively. The K/L_∞ relationship of pelagic species changed comparatively less than the mortality parameters, and

the exponent (e_{pel}) remained within the interval -1.17 to -1.38, irrespective of the large changes in fecundity and in post-larval mortality. Halving $M1$ resulted in a $<2\%$ change in any of the parameter values.

Using a simpler model with no difference between habitats

When natural mortality was assumed to scale with individual length, L, only, solutions minimizing the across-species difference in R (in the L_∞ range 10–180 cm, corresponding to the range found for common North Sea species) resulted in a scaling exponent $n = -1.28$, and values of adult total natural mortality in the order of 0.32 year^{-1} for a 50-cm fish and 0.19 year^{-1} for a 100-cm fish. These values of M are not unlike those currently used for demersal species in North Sea stock assessments. However, the replacement curve increased monotonically as a function of L_∞, suggesting that coexistence of different-sized species of fish was unattainable (Figure 3). Comparing species with an L_∞ of 20 and 100 cm, the latter were predicted to produce a 927 $\times$ higher R than the former, a difference hardly conceivable to be conducive for coexistence.

Pauly (1980) described natural mortality as a function of K, L_∞, and ambient temperature. Using Pauly's formula with an ambient temperature of 12°C to calculate natural mortality from the post-larval stage on, a steadily increasing replacement curve was obtained. With a constant M (independent of individual length), R for a species with $L_\infty = 100$ cm was 44 times larger with the model of Pauly (1980) than R for a species with $L_\infty = 20$ cm (Figure 3).
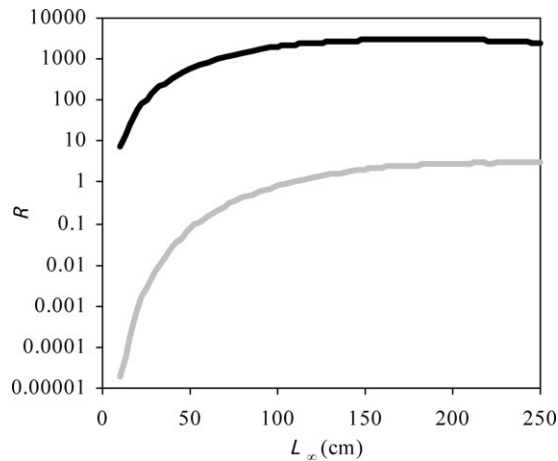
Figure 3. Estimates of net reproductive rate (*R*) plotted against asymptotic length (*L*∞) for two models: black line, constant size-independent natural mortality estimated using Pauly's (1980) equation; grey line, natural mortality depending only on individual length (see text for more explanation).

Checking the results from the key-run against independent data

Recent estimates of quarterly predation mortality from a North Sea MSVPA (1963–2003; excluding seals) were kindly provided by Morten Vinther (of DTU-Aqua). The average quarterly predation mortality (*M2*) for cod, haddock, whiting, Norway pout, herring, sprat, and sandeel was calculated across all years and regressed against average length (Figure 4) using the model $\ln (M2_{L,j}) = \ln(h) + i\ln(L_{\infty,j}) + n\ln(L)$, where *j* is the species, length (*L*) was calculated from MSVPA weights-at-age, and the other parameters correspond to Equation (8). The model explained 51% of the total variance of the data and was highly significant [$r^2 = 0.51$, $F = 49.7$, $\Pr(F) < 0.001$, n = 98]. Introducing separate slopes and intercepts for individual species did not produce parameter estimates that differed significantly from the overall.

Fitting the model separately for demersal (cod, haddock, whiting, Norway pout, and sandeel) and pelagic species (herring and sprat), the parameter estimates for demersal species were all significantly different from zero and their confidence limits contained the theoretical values estimated by the size-based model (Table 3). The exponent *i* of the M_L/L_{∞} relationship was here estimated as 0.71 compared with 0.80 in the key-run, the exponent *n* in the M_L/L relationship was −2.11 rather than −1.66, and the parameter $\ln(h)$ was 1.45 vs. 0.54 in the key-run. For pelagic species, *i* was not significantly different from zero, but *n* was significantly different from zero (−0.99), and its confidence limits contain the −1.66 estimated in the key-run, and $\ln(h)$ (1.03) had confidence limits large enough to contain the 3.31 estimate from the key-run.

Values of *L*∞ and *K* for selected families of demersal and pelagic teleosts were obtained from FishBase (Froese and Pauly, 2006). Only data from families for which >100 individual estimates
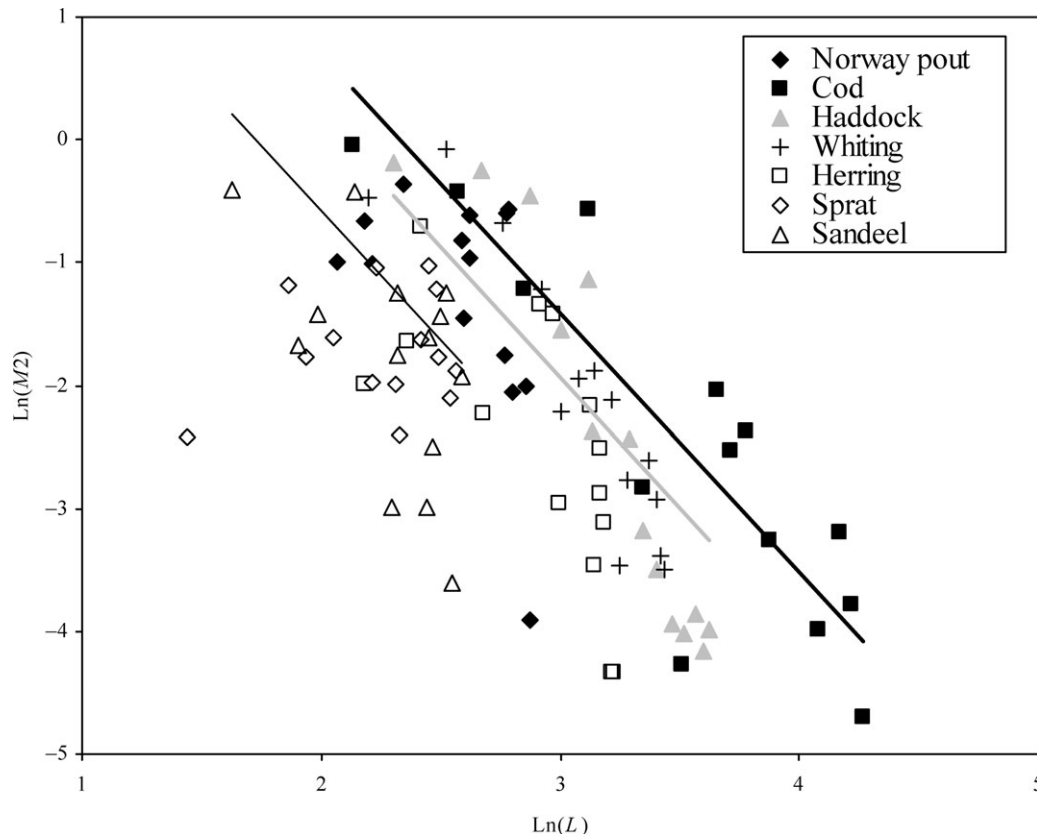
Figure 4. Quarterly estimates of ln predation mortality (*M2*) for seven North Sea fish species from MSVPA plotted against ln length (*L*, cm). The straight lines plotted are the regression lines for cod (upper), haddock (intermediate), and sandeel (lower).

Table 3. Parameter estimates (95% CI in parenthesis) obtained when fitting the model of length-dependent natural mortality to MSVPA estimates of quarterly predation mortality in the North Sea for demersal species (cod, haddock, whiting, Norway pout, and sandeel; r^2 = 0.59, F = 48.5, Pr(F) < 0.0001, n = 70), and pelagic species (sprat and herring; r^2 = 0.32, F = 6.0, Pr(F) < 0.0074, n = 28).

Habitat	Parameter	Estimate	*t*-value	Pr > ||t|
Demersal	ln(h)	1.45 (0.3, 2.62)	2.51	0.0145
	n	−2.11 (−2.58, −1.64)	−8.97	<0.0001
	i	0.71 (0.3, 1.12)	−3.43	0.001
Pelagic	ln(h)	1.03 (−2.02, 4.11)	0.70	0.492
	n	−0.99 (−1.03, −0.06)	−2.19	0.038
	i	−0.19 (−1.58, 1.2)	−0.29	0.777

were available, and with few multiple estimates for individual species, were included. Non-linear regression was used to estimate the parameters d and e (Table 4). Fitting a linear model with separate intercepts and slopes for demersal and pelagic fish to log-transformed values of L_∞ and K revealed a significant difference in slope between the two groups ($F = 9.7$, $p < 0.0019$), the slope being consistently more negative for pelagic species than for demersal. Except for the Sciaenidae, the exponent was between −0.85 and −0.63 for demersal families, and between −1.57 and −1.08 for pelagic families, conforming to the difference in growth patterns suggested by the model where the estimated exponent for the pelagic species was −1.34, different from the −0.64 estimated for demersal fish.

Denney *et al.* (2002) found an inverse relationship between the natural logarithm of the maximum R/SSB and maximum body length. Re-analysing these data (in their Table A1) revealed that maximum recruitment scaled with maximum length raised to a power of −3.03 [$r^2 = 0.63$, $F = 87$, $p < 0.0001$, n = 54, 95% confidence intervals (−2.38, −3.69)].

Many commercially exploited North Sea species are close to or at levels of spawning–stock biomass where recruitment is impaired. In accord with Denney *et al.* (2002) and others (Myers *et al.*, 1999; Barrowman and Myers, 2000), we assumed that the effect of density dependence on recruitment would be negligible in this situation and that R/SSB was close to the maximum possible. However, the maximum R/SSB reported by Denney *et al.* (2002) were derived from VPA and represent cohort strength before the cohorts enter the exploited phase. In the size-based

model, small species are subject to fishing in their first year of life, and the maximum number of 1-year-old recruits generated per unit of SSB was hence obtained at zero fishing mortality. Changing F from its current level to zero in the key-run without changing the other parameters generates a scaling of recruitment at age 1 with L_∞ with an exponent of −2.69 for demersal species and −2.96 for pelagic species. Both values fall well within the confidence intervals of the estimate derived from the data of Denney *et al.* (2002).

Discussion
Scaling relationships and coexistence
The model describes a teleost community where the species share a common set of habitat-dependent scaling relationships describing how growth, maturity, and mortality depend on length and asymptotic length. We assume that these scaling relationships have evolved in response to interactions with co-occurring species, to habitat characteristics, and to phylogenetic and physiological constraints. Most of the parameters in the model can be gathered from published data on growth, maturity, and fecundity, but assuming that both small and large species are able to replace themselves, the remaining parameters describing natural mortality and, for pelagic species, the parameters linking growth to asymptotic length have to be estimated within the model. This was done by minimizing the standard deviation of the net reproductive rate (R) across the range of asymptotic lengths found in the community, subject to the constraint that, on average, R should equal 1.0 across the range of asymptotic lengths.

We have used the model to explain a general scaling of SSB/R with L_∞. This scaling is puzzling because of its magnitude—three orders of magnitude for a one-order change in asymptotic length—and important because of its potential consequences for species coexistence. The trivial explanation for the scaling of SSB/R that spawners of a species with large L_∞ necessarily accumulate more biomass per recruit than a species with small L_∞ must be placed in the fuller context of how many equally sized recruits of both species will be produced per kilogramme of spawner. M or K simultaneously has to scale in some way to produce a long-term expectation of one spawner per spawner ($R = 1$) for all species to persist in the community. The solutions obtained with the simpler models (with M depending only on individual length, and with M depending only on L_∞) produce large differences in R among species. This demonstrates that

Table 4. Estimates of the parameters d and e (with 95% CI in parenthesis) in the relationship $K = dL_\infty^e$ for different families of fish.

Habitat	Family	d	e
Pelagic	Carangidae n = 252	37 (9, 66)	−1.16 (−0.93, −1.39)
	Clupeidae n = 629	94 (80, 108)	−1.57 (−1.50, −1.64)
	Engraulidae n = 233	22 (12, 32)	−1.08 (−0.9, −1.27)
	Scombridae n = 375	117 (48, 187)	−1.33 (−1.16, −1.51)
Demersal	Gadidae n = 408	5.6 (4.1, 7.1)	−0.74 (−0.68, −0.81)
	Pleuronectidae n = 146	3.7 (-0.7, 8.1)	−0.70 (−0.38, −1.02)
	Sparidae n = 200	5.4 (1.7, 9.1)	−0.85 (−0.66, −1.04)
	Lutjanidae n = 219	3.2 (1.7, 4.8)	−0.63 (−0.51, −0.76)
	Serranidae n = 123	3.0 (1.2, 4.8)	−0.64 (−0.48, −0.80)
	Sciaenidae n = 187	22 (9, 34)	−1.02 (−0.86, −1.19)

The data are from FishBase (Froese and Pauly, 2006).

there would be little opportunity for coexistence of large and small species of fish in a simple single-factor model where M is assumed to scale either with individual body length within species ($i = 0$) or with L_∞ across species ($n = 0$).

The scaling problem may be solved by allowing small species to produce more eggs than large species, by subjecting large species to a higher M than small species, or by letting small species grow more rapidly than large species. The regression of the number of eggs produced per gramme of female provided little evidence for a general scaling of relative fecundity with L_∞, and a trial run where the estimates of u and v given in Table 1 were used to calculate relative fecundity did not produce results that differed significantly from the key-run. Relative fecundity may vary over time within species, but the variation seems to be relatively modest (Oskarsson *et al.*, 2002; Yoneda and Wright, 2004; Thorsen *et al.*, 2006). RE may also increase somewhat with size within species (Kamler, 2005), but this would only aggravate the problem by affecting large species more than small species. No evidence was found in the literature (e.g. Pepin, 1991; Houde and Zastrow, 1993) to support a scaling of larval growth and mortality with L_∞. We also cannot find a plausible explanation as to why the mechanisms regulating growth and survival in the pelagic larval and early juvenile stages should work quite differently for species with different L_∞, when their larval and early juvenile stages are of similar size. We therefore consider a scaling of the survival of pelagic prerecruits of the necessary magnitude to be unlikely and propose an alternative hypothesis where differences between pelagic and demersal habitats are used to explain how small and large species can coexist in the North Sea.

Demersal species

For demersal fish, the observed scaling of K with L_∞ implies that the rate of growth immediately after metamorphosis and settling differs between small and large species. In the von Bertalanffy growth equation, the rate of growth in length approaches a maximum of $L_\infty \times K$ as length moves towards zero. If L_∞ were exactly inversely proportional to K, all species would have the same maximum growth rate. When the exponent differs from -1, maximum growth rate is a function of L_∞. For exponents < -1, the maximum growth rate of a large species is lower than the maximum growth rate of a small species. For exponents > -1, the opposite occurs. With an estimated exponent of -0.64 in the scaling of K with L_∞, the initial slope of the growth curve is much steeper for large demersal species than for small. At a size of 4 cm, the growth rate of a demersal species with $L_\infty = 130$ cm is four times the growth rate of a species with $L_\infty = 10$ cm.

Securing the food necessary to maintain a fast growth rate may entail a fish being exposed to a higher M (Sogard, 1997), in particular during and immediately after major life-history transitions such as settling. Moreover, many of the small demersal species in the North Sea seem better protected against predation than large species fish of similar size (Figure 5). They typically possess antipredator defences such as (venomous) spines, flat body shapes, or cryptic behaviour, or they live in habitats where they can hide from predation (e.g. sandeel and species associated with structurally complex habitats such as rocky seabeds). Developing predator defences or hiding may involve a metabolic cost or reduce their food intake and affect growth. For example, hiding by fresh-water fish reduces food intake while decreasing predation mortality (Mittelbach, 1986; Werner and Hall, 1988). In their analyses of
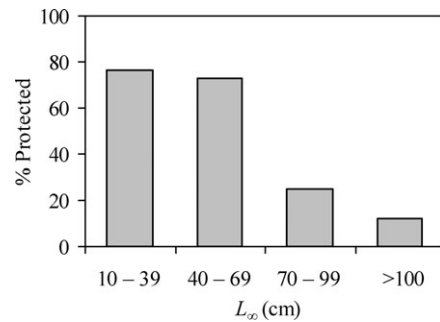
Figure 5. Proportion of species protected by either spines, venom, bone plates, being cryptic, flattened, or buried plotted against L_∞. Data are from Appendix Table A2.

empirical estimates of the natural mortality of 173 fish species, Griffiths and Harrod (2007) found species that were cryptic, hid in burrows, or had morphological defence against predators to have the lowest natural rates of mortality. We therefore hypothesize that the scaling of M with L_∞ reflects a trade-off between growth and mortality. Demersal fish with small L_∞ may have a lower maximum growth rate at the larval/juvenile transition than fish with a large L_∞, specifically because they adjust their behaviour or morphology to reduce predation.

Our model shows that the difference in R with L_∞ can be largely solved for demersal species by making M after settling a function of individual length and L_∞. Many authors have identified settling as an important life-history event and have found density-dependent predation in the post-settlement phase to be important (Myers and Cadigan, 1993; Van der Veer *et al.*, 2000; Hixon and Webster, 2002; Almany and Webster, 2006). To our knowledge, whether mortality immediately after settling generally scales with L_∞ has so far not been investigated. Our results suggest that M after settling should be almost directly proportional to L_∞. This proportionality obviously depends on the input parameters. Changes in larval mortality and relative fecundity alter the results substantially, but the values of the mortality parameters from the key-run are not significantly different from those generated by an independent analysis of the average predation mortalities estimated by North Sea MSVPA.

For demersal species, our estimate of the exponent in the relationship between M and size is in general accord with the values reported. M and body weight or length scale with an exponent close to -0.25 or -0.75, respectively (Peterson and Wroblewski, 1984; McGurk, 1986; Brown *et al.*, 2004). At first glance, our results may seem to suggest that M should scale with length raised to a power of -1.66 rather than with length raised to -0.75 (Table 2). However, this apparent difference can be explained by the confounding effect of the L_∞ term for demersal species. Assuming that the values of M for adult fish used by the authors cited above were derived mainly from demersal fish of a length corresponding to a constant fraction (μ) of their L_∞, their predation mortality should scale as $h \times (L_\infty)^i \times (\mu L_\infty)^n$, i.e. as $i + n$. We estimate $i + n$ to equal -0.86 (Table 2), so the overall exponent relating M to weight is estimated to be $-0.86/3 = -0.29$, close to the -0.25 reported by others. Further, the exponent relating M to larval body weight is reported to be significantly more negative than it is for adults (McGurk, 1986; Houde, 1987). In our model, the exponent for the post-larvae is $-1.66/3 = -0.55$ on a weight basis, compared with the -0.29

estimated for adult fish. Finally, in an empirical analysis of 175 fish stocks, Pauly (1980) found that M at a given temperature was proportional to $K^{0.654} \times L_\infty^{-0.28}$. Inserting $K \sim L_\infty^{-0.64}$ (Table 2) in this relationship, we find that natural mortality should scale to asymptotic length raised to -0.70, not far from the value of -0.86 derived above.

Pelagic species

For pelagic species, the model predicts that K should scale with L_∞ raised to a power of -1.34. Although this result is based on very few species, an analysis of L_∞ and K from FishBase resulted in exponents for four pelagic families ranging from -1.08 for Engraulidae to -1.57 for Clupeidae, significantly lower than those for most demersal families (Table 4). Hence, the growth pattern appears generally different among the two habitats. Small pelagic species seem initially to grow faster than their larger counterparts, and this may explain how the former are able to sustain the higher levels of M associated with a smaller body size, by being exposed to size-dependent M for less time at each size. Where demersal species seem to solve the apparent difference in replacement of large and small species by modifying their growth and vulnerability to predation, pelagic species may overcome the problem by changing their growth rate with asymptotic size.

Ideally, we should have used estimates of L_∞ and K for pelagic and demersal species from different fish communities and analysed their relationship allowing for differences in intercepts and exponents between communities. However, for pelagic species, we could not find sufficient estimates of growth parameters from separate communities to perform such analyses. By analysing the data at a family level, we may have introduced additional variation caused by differences between fish communities in, for instance, ambient temperature and exploitation. Despite the likely inflation of overall variance caused by these differences, the difference in the slope of the K/L_∞ relationship between pelagic and demersal families of fish proved highly significant. Our analysis not only confirms the overall difference between pelagic and demersal species suggested by the model, but it shows that this difference is present also at a family level.

Scaling of maximum R/SSB

Our model can reproduce the scaling of maximum R/SSB with L_∞ reported by Denney et al. (2002). Calculating the maximum survival from egg to age 1 by assuming that only M operates during this period results in numbers of R/SSB for both demersal and pelagic species that scale with L_∞ raised to powers that are close to the estimate of -3.03 based on their data from the Northeast Atlantic. This scaling cannot be reproduced by a model where natural mortality depends only on individual length and where the combined scaling of L_∞ and K is used to model growth.

The importance of stabilizing and equalizing mechanisms for species coexistence

We base our conclusions on a simple model of coexistence in which populations are assumed to be in steady state. In line with common approaches in life-history theory (Stearns, 1992; Charnov, 1993), we attempt to capture the general patterns in the average life-history characteristics of demersal and pelagic teleosts. For the sake of simplicity, we used a model with an unstable equilibrium, providing no mechanism for recovery of species with a less than one-for-one replacement.

Species can coexist in variable environments if they respond differently to differing conditions and can persist through unfavourable periods or retract to favourable areas, and stage structure, resource partitioning, non-linear competition, and density-dependent biological interactions are able to promote coexistence (McCann and Yodzis, 1998; Chesson, 2000; Abrams and Holt, 2002; Bonsall and Hastings, 2004; Chase, 2005). We recognize that periods of decline or increase are common in fish populations, and that stabilizing mechanisms must be important for their long-term persistence. Still, when the species in a community manage to persist over long time-spans, their net rates of population growth are bound to be close to zero (Hubbell, 2001). This can only be realized if their growth, mortality, and reproductive characteristics on average generate spawner-for-spawner or egg-for-egg replacement, irrespective of the nature of the mechanisms involved. Although long-term persistence will be achieved by both fitness-equalizing and -stabilizing mechanisms (Chesson, 2000; Adler et al., 2007), there is no obvious reason why stabilizing mechanisms should result in a relationship between R/SSB and L_∞, producing a three orders of magnitude difference in recruitment for a single order change in L_∞. Rather, stabilizing mechanisms alone are unlikely to be responsible for more than a single-order change in replacement. In their analysis of >700 time-series of spawners and recruitment for different populations and species of fish, Myers et al. (1999) found that the maximum relative growth rate of fish populations is typically around 1–7 replacement spawners per spawner per year, suggesting that a factor of 10 is the likely maximum difference in average replacement that stabilizing mechanisms could effectively buffer against. The net reproductive rate is the proper fitness measure to use when populations are regulated by density-dependence early in life (Mylius and Diekmann, 1995). Still, by neglecting other stabilizing mechanisms and assuming populations to be in steady state, we cannot be completely sure that the model will generate life-history strategies that are evolutionarily stable. Therefore, investigating the consequences of our model assumptions in an evolutionary context is a clear target for further research.

Model limitations and applicability

Using a simple scaling model to capture variations in life-history parameters across a multitude of species makes it likely that some species rely on life-history features not adequately accounted for by the model to compensate for insufficient replacement. This is, for instance, reflected by the spread of the observations of L_∞ and K around a log-linear relationship (Figure 1a). It is therefore unrealistic to expect general scaling relationships to produce an exact one-for-one replacement at any one time. Additional trade-offs between growth, mortality, and reproductive investment should allow species with identical L_∞ to achieve a one-for-one replacement, e.g. if they counteract a reduction in growth rate with an increase in fecundity or a reduction in M (Gunderson, 1997). Species of similar L_∞ may be found on a continuum from sit-and-wait strategists to active swimmers hunting for food or use parental care to increase egg survival, as several of the smaller North Sea demersal species do.

Our model is primarily aimed at describing marine fish communities typical of temperate continental shelves with sandy and muddy seabeds, and it mimics the basic life-history features of determinate spawners with pelagic eggs. Although we applied information from North Sea species, the model could be applied

easily to other shelf areas to test our prediction that for a given individual length, large demersal species after settling should suffer greater mortality than small demersal species. Size-based scaling of life-history parameters across species may also be used to compare replacement and to explore trade-offs among life histories in other types of communities, such as in deep-water fish communities where the light intensity shapes the trade-offs between feeding and predation (Strand *et al.*, 2002; Fiksen *et al.*, 2005), or in reef-fish communities where species diversity is linked to habitat complexity (Gratwicke and Speight, 2005). These may be particularly interesting systems for studying size-based trade-offs, because superimposed on the processes considered here, complex habitats offer the various species a multitude of possibilities for composing their own particular life-history strategy to secure their persistence, constrained by size as a factor in securing shelter and reduced predation mortality. However, where shelter favours certain sizes, it may not suffice to model predation mortality by an expression where a single exponent is used to relate predation mortality to length.

The surprisingly good fit to the estimated predation mortalities from the North Sea MSVPA calls for further investigations of our model's ability to fit existing estimates of M for various species and sizes of fish, and for a revision of the formula for estimating M derived by Pauly (1980). This formula ignores the within-species length dependence frequently reported for fish (Lorenzen, 1996; Sogard, 1997; Bax, 1998). It has been widely used to estimate M for fish populations in situations where research costs would prohibit empirical observations, but many of the empirical values used in its derivation refer to inferred values (such as 0.1 or 0.2 for many temperate commercial fish stocks) rather than independent estimates. Often, estimates of M derived from the formula have been used in stock assessments leading to management advice. Taking the length dependence of M into account is likely to change predictions of the effects of size-based management measures such as mesh-size regulations, as well as predictions of responses of fish communities interlinked by predation to ecosystem-based harvesting strategies.

Acknowledgements

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Appendix

Table A1. Variables and constants used in the model.

Type	Parameter	Description	Unit	Value	Source
Independent parameter	L_∞	Asymptotic length	cm	–	–
Internal variables	L	Length	cm	–	Equations (3) and (5)
	t_L	Age at length	year	–	Equation (4)
	N_L	Numbers at length	–	–	Equations (1), (11), and (12)
	$\tilde{N}_{L, L+\Delta L}$	Average annual number of individuals in length interval from L to $L+\Delta L$	–	–	Equation (13)
	W_L	Body weight at length	g	–	Equation (14)
	K	von Bertalanffy growth parameter	$year^{-1}$	–	Equation (7)
	L_{mat}	Length at first maturity	cm	–	Equation (15)
	t_0	Parameter in the von Bertalanffy growth equation generating a fish of length L_{met} at age $t_{L_{met}}$	year	–	Equation (6)
	F_L	Fishing mortality at length	$year^{-1}$	–	Equation (10)
	M_L	Natural mortality at length	$year^{-1}$	–	Equations (8) and (9)
	RE	Relative fecundity	g^{-1}	–	Equation (16)
	E_{1,L_∞}	Total lifetime egg production	–	–	Equation (17)
	R_{L_∞}	Net reproductive rate	–	–	Equation (18)
Constants estimated by the model	n	Exponent relating predation mortality to L	–	–	–
	i	Exponent relating predation mortality to L_∞ in the demersal habitat	–	–	–
	h_{dem}	Constant used to link predation mortality to L_∞ and L in the demersal habitat	$cm^{-(i+n)} \, year^{-1}$	–	–
	e_{pel}	Exponent used to scale K to L_∞ for pelagic species	–	–	–
	d_{pel}	Constant used to scale K to L_∞ for pelagic species	$cm^{-e} \, year^{-1}$	–	Estimated from e_{pel} and $K_{32.1}$. Equation (21)
	h_{pel}	Constant used to link predation mortality to L in the pelagic habitat	$cm^{-n} \, year^{-1}$	–	Estimated from n, $M1$, and M_{L_0}. Equation (22)
User-specified constants	$M1$	Mortality attributable to non-size-related causes of death	$year^{-1}$	0.1	See text
	ΔL	Width of length interval	cm	0.25	See text
	L_{met}	Length at end of post-larval stage	cm	4.0	See text
	E_0	Initial number of eggs	–	10^6	See text
	C_e	Fraction of eggs surviving to hatch	–	0.435	Pepin (1991)
	C_y	Fraction of yolk-sac larvae surviving to post-larval stage	–	0.074	Pepin (1991)

Continued

Table A1. *Continued*

Type	Parameter	Description	Unit	Value	Source
	L_0	Length of post-larvae at first feeding	cm	0.5	Russell (1976)
	M_{L_0}	Daily mortality of post-larvae in initial length class	year^{-1}	59.7	Pepin (1991)
	a	Constant in post-larval growth equation	cm$^{(1-b)}$ year^{-1}	0.064	Pepin (1991)
	b	Exponent in post-larval growth equation	–	0.54	Pepin (1991)
	e_{dem}	Exponent used to scale K to L_∞ for demersal species	–	−0.64	Estimated from Table A2
	d_{dem}	Constant in equation used for scaling K to L_∞	cm^{-e} year^{-1}	3.15	Estimated from Table A2
	F	General overall level of fishing mortality	year^{-1}	0.7	Pope *et al.* (2006)
	δ	Proportion of L_∞ at 50% gear selection	–	0.33	Pope *et al.* (2006)
	γ	Constant used to generate the slope of the exploitation curve with respect to length	cm^{-1}	0.2	Pope *et al.* (2006)
	λ	Constant used to link the level of fishing mortality to L_∞	cm	70	Pope *et al.* (2006)
	κ	Constant expressing how fast the level of fishing mortality changes with respect to L_∞	cm^{-1}	0.0035	Pope *et al.* (2006)
	q	Constant used to scale L_{mat} to L_∞	cm$^{(1-s)}$	0.72	Estimated from Table A2
	s	Exponent used to scale L_{mat} to L_∞	–	0.93	Estimated from Table A2
	u	Constant used to scale relative fecundity to L_∞	cm$^{(1-v)}$	977	Estimated from Table A2
	v	Exponent used to scale relative fecundity to L_∞	–	0.0	Estimated from Table A2

Table A2. Growth parameters (L_∞, K), length at first maturity (L_{mat}), egg diameter (EggD), relative fecundity (RE) in eggs g female body weight^{-1}, and predator defence (Pdef) of North Sea teleosts. L_{mat}, EggD, and Pdef from FishBase (Pl, plates; B, bury; F, flat; S, spiny; V, venomous; N, nearshore; Blank, no apparent predator defence).

Species	L_∞ (cm)	K (year^{-1})	Source[a]	Demersal/Pelagic	L_{mat} (cm)	EggD (mm)	RE	Source[a]	Pdef
Agonus cataphractus	15.0	0.48	1	D	9.2	1.9	–	–	Pl
Ammodytes marinus	21.8	0.89	2	D	16.3	1.0	790	2	B
Anarhichas lupus	115.0	0.11	3	D	55.0	6.0	–	–	–
Arnoglossus laterna	15.8	0.84	4	D	–	0.7	–	–	F
Aspitrigla cuculus	41.7	0.46	5	D	25.0	1.6	–	–	S
Brosme brosme	89.0	0.08	6	D	50.0	1.3	–	–	–
Buglossidium luteum	11.7	0.54	4	D	7.0	0.8	–	–	F
Callionymus lyra	17.5	0.55	7	D	13.3	0.9	–	–	S, B
Chelidonichthys lucernus	48.4	0.33	5	D	–	1.4	–	–	S
Clupea harengus	30.0	0.38	8	P	25.7	1.2	310	33	–
Dicentrarchus labrax	72.3	0.14	9	D	42.0	1.2	–	–	–
Echiichthys vipera	15.0	0.33	10	D	–	1.2	–	–	V, S, B
Enchelyopus cimbrius	36.0	0.20	11	D	14.0	0.8	–	–	–
Eutrigla gurnardus	46.0	0.16	12	D	23.0	1.3	–	–	S
Gadus morhua	132.0	0.20	8	D	69.7	1.4	500	33	–

Continued

Table A2. *Continued*

Species	L_∞ (cm)	K (year^{-1})	Source[a]	Demersal/Pelagic	L_{mat} (cm)	EggD (mm)	RE	Source[a]	Pdef
Glyptocephalus cynoglossus	46.1	0.20	13	D	20.0	1.2	–	–	F
Gobius niger	9.5	0.43	14	D	–	1.5	–	–	N
Hippoglossoides platessoides	25.0	0.34	15	D	15.1	2.3	1300	33	F
Labrus bergylta	44.4	0.10	16	D	–	1.0	–	–	–
Lepidorhombus whiffiagonis	61.1	0.13	17	D	25.3	1.1	–	–	F
Limanda limanda	27.0	0.26	18	D	13.8	1.0	3300	33	F
Lophius piscatorius	137.0	0.16	19	D	75.0	2.7	–	–	S
Lumpenus lampretaeformis	47.6	0.21	19	D	–	–	–	–	B
Melanogrammus aeglefinus	63.5	0.26	20	D	31.5	1.5	500	33	–
Merlangius merlangus	40.0	0.29	21	D	20.2	1.2	1700	33	–
Merluccius merluccius	103.6	0.11	13	D	50.0	1.0	–	–	–
Microchirus variegatus	20.7	0.37	4	D	14.0	1.3	–	–	F
Micromesistius poutassou	37.1	0.23	22	D	25.1	1.1	–	–	–
Microstomus kitt	37.1	0.42	23	D	27.0	–	470	33	F
Molva dipterygia	155.0	0.13	24	D	85.0	–	–	–	–
Molva molva	183.0	0.12	24	D	–	–	–	–	–
Myoxocephalus scorpius	26.7	0.54	25	D	15.0	2.2	–	–	S
Platichthys flesus	46.5	0.30	26	D	–	1.0	–	–	F
Pleuronectes platessa	70.0	0.08	8	D	26.6	1.9	265	33	F
Pollachius pollachius	85.6	0.19	27	D	–	1.2	–	–	–
Pollachius virens	107.0	0.19	28	D	55.4	1.1	750	33	–
Pomatoschistus minutus	9.2	0.93	29	D	–	1.2	–	–	N
Psetta maxima	64.8	0.26	30	D	46.0	1.0	1100	33	F
Scomber scombrus	39.0	0.43	19	P	26.2	1.2	1275	33	–
Solea vulgaris	39.0	0.40	8	D	24.8	1.2	750	33	F
Sprattus sprattus	16.0	0.65	19	P	13.0	1.1	–	–	–
Trachinus draco	38.3	0.15	31	D	16.0	1.0	593	31	V, S, B
Trachurus trachurus	43.4	0.18	32	P	18.5	0.9	1655	33	–
Trisopterus esmarki	22.6	0.52	23	D	18.6	1.0	700	33	–
Trisopterus minutus	20.0	0.51	23	D	13.0	1.0	–	–	–

[a]Sources: 1, Le Gall (1969); 2, Macer (1966); 3, Liao and Lucas (2000); 4, Deniel (1990); 5, Baron (1985); 6, Bergstad (1988); 7, Chang (1951); 8, Beverton and Holt (1959); 9, Holden and William (1974); 10, Creutzberg and Witte (1989); 11, Albert (1993); 12, Damm (1987); 13, Greenstreet and Rogers (2006); 14, Nash (1984); 15, Ntiba (1989); 16, Dipper *et al.* (1977); 17, Robb (1973); 18, Rijnsdorp *et al.* (1992); 19, Pauly (1978); 20, Jones (1983); 21, Knudsen (1964); 22, Jennings *et al.* (1998); 23, Jennings *et al.* (1999); 24, Joenoes (1961); 25, Hass (1937); 26, Saeger (1974); 27, Moreau (1964); 28, Beverton and Holt (1959); 29, Fonds (1973); 30, Jones (1974); 31, Bagge (2004); 32, Sahrhage (1970); 33, Knijn *et al.* (1993).