Optimal state-dependent allocation to growth or reproduction in cod

Øyvind Fiksen[1] and Brian R. MacKenzie[2]

[1]Department of Fisheries and Marine Biology, University of Bergen, HiB, Pb 7800, N-5020 BERGEN, Norway. email: oyvind.fiksen@ifm.uib.no. [2]Department of Marine Ecology and Aquaculture, Danish Institute for Fisheries Research, Kavalergården 6, DK-2920 Charlottenlund, Denmark

Abstract

Several studies have revealed that a fraction of the mature stock in various fishes occasionally skip spawning and reabsorb their initial investment in gonads. We have developed a simple life history model that explores the evolutionary benefits to individuals that adopts this strategy, using cod as our model organism. If there is an increased mortality risk or physiological cost associated with spawning, fish can increase their lifetime reproductive output by allocating surplus energy to growth instead of reproduction, particularly in years with reduced food intake (low surplus energy). The model provides a framework to study possible causes and consequences of skipped spawning in fish.

Introduction

At the heart of life history theory is the trade-off between growth and reproduction (Roff 1992, Stearns 1992, Heino & Kaitala 1999). A special case of the allocation problem is the optimal age and size at maturation, and the long-term effects of harvesting on this trait. Law (2000) recently reviewed the evolutionary change induced by fisheries, and he pointed to the potentially large long-term loss of yield caused by adaptive changes in age and size at maturity. These questions have been addressed repeatedly recently (e.g. Law & Grey 1989, Rijnsdorp 1990, Reznick 1993, Heino 1998), but has mainly focussed on the optimal age at maturity as a function of harvesting. In light of the major role of fat storage in the life history and general biology of many organisms (e.g. Adams1999), life history analyses would benefit by incorporation of this state variable.

Northeast Arctic (NEA) cod is an example of a species that has evolved a life history where energy storage plays a major role. Among the most important prey to cod is the lipid-rich capelin, and the annual and seasonal variability in lipid reserves in NEA cod is correlated with the availability of capelin (Yaragina & Marshall 2000). Lipids are stored in the liver, and fuel metabolism in periods with reduced food intake (Karlsen & al. 1995) and the maturation-cycle of gonads (Kjesbu & al. 1991). In fact, it has been suggested that in years when lipid content (feeding levels) are low, a larger fraction of the mature individuals may have skipped spawning altogether (Oganesyan 1993, Marshall & al. 1998). This has also been observed in northern cod (Burton & al. 1997, Rideout & al. 2000) and other species (Rijnsdorp 1990, Bromley & al. 2000). Further, much effort has recently been allocated to explore the relationship between recruitment success and total liver energy in the spawning stock of NEA cod (Marshall & al 1998, 1999, 2000, Kjesbu & al. 1998, Yaragina & Marshall 2000). This work has demonstrated that the total liver energy of the spawning stock is a better index of the total egg production of the stock than the traditional spawning stock biomass. However, much variance remains unexplained, and it is possible that the estimated total liver energy in the spawning population as an index of egg production is biased if a large fraction of mature females skip spawning (Marshall & al. 1998). This bias is potentially even larger for the more frequent situation in which spawning stock biomass itself is used as an index of egg production and as an explanatory variable in recruitment models (MacKenzie & al. 1998; Marshall et al.

1998, 2000). The inclusion of a reaction norm defining the probability of participation in spawning as a function of body size and condition and having a direct coupling to individual size-specific fecundity may improve the general coherence between total liver energy, egg production and recruitment success in NEA cod.

Model and results

Here, we develop a simple, first attempt to clarify the reasons that could cause fish such as cod to regulate their investment in offspring between years. We take an optimality approach, and calculate the allocation rule (reaction norm) that yields maximum expected lifetime reproduction using basic life history theory (Houston & McNamara 2000).

Maximum fitness $F(L,t)$ and optimal allocation rule $\alpha^*(L)$ in a stable environment is found from

$$F(L,t) = \max_{\alpha}\left\{\begin{array}{l} b(g_L,\alpha) + \\ (1-u_L)F[L+(1-\alpha)g_L,t+1] \end{array}\right\}$$

(1)

where L is body length (cm), t is time (years), fecundity b is a function of size and allocation decision, and mortality u_L is size dependent (Fig. 1). In this simple case, the optimal allocation rule (i.e. an individual maturity ogive) will depend on body size only (Fig. 2a). Intermediate allocation will occur only within a narrow length category (age 8 and 9, Fig. 2b).

The problem is more interesting in a variable environment (Fig. 3). Under these conditions, the optimal allocation schedule can be found from:

$$F(L,t) = \sum_{j=0}^{J} P_j \max_{\alpha(L,j)}\left\{\begin{array}{l} b(g_{L,j},\alpha) + \\ (1-u_L)F[L+(1-\alpha)g_{L,j},t+1] \end{array}\right\}$$

(2)

where P_j and $g_{L,j}$ are given in Fig. 3. Now, we have to summarise over all environmental states and their probabilities of occurrence, and the optimal allocation rule $\alpha^*(L,j)$ now depends on both size L and environment j. This may be interpreted as if the animal make its decisions based on length and condition, if condition is sensitive to annual surplus energy. The optimal allocation rule resulting from Eq. 2 is shown in Fig. 4a, and some stochastic realisations are presented in Fig 4b.

To increase the realism of our analysis further, we introduce spawning costs. These costs may be energetic (c), i.e. the energy required to carry roe or to migrate to the spawning areas, or costs in terms of lower survival probability u_s. Such costs can easily be introduced in the optimisation procedure:

$$F(L,t) = \sum_{j=0}^{J} P_j \max_{\alpha} \left\{ \begin{array}{l} b(g_{L,j},\alpha) - c + \\ [1-(u_L + u_s)]F[L+(1-\alpha)g_{L,j},t+1] \end{array} \right\}. \tag{3}$$

If we assume c is equivalent to 0.5 million eggs and u_s is 5%, then the optimal reaction norm (allocation rule) will depend very much on the environmental (or internal) conditions (Fig. 5a). Clearly, unless a minimum amount of offspring can be produced, it is profitable to skip spawning and invest surplus energy in growth instead. The benefit of increasing size is larger for smaller individuals, and these will only participate in spawning at higher conditions. The consequence of this reaction norm is that realised fecundity of individuals at the spawning grounds will be higher than in the previous examples, and skipped spawning will be more common (Fig. 5b).

Interestingly, there will also be a tendency towards indeterminate growth when some costs of spawning is included (Fig. 5b).

There are some interesting ecological consequences of the evolutionary arguments presented above. In bad years, the fecundity will generally be lower for all individuals, and the probability of skipped spawning increase with lower condition, especially if we include some costs. In fact, low fecundity should be less common under increasing spawning costs, while the variance in the spawning population will be lower. At high spawning costs, individuals should be expected to have quite high fecundity before participating in the spawning, while fecundity would reflect the environmental variance at low costs. That is illustrated in the difference between Figs. 4b and 5b.

Discussion

We have developed a framework where the causes of skipped spawning can be studied. The model demonstrates that young cod should be more likely to skip spawning than older cod. The implication of this is that the spawning stock biomass can be greatly reduced in situations where abundant age classes about to recruit (or

first time spawners) face harsh growth conditions. In order to maximise their lifetime reproductive output, these low-condition individuals should not participate in spawning, particularly if there are energetic or survival costs involved in spawning. However, the probability that these size groups will participate in spawning next year increases, as larger animals have increased propensity to spawn.

The general importance of fat storage in life history theory and growth patterns of fish has not been fully realised (Adams 1999). Additionally, it could well be that physiological constraints, such as storage limitations of liver and gonads can affect allocation decisions in cod in a similar way as in clam (Heino & Kaitala 1996). Thus, model studies on energy flows, acquisition and the reaction norm of energy allocation as a function of state (fat and body size) are warranted, not only in cod, but also in fish in general.

To parameterise our model, we would need information on the variability of surplus energy (or condition, e.g. liver index), physiological constraints on fecundity and growth, and costs involved in spawning activity. These issues will be pursued further to increase the realism of the model.

References

Adams, SM. 1999. Ecological role of lipids in the health and success of fish populations. In: *Lipids in freshwater ecosystems*. Eds.: Arts MT & Wainman BC. Springer-Verlag, New York. pp. 132-160.

Burton MPM, Penney RM, Biddiscombe S. 1997. Time course of gametogenesis in Northwest Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. 54(Suppl. 1):122-131.

Bromley PJ, Ravier C, Witthames PR. 2000. The influence of feeding regime on sexual maturation, fecundity and atresia in first-time spawning turbot. J. Fish Biol. 56:264-278.

Heino M. 1998. Management of evolving fish stocks. Can. J. Fish. Aquat. Sci. 55:1971-1982.

Heino M., Kaitala V.1996. Optimal resource allocation between growth and reproduction in clams: why does indeterminate growth exist? Functional Ecology 10:245-251.

Heino M, Kaitala V. 1999. Evolution of resource allocation between growth and reproduction in animals with indeterminate growth. J. Evol. Biol. 12:423-429.

Houston AI & McNamara JM. 1999. *Models of adaptive behaviour: an approach based on state.* Cambridge University Press, Cambridge, UK. 378 pp.

Karlsen Ø, Holm JC, Kjesbu OS. 1995. Effects of periodic starvation on reproductive investment in first-time spawning Atlantic cod (*Gadus morhua* L.). Aquaculture 133:159-170.

Kjesbu OS, Klungsør J, Kryvi H, Witthames PR, Greers Walker M. 1991. Fecundity, atresia, and egg size of captive Atlantic cod (Gadhus morhua) in relation to proximate body composition. Can J Fish Aquat Sci 48:2333-2343.

Kjesbu OS, Witthames PR, Solemdal P, Greer Walker M (1998) Temporal variations in the fecundity of Arcto-Norwegian cod (*Gadus morhua*) in response to natural changes in food and temperature. J Sea Res 40:303-321.

Law R. 2000. Fishing, selection, and phenotypic evolution. ICES J. Mar. Sci. 57:659-668.

Law R, Grey DR. 1989. Evolution of yields in populations with age-specific cropping. Evol. Ecol. 3:343-359.

MacKenzie BR, Tomkiewicks J, Köster F, Nissling A. 1998. Quantifying and disaggregating the spawner effect: incorporation of stock structure, spatial distribution and female influences into estimates of annual population egg production. ICES CM 1998/BB:11.

Marshall CT, Kjesbu OS, Yaragina NA, Solemdal P, Ulltang Ø. 1998. Is spawner biomass a sensitive measure of the reproductive and recruitment potential of Northeast cod? Can J Fish Aquat Sci 55:1766-1783.

Marshall CT, Yaragina NA, Lambert Y, Kjesbu OS. 1999. Total lipid energy as a proxy for total egg production by fish stocks. Nature 402: 288-290.

Marshall CT, Yaragina NA, Ådlandsvik B, Dolgov AV. 2000. Reconstructing the stock-recruitment relationship for Northeast Arctic cod using a bioenergetic index of reproductive potential. Can. J. Fish. Aquat. Sci. 57:2433-2442.

Oganesyan SA. 1993. Periodicity of the Barents Sea reproduction. ICES CM 1993/G:64.

Reznick DN. 1993. Norms of reaction in fishes. In *The exploitation of evolving resources*, pp 72-90. Stokes TK, McGlade JM, Law R (eds). Lecture Notes in Biomathematics 99. Springer-Verlag, Berlin. 264 pp.

Rideout RM, Burton MPM, Rose GA. 2000. Observations of mass atresia and skipped spawning in northern Atlantic cod, from Smith Sound, Newfoundland. J Fish Biol. 57:1429-1440.

Rijnsdorp AD. 1990. The mechanism of energy allocation over reproduction and somatic growth in female North Sea plaice, *Pleuronectes platessa* L. Neth. J. Sea Res. 25:279-290.

Roff DA. 1992. *The evolution of life histories*. Chapman and Hall, New York, USA. 535 pp.

Stearns, S. C. 1992. *The evolution of life histories*. Oxford University Press, Oxford.

Yaragina NA, Marshall CT. 2000. Trophic influences on interannual and seasonal variation in the liver condition index of Northeast Arctic cod (*Gadus morhua*). ICES J. Mar Sci. 57:42-55.
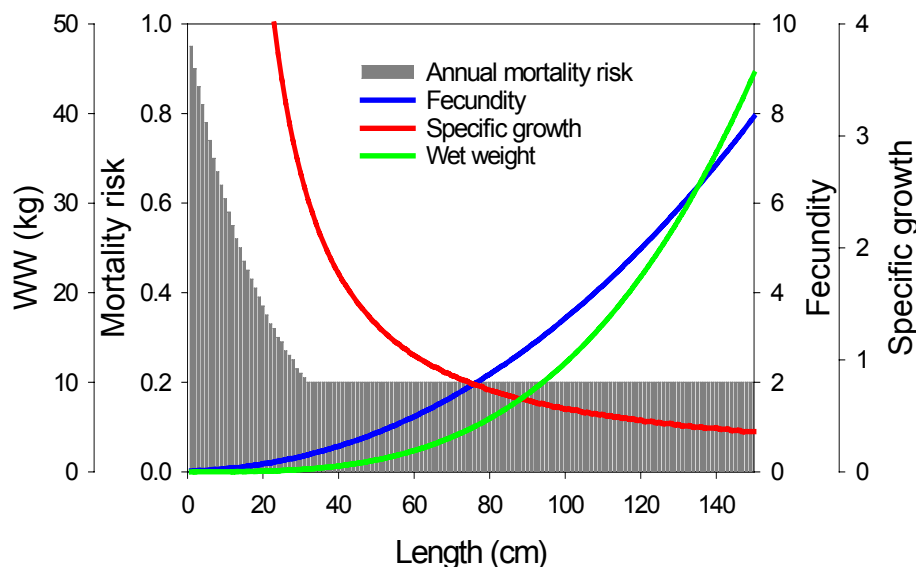
Figures

Fig. 1. The length-dependence of specific growth (g g^{-1} year^{-1}), body weight (kg wet weight), mortality risk and fecundity (10^{-6}) used in the analysis. We have assumed a maximum annual length increment of 15 cm year^{-1}, the length-weight relationship from Svåsand & al. 1996, and 500 egg g^{-1} to estimate potential fecundity if all energy is devoted to egg production.
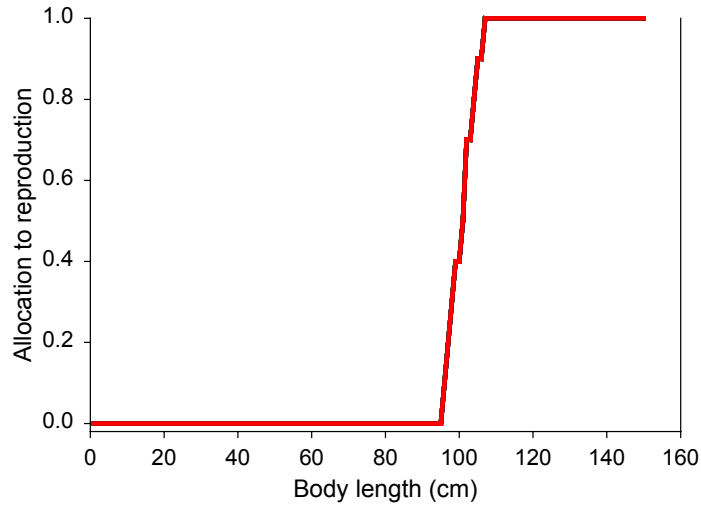
Fig. 2a. The optimal allocation rule $\alpha^*(L)$ in a deterministic world, with growth and mortality schedules as in Fig. 1, and fitness from Eq. 1.
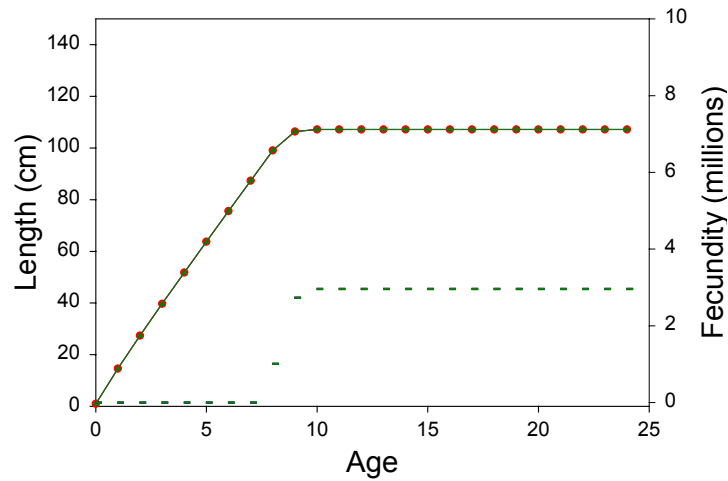

Fig. 2b. The resulting time development of body length and fecundity from the optimal allocation schedule in a stable environment.
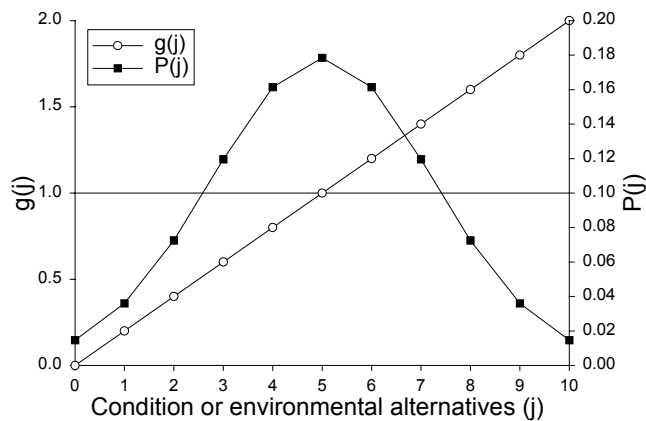

Fig. 3. We define 10 environmental 'states', which take on a normal probability distribution P(j) around the mean state (j=5). The expected state is similar to the one used in the stable environment simulations. The 'environmental state' j indicates annual surplus energy or matter available for growth or reproduction. In terms of the growth-relation in Fig. 1, it varies between 0 (j=0) and 2 (j=10) times the value from Fig. 1.
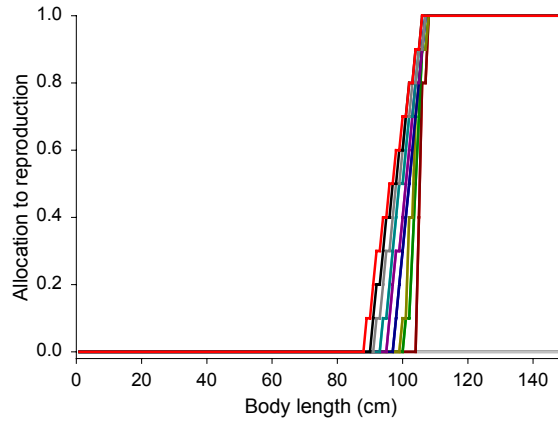
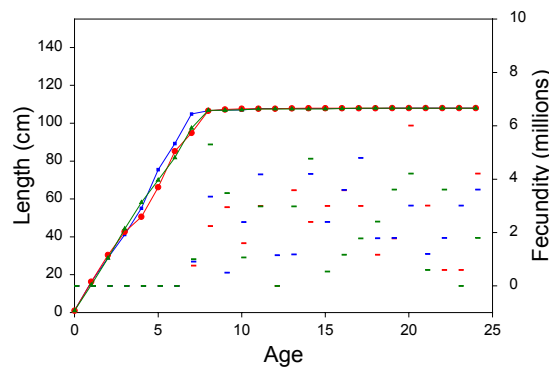Fig. 4a. Optimal allocation rule $\alpha^*(L,j)$ for all lengths (*L*) and environments (*j*) from eq. 2.

Fig. 4b. Three independent stochastic realisations of the life history (length and fecundity) generated from the environment specified in Fig. 3 and the optimal allocation rule from Fig. 4a. The variability in fecundity is here a result of environmental fluctuations, good years give high fecundity while bad years (low j) give low fecundity.
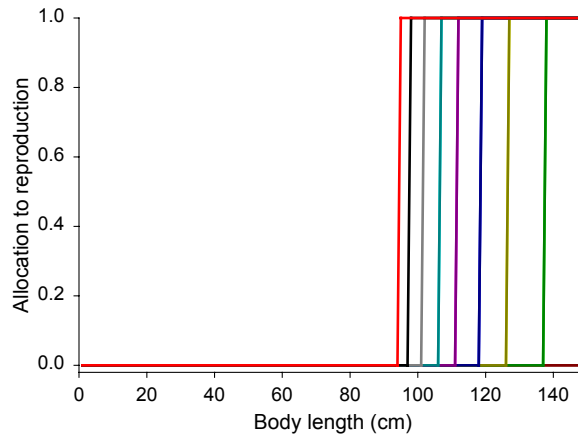

Fig. 5a. The optimal allocation rule when spawning involves an energetic cost (c) of 0.5 million eggs and a mortality risk of 5%. There is one line for each of the environmental situations (j) from Fig. 3, and the best condition (j=10) first elicits reproduction. For j=0, spawning is of course never profitable.
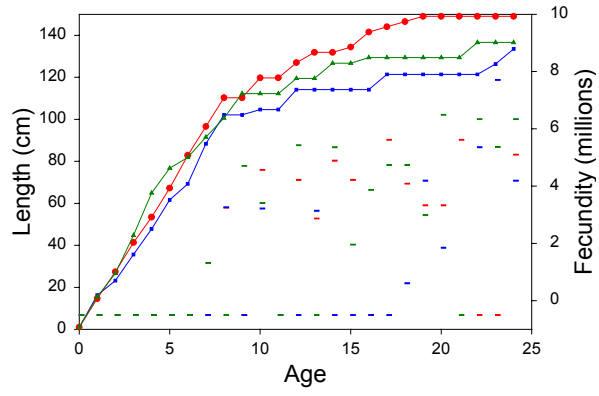
Fig. 5b. Three independent stochastic realisations of growth- and fecundity-trajectories for individuals obeying the reaction norm presented in Fig. 5a.