

Comparing Adaptive Dynamics and Optimisation Models for Predicting Energy Allocation in a Harvested Species

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Goal

To understand the evolution of energy allocation to growth and reproduction in a harvested species by comparing optimisation models and adaptive dynamics models for predicting the consequences of fisheries-induced selection.

Background and motivation

Life-history theory has evolved from simple trade-offs (e.g., Williams 1966) through analyses including environmental stochasticity (Yoshimura and Clark 1993) and individual state (e.g., McNamara and Houston 1996) to the current paradigms of adaptive dynamics (Metz et al. 1992; Dieckmann 1997; Heino 1998) and evolving ING models (individual-based neural network genetic algorithm; Giske et al. 1998; Huse and Giske 1998; Huse et al. 1999; Strand et al. 2002). These developments have increased the realism of life-history models, but have also shifted the balance in the underlying 'complexity trade-off' to near its intractable end.

The present project will explore and compare modern approaches in life-history theory by using cod as model organism. The focus will be on patterns of energy allocation in cod and on the role of body reserves. Part of the allocation problem is understanding the optimal age and size at maturation. Evolutionary changes induced by fisheries were recently reviewed by Law (2000), pointing to the potentially large long-term loss of yield caused by adaptive changes in age and size at maturity. These questions have been addressed for several populations and species (e.g., Law and Grey 1989; Rijnsdorp 1990; Heino 1998). However, to my knowledge an evolutionary study satisfyingly linking a realistic physiology to population level responses has hitherto not been conducted.

Optimization models have almost invariably predicted determinate growth when allocation to growth and reproduction is modeled in a life-history perspective (Cichon 1999): energy is first allocated to growth, until, at an optimal point in life, it is fully diverted to reproduction (Heino and Kaitala 1996; Heino and Kaitala 1999). Indeterminate growth – a continuation of growth after reaching sexual maturity – is, however, frequently occurring across several taxa. Structural constraints and age-dependent rates of mortality and reproduction were found to favor indeterminate growth in clams (Heino and Kaitala 1996), whereas environmental stochasticity was found to select for prolonged reproductive lifespan in general (Murphy 1968; Schaffer 1974) as well as for a prolonged reproductive period and a more indeterminate strategy in a small teleost (Strand et al. 2002). In a numerical model developed by Cichon (1999), determinate growth was found to be the optimal strategy in all situations. The differences in fitness between the optimal determinate strategy and sub-optimal indeterminate growth strategies were, however, in many cases very small. Based on a genetic approach, he

furthermore argues that stochasticity, either in the natural environment or at the genetic level during reproduction, can make indeterminate growth persist as a sub-optimal strategy.

Another implication is that Von Bertalanffy growth should not be used, since it already assumes indeterminate growth (Day and Taylor 1997; Czarnoleski and Kozlowski 1998). Instead, a more descriptive physiological model for energy flow during feeding, allocation, and reproduction combined with a realistic bioenergetics model will allow for an undisturbed exploration of growth and allocation patterns. In light of the major role of fat storage in the life history and general biology of many organisms (Adams 1999), life history analyses would benefit from incorporating energy stores as a state variable (e.g., Fiksen and Carlotti 1998; Fiksen 2000). Stored energy can be viewed as the common currency linking food variability with life-history decisions at the individual level, and producing population-level responses through recruitment success and population dynamics (Adams 1999).

Northeast Arctic cod *Gadus morhua* has evolved a life history in which energy storage plays a major role. Lipids are primarily stored in the liver, and are used to fuel metabolism during periods of reduced food intake (Karlsen et al. 1995), as well as during the maturation cycle of gonads (Kjesbu et al. 1991). Recent 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 traditional spawning stock biomass (Marshall et al. 2000). Yet, much variance remains unexplained. It has been suggested that in years when lipid content (feeding levels) are low, a larger fraction of the adult individuals may skip spawning altogether (Marshall et al. 1998). It is possible that 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 et al. 1998). In addition, skipped spawning will affect the shape of maturity ogives when presence at the spawning grounds is interpreted as sexual maturity.

Research questions

A multiplicity of approaches to behavioral and life-history evolution has recently been emphasized by Houston and McNamara (1999) and Clark and Mangel (2000). Stochastic dynamic optimization models (Clark and Mangel 2000) calculate *the* optimal solution to a problem, but will – in terms of biological realism and the inter-connectedness of variables – quickly be constrained by the complexity of the problem. Adaptive models are advantageous for complex scenarios, and also have the appealing ability to embody biological measures such as heritability and genetic variance (Clark and Mangel 2000, p. 227) and intrinsic fitness measures (no definition of fitness is required, e.g. Strand et al. 2002).

The aim of the present project is therefore to compare predictions resulting for the same life-history problem from two types of models: the modeling framework of adaptive dynamics theory (Dieckmann and Law 1996; Dieckmann 1997; Geritz et al. 1998) will be applied to study energy allocation in cod, and the model's predictions will be compared with those derived from an optimization model (stochastic dynamic programming, Houston and McNamara 1999; Clark and Mangel 2000). As optimization models are much constrained in the biological complexity they can capture, special attention will be paid to the qualitative differences in the resulting predictions as complexity is added to

the adaptive dynamics model. This combined approach will draw on the strengths of optimization models under simpler conditions, and highlight the adaptive approach for more complex problems. Possible effects of the selection pressures enforced by fisheries will be explored.

If time permits, it would also be of great interest to extend the comparison of models to include ING models (Huse and Giske 1998; Huse et al. 1999; Strand et al. 2002), another type of adaptive modeling tool suited for studying complex biological settings.

Methods and work plan

The models that will be used in this project are parameterized for Northeast Arctic cod, and predict monthly allocation strategies and spawning events in a stochastic environment. Various subsets of the population will be subject to harvest, resembling present and past harvesting regimes. The adaptive dynamics and optimization models will be built on the same set of equations describing environment, mortality, and physiology, but more ecological and demographic complexity will be added to the adaptive dynamics model.

Preliminary results from the optimization model show both indeterminate growth and skipped spawning: stochasticity seems to be a requirement for these two life-history patterns. Further, age and size at maturity, variation in allocation strategies, and effects of human exploitation on these life-history traits are worth focusing on. Mortality regimes greatly affect the optimal age and size at maturation. By simulating numerous individuals experiencing the same level of stochasticity but not in identical sequence, reaction norms for age and size at maturity can be extracted from the model. Examples of density-dependent effects that may be added in the adaptive models are as follows:

- Density dependence at the larval stage. This kind of density dependence can have the effect of making skipped spawning less attractive, since a given reproductive effort has a relatively higher value in years when the population as a whole produces fewer offspring.
- The time-lagged density dependence when older juveniles (2-group) cannibalize on young-of-the-year larvae as they are settling toward the bottom.
- Density dependent food intake. At least during periods of high population levels, food availability is likely to affect growth and reproduction. A connection between capelin abundance and condition of cod is well documented (e.g., Yaragina and Marshall 2000), and, if desirable, historic abundance estimates of capelin can be incorporated into a model to compare the model's life-history predictions with field observations.

Relevance and link to ADN's research plan

This project will apply adaptive dynamics modeling to a specific life-history problem that links directly to ADN's research focus on *Fisheries-Induced Adaptive Change*.

Expected output and publications

This work is intended for publication as a co-authored research article and will also be included in my PhD thesis.

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