

Young Scientists Summer Program 2003

Three Research Projects

**Adaptive Dynamics Network
International Institute for Applied Systems Analysis
Laxenburg, Austria**



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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Evolutionary Suicide in Spatial Host-Pathogen Systems

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Goal

To investigate the phenomenon of evolutionary suicide in spatial host-pathogen systems.

Background and motivation

Evolution can sometime lead populations to extinction (Darwin, 1859 and 1871; Matsuda, 1994a and 1994b). This is possible because some individual advantages (gained by the mutation of traits) can have disastrous effects on the population as a whole (Hardin, 1968). For example, a predator the traits of which mutated toward extreme voracity is likely to abound initially, but when its prey becomes too scarce, it is going to starve and could even go extinct. We refer to *evolutionary extinction* as evolution toward trait values at which a population can no longer persist. There exists a distinction between '*evolutionary suicide*' and '*evolutionary murder*,' depending on whether an evolutionary extinction is caused, respectively, by the mutation of the extinguishing population itself, or by the mutation of another population in the same environment. It turns out that evolutionary suicide is a quite frequent phenomenon under frequency-dependent selection (Ferrière, 2000).

My interest in the field of spatial evolutionary dynamics is recent, but motivated by my Ph.D. studies on spatial dynamics and synchronization of oscillators.

Research questions

My project is to investigate evolutionary suicide in a spatial host-pathogen system where one or more traits of the populations are allowed to evolve. Previous work (Rand *et al.*, 1995; Keeling, 2000) has shown that in a spatial explicit PCA (Probabilistic Cellular Automaton) model pathogens are at risk of extinction when their transmissibility is too high. In other words, if a pathogen "burns out" too quickly all the hosts it can reach, it will go extinct. Also using the so-called PATCH (Partitioning, Allocation, Transmission, and Coalescing of Habitats) model it has been shown that the evolving transmissibility of the pathogen tends to a critical value, beyond which the pathogen cannot persist.

However, it is not yet clear if evolution of the pathogens will lead the population to hover just below the critical value of transmissibility, or whether evolution will take it all the way to extinction. The former could happen in spatially extended host-pathogen populations through cluster-level selection: pathogens that transmit too efficiently remove themselves from the pathogens by eradicating their host clusters. In the first case I will turn my attention to elucidating the mechanism of cluster-level selection in more detail, possibly by using the PATCH model, or by developing another suitable model approximation. In the latter case, instead, I will focus on the extinction process, investigating the extinction bifurcation: according to Gyllenberg *et al.* (2000) this would have to involve a discontinuous transition to extinction.

Methods and work plan

My work will be primarily based on two models.

- One model is a spatially explicit PCA (Probabilistic Cellular Automaton) composed of a square lattice of sites with periodic boundary conditions. Each site can be in one of three states: empty, occupied by a healthy host, or occupied by a parasitized host (i.e., occupied by a host and a pathogen that eventually will kill the host). At each step of the simulation, a site can change its state with a probability determined by the configuration of its four nearest neighbours. In particular, if a healthy host is located near one or more parasitized hosts, it can in turn become infected, with a probability that increases with the pathogen's transmissibility.
- The other, spatially implicit, model is called PATCH model, because simulation steps are broken up into a sequence of four macroscopic steps: Partitioning, Allocation, Transmission, and Coalescing of Habitats. The model's dynamical variables are the number of patches of different size, and the simulation steps involve interactions between patches and within patches. The PATCH model offers two advantages compared with the PCA model: first, it remove stochasticity from the simulations, and second, simulations are much faster, because the PATCH model is based on a set of deterministic equations. Of course, because the PATCH model is an approximation only concerned with large-scale patterns, it cannot describe small-scale dynamics due to local correlations.

Based on these models, I will investigate the question whether or not evolutionary suicide occurs when the transmissibility of the pathogen is allowed to evolve in the PCA model. There are two possible scenarios:

- On the one hand, the pathogen could go extinct because it causes excessive host infection. Should this happen, I would continue with the following problem. A work by Gyllenberg *et al.* (2000) investigated evolutionary bifurcations in a structured metapopulation model in which the dispersal rate of an organism is allowed to mutate and showed that for evolutionary suicide to occur the population has to undergo a discontinuous transition to extinction. I would therefore try to understand whether this conclusion holds for the PCA and the PATCH models, too.
- On the other hand, it is also possible that extinction does not happen, so that pathogens that are slightly beyond the critical value of transmissibility will kill themselves by locally "burning out" their host clusters, while pathogens that are slightly below the critical value will persist. This would result in an interesting example of group selection to focus on, since evolution, instead of being driven by individual fitness only, would be driven by cluster-level fitness, too.

If time permits, the following extensions of the project could be considered:

- To introduce the evolution of other pathogen strategies in addition or instead of transmissibility;
- To consider also evolution of the host (specifically, by allowing for adaptive variation in the host's resistance or dispersal rate); and

- To investigate more complex mechanisms of spatial spread, like infections occurring over longer distances or the possibility for the pathogens to travel through host-free environment.

Relevance and link to ADN's research plan

This project aims at establishing further insight into the phenomenon of evolutionary suicide, which has already been a focus of ADN's studies (Ferrière, 2000). In particular, this work will help understanding whether a spatial model composed of hosts and pathogens, as proposed by Rand *et al.* (1995) and Keeling (2000), can evolve toward host extinction, and under which general ecological conditions this can happen. Additionally, this project is putting a result previously obtained by ADN (Gyllenberg *et al.*, 2000; on discontinuous transitions to extinction) to a test in a more complex ecological scenario.

Expected output and publications

The study envisaged here is expected to be published in at least one jointly authored paper and will be integrated as one chapter in my Ph.D. thesis.

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Reproductive Strategies In Cooperative Breeders

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Goal

To develop a dynamic model that predicts the evolution of reproductive skew in cooperative breeders.

Background and motivation

Social systems are characterized by complex interactions between individuals, involving both cooperative behavior and reproductive competition between group members. Evolutionary mechanisms such as kin selection (Hamilton 1964), reciprocal altruism (Trivers 1971; Nowak & Sigmund 1998), ecological constraints (Emlen 1982), prestige (Zahavi & Zahavi 1997), and similarity (Riolo et al. 2001) have been proposed to explain why social animals stay together and cooperate with each other.

Since the work of Vehrencamp (1979, 1983) the evolution of cooperative breeders has been studied in the framework of reproductive skew theory (see Johnstone 2000 and Reeve 2001 for reviews). Reproductive skew is defined as any unevenness in the partitioning of reproduction across members of a group. In particular, this approach aims at predicting the distribution of reproduction between dominant and subordinate group members (the latter are also called 'helpers'). The models assume that the possibility to increase own reproductive success may be an incentive to cooperate and live in groups, and predict the reproductive skew in a group as a function of factors such as relatedness, ecological constraints, group productivity, and depending on who controls reproduction. There also have been some attempts to explain delayed dispersal by dynamic models and to determine the importance of future fitness effects (Lucas et al. 1997; Kokko & Johnstone 1999; Ragsdale 1999; Kokko et al. 2002).

I argue that models formulated to explain the reproductive distribution in cooperative breeders have to incorporate further aspects of an animal's life history, such as (i) trade-offs between direct and indirect reproductive benefits, (ii) trade-offs between current and future benefits, (iii) repeated decision options, (iv) the dynamics of the conflict of interest between dominants and subordinates, and (v) realistic measures of the different fitness costs and benefits associated with the behavioral alternatives. I used a state space approach (see Houston & McNamara 1999 for an introduction to dynamic state variable models) to cover these different aspects of behavioral strategies of helpers (Skubic et al. ms) of the social cichlid fish *Neolamprologus pulcher* to predict optimal reproductive decisions. This approach revealed that behavioral strategies of subordinates (determining whether to refrain from reproducing or to parasitize the reproduction of dominant breeders) depend on a complex interplay between reproductive benefits and life-history costs. The risk of expulsion when helpers parasitize the breeders' reproduction turned out

to be of major importance for the reproduction of subordinates. In particular, I have shown that there are two thresholds, with parasitism optimal for small fish and large fish, but not optimal at intermediate size. Thus, a conditional reproductive strategy might be expected in subordinates: (i) while small, these would start to reproduce shortly after maturity (as found in many fish species; Taborsky 1994), and (ii) once large, helpers would invest into long-term survival, and future reproduction in an own territory.

In general, social animals have to pass through a phase of subordinate status during their life history before being able to become breeders and maintain a territory of their own. Depending on their growth rate, some individuals might reach a critical body size at which to become independent from their natal group more quickly than others. This suggests that reproductive strategies might be polymorphic during life history. Especially in fish, but also in mammals and social insects, fighting ability and female fecundity increase with body size. The body size of an individual relative to its competitors and thus the distribution of body sizes within a population may strongly influence the opportunity of a given individual to reproduce independently. The size distribution and the frequency of different reproductive strategies may therefore be important aspects of social systems and a model that links individual behavior to population dynamics is needed. To incorporate such population-level feedback into models of reproductive skew, by using methods from the theory of adaptive dynamics, is thus the primary goal of my summer project.

Research questions

I will determine evolutionary outcomes of behavioral evolution affecting reproductive skew in populations of cooperative breeders. The specific topics I plan to study during my research stay at IIASA are the following:

- To determine the evolutionarily stable body sizes for switching from one reproductive strategy to another.
- In this context, to investigate the evolutionarily stable coexistence of alloparental brood care, reproductive parasitism, and breeding in an own territory.
- To compare the effect of different ecological environments on the distribution of reproduction within social systems.

Methods and work plan

I will consider the social cichlid *N. pulcher* as a model system and extend my previous approach of dynamic programming by developing a population model that links individual decisions affecting reproduction to population dynamics. I assume that all individuals invest in alloparental brood care and defense, i.e., that they help in raising offspring, potentially of other group members. At any point in their life, individuals can 'decide' whether they (i) do not reproduce on their own, (ii) parasitize the reproduction of dominants, or (iii) try to obtain a territory of their own and become a dominant breeder. The corresponding shifts in reproductive strategy are assumed to be irreversible.

I will develop a deterministic size-structured population model assuming that individuals invest in care for non-descendant kin when they are small and switch to reproduction at larger body sizes. Body size and growth are continuous life-history variables, and we consider a continuum of possible switch sizes from pure helping to

parasitic reproduction and to breeding. Thus, the switch sizes from one reproductive role to another are the phenotypic variables of interest. First, I will assume two switch size variables in the model.

The population is characterized by the densities of the different reproductive roles. I incorporate an environmental feedback by taking the dynamics of density-dependent individual growth into account. The frequency distributions of the reproductive roles are considered to be strongly determined by size-dependent predation, the expulsion probability of helpers, and by the help that other individuals provide. I assume that the density of helping individuals results in fitness benefits in terms of fertility and growth (the helper effect). Population densities vary according to processes of size-dependent growth, fertility, and mortality. Spatial structure is included implicitly.

For numerical analysis, I will use the approximation of envisaging a continuously size-structured population as a collection of many size cohorts, characterized by their average body size and by the number of individuals they contain. This method is known as the 'Escalator Boxcar Train' (Tuljapurkar & Caswell 1997). I will determine the population dynamics of the resident strategy and determine the equilibrium size distributions of the three reproductive roles.

To analyze the evolutionary change of switch sizes I will apply methods of adaptive dynamics theory. Following other game theoretic approaches I assume that mutations occur rarely and that successful invasion by a mutant implies its replacing the resident strategy. Each resident set of switch sizes will result in stable equilibrium size distributions of non-reproducing, parasitizing, and breeding individuals. I then will consider mutant strategies that slightly deviate from the resident population strategy in their switch sizes and determine their invasion fitness. On this basis I will determine the selection gradient and thus the evolutionary attractor in the trait space of switch sizes.

The following scenarios will be investigated:

- To start I will examine the fitness consequences of the model described above with two possible switch size variables. In this analysis I assume that there are no differences in the reproductive roles between the sexes. However, there may be a variation in the equilibrium switch sizes between them and equilibrium solutions of both types will be examined separately.
- In a second approach I will allow for a difference in the roles between females and males and include the possibility of a non-reproductive phase before becoming a breeder.
- Thirdly, I will examine the influence of different environmental effects on the equilibrium densities of helpers, reproductive parasites, and breeders. In particular, the evolutionarily stable reproductive strategies will be investigated in response to a variation in mortality due to predation and in the helper effect.

I will use the deterministic model to determine possible evolutionarily singular points and examine their properties based on pairwise invasibility plots. Lastly, if time permits, I will construct a stochastic individual-based version of the model to investigate the robustness of the derived predictions.

Relevance and link to ADN's research plan

Including the environmental feedback between individual reproduction and population regulation, this adaptive dynamics study will determine evolutionary pathways of reproductive strategies involving cooperative breeding behavior. Understanding the effect of different environmental settings on these strategies will allow to compare data from different populations and species, and might propose a general pattern for explaining the observed high natural variation in cooperative behavior and reproductive skew.

Based on a model by Claessen & Dieckmann (2002), continuous-time adaptive dynamics (Dieckmann 1997; Tuljapurkar & Caswell 1997; Dieckmann 2003) will be used. The proposed project is related to ADN's research foci on the foundations of adaptive dynamics, on the evolution of cooperation, and on fisheries management. In particular, I will extend the application of adaptive dynamics models to understanding reproductive skew in the evolution of social systems.

Expected output and publications

The research described here might be integrated in one chapter of my PhD thesis and is expected to be published in a jointly authored paper in an international scientific journal.

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