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Seven Research Projects

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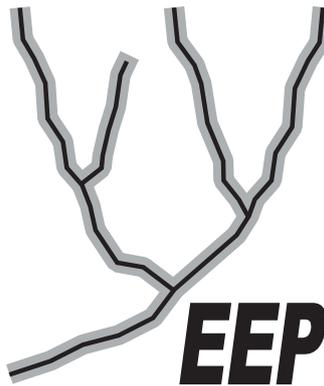
Mutualism evolution on heterogeneous landscapes

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Goal

To investigate the evolution and stability of mutualistic interactions based on changing interaction topologies, spatially heterogeneous habitats, asymmetries in partner numbers, and processes of partner fidelity and partner choice.

Background and motivation

Numerous effects sustaining cooperation have been identified since the very first models of cooperation and mutualistic interactions were published. In particular, these early models incorporated mainly static interaction topologies. Such topologies were designed so that a certain member of the population was interacting either within a fixed neighborhood or with the whole population. In contrast, biological experience often shows that individuals can select their interaction partners from an assembly of potential "applicants" (Schwartz & Hoeksema 1998). Once an interaction is established, an individual can also interrupt it again if it is not satisfied with the benefit it thus gains (West et al. 2002). Thus the number and the quality of interactive links of an individual are often expected to change across the population and over time, leading to a dynamic interaction topology. Such dynamism may apply to interactions involving both interspecific and intraspecific cooperation.

Even when mutualistic relationships are obligatory for the participants, a particular interaction with a single partner can thus still be conditional. The larger the supply of potential partners, the easier it is to dispose non-mutualistic partners (cheaters) and seek out better mutualistic partners. This leads to the dynamic formation and loss of contacts between individuals, resulting in a changing composition of interacting groups.

The distinction between partner fidelity (PF) and partner choice (PC) models was first considered by Bull and Rice (1991). PF models focus on the termination of contacts between individuals of two species, while PC models, interpreting the cooperative act as a good offered in a biological marketplace, focus on the initiation of contacts between individuals of two species.

The majority of modeling work in the field of cooperation and mutualistic interactions has incorporated partner fidelity. The same applies to a model of mutualism by Doebeli and Knowlton (1998), which I have previously used to explore the effects of spatial heterogeneity on the evolution and stability of mutualism (Boza and Scheuring 2004). My previous model was based on a fixed interacting neighborhood, so that an individual could only choose its partner from the same location on a grid. Only the intraspecies competition could lead to changes in the interspecific allocation of partners. A spatial game-theoretical model incorporating both partner fidelity and partner choice will extend this earlier work and will serve as a natural next step in understanding mutualism.

The main idea for the summer project is to generalize Axelrod's well-known Pavlov strategy from game theory, also known as „win stay–lose shift", to describe part-

ner fidelity in mutualistic interactions. Addressing the so far uninvestigated issue of asymmetry in partner numbers, the formation of mutualistic groups will allow the participation of one or more individuals from one of the two mutualistic species, with the other species being referred to as the host. Incorporating partner choice, such groups will be established based on the initial offer from applicants. Incorporating partner fidelity, the maintenance of these groups will depend on the level of satisfaction with the benefits participants are receiving. To explore the implications of spatial structure, we will focus on systems with limited dispersal. Plant-mycorrhizal (Hoeksema and Kummel 2003) and plant-rhizobium (Simms and Taylor 2002) interactions are the most important natural systems motivating the design of our model.

Research questions

The main purpose of this project is to study the evolution and stability of mutually beneficial interactions based on dynamically changing interaction topologies. We will examine the optional mix of partner fidelity and partner choice processes.

Our specific research questions are as follows:

- What are the effects of different acceptance and rejection levels of the host in choosing adequate partners? Are these mechanisms enough to filter out cheaters?

- Is there an interaction between the processes and traits describing partner choice and partner fidelity? What happens when both processes are instead characterized by a single fixed parameter, or a single evolving trait, describing an individual's satisfaction level?

- Will the interaction of one host with several symbiotic partners (instead of one host with a single symbiotic partner) help or hinder the evolution of mutualistic interactions? What are the evolutionary consequences of allocating to each host several nodules, within each of which mutualistic interactions with a group of symbiotic partners are occurring?

- What are the implications of different search ranges of the host for the stability of mutualism? What is the evolutionarily optimal search range? Are larger search ranging helping to find more adequate partners, or do they only give more opportunity for cheaters to spread?

Methods and work plan

The environment in which the hosts reproduce and compete is represented by a lattice consisting of $L \times L$ sites with periodic boundary conditions. Each host has n nodules harboring m symbionts each.

Traits of the host

The host is characterized by its search range (s), acceptance level (α), and rejection level (δ). In addition, we use a linear reaction norm for determining the investment of a host individual in dependence of the payoff it has received from the symbionts, with a given intercept (a_H) and slope (b_H). The search range is the spatial radius of the neighborhood in which the host searches for new symbiotic partners. The acceptance level is the initial offer of the symbiont above which the host accepts the partner with more than 50% probability. The rejection level is the benefit obtained from the mutualistic interaction below which the interaction is broken more than 50% probability.

Traits of the symbiont

Also for the symbionts, we use a linear reaction norm for determining the investment of a symbiont individual in dependence of the payoff it has received from the host, with a given intercept (a_S) and slope (b_S).

Population dynamics of the host

Each site in the lattice is occupied by a host. Hosts are picked for update randomly. The population dynamics is governed by one of three alternative update rules to be considered (see below). On occasion of an update of the host, it is replaced by an offspring of a host from its neighborhood (by default we will use the von Neumann neighborhood, consisting of the focal individual and its four closest neighbors).

With the *proportional update rule*, the chance of host j to get to occupy the focal site is proportional to its payoff in relation the payoff of the others $P_j / \sum_{i=1}^{m} P_i$ (see below for how to calculate payoffs). Here, also the offspring of the focal individual can be the winner of the competition. We will also consider a *death-birth update rule*. This is similar to the proportional update rule, but here the focal individual itself cannot reproduce. With the *pairwise update rule*, reproduction to the focal site is determined by the difference in the payoffs between the focal individual and one of its neighbors. The higher the neighbor's payoff, the higher is its chance to reproduce to the focal site. In all three cases, the new individual inherits its parent's trait. In addition, mutations occur with a certain small probability independently in all five phenotypes (S, δ, α, a, and b).

Population dynamics of the symbiont

Symbionts are considered to reproduce constantly and create a symbiont pool at their site. The densities of free-living symbiont phenotypes will be assumed either to be proportional to the payoffs of symbiont phenotypes within nodules, or they will be subject to a logistic death rate in combination with birth rates that are proportional to the payoffs of symbiont phenotypes within nodules. In the second case, symbionts can reproduce in the soil outside of nodules, as well as inside a nodule. However, the symbionts' reproduction rate in a nodule is much higher, because of the benefits of the mutualistic interaction.

Symbiont can enter an interaction with a host (1) when the host has newly reproduced to the site or (2) after the host has rejected one of its nodules (see below). Again, new symbiont individuals (entering a newly formed nodule) inherit the traits of their parent, potentially with mutations.

Mutualistic interaction

According to their phenotype, a host invests to nodule i the amount $I_{H_i} = a_H + b_H P_{H_i}$, where P_{H_i} denotes the payoff gained from nodule i the previous round. In the first round of an interaction, we always have $P_{H_i} = 0$. A symbiont j in nodule i invests $I_{S_{i,j}} = a_{S_{i,j}} + b_{S_{i,j}} P_{S_{i,j}}$, where $P_{S_{i,j}}$ denotes the payoff gained from the host in the previous round. The symbionts' investments are pooled for a given nodule, so that the host receives an average investment of $I_{S_i} = \frac{1}{m} \sum_{j=1}^{m} I_{S_{i,j}}$ from nodule i. Symbionts either get the full benefit of the host's investment, or share it equally.

The investments of symbionts and hosts imply a cost for the investor ($C(I_{receiver})$) and a benefit for the receiver ($B(I_{investor})$). The cost is a linear function of the investment, $C(I_{receiver}) = C_0 \cdot I_{receiver}$, while the benefit is a saturating function of the investment, $B(I_{investor}) = B_0 \cdot (1 - \exp(-B_1 \cdot I_{investor}))$. C_0, B_0, and B_1 are parameters of the model that

can be different between the hosts and the symbionts or can be considered identical for both species. Thus, the payoffs gained in one round of the potentially mutualistic interaction between the host and its symbiont are as follows:

$$P_{H_i,t} = B(I_{S_i,t}) - C(I_{H_i,t}) = B_0[1 - \exp(-B_1 \cdot \tfrac{1}{m} \sum_{j=1}^{m} (a_{S_{i,j}} + b_{S_{i,j}} P_{S_{i,j},t-1}))] - C_0(a_{H_i} + b_{H_i} P_{H_i,t-1}),$$

$$P_{S_{i,j},t} = B(I_{H_i,t}) - C(I_{S_{i,j},t}) = B_0[1 - \exp(-B_1 \cdot (a_{H_i} + b_{H_i} P_{H_i,t-1}))] - C_0(a_{S_{i,j}} + b_{S_{i,j}} P_{S_{i,j},t-1}).$$

In order to include the effect of *b* in partner choice, two rounds of interaction take place right at the (potential) beginning of a new mutualistic relationship. Further (single) rounds of interaction occur until the rejection of a nodule or until the death of the host.

During one interaction step of the model, a host and one of its nodules are chosen randomly and updated. Payoffs are calculated, and the host can choose to reject the nodule based on its rejection level and the payoff gained from the interaction. The probability of rejection is $[1 + \exp((\delta - P_{H,t})/\kappa_R)]^{-1}$, where κ_R is the slope of this function at its inflection point and measures how imperfectly the host perceives the payoff obtained from the symbionts. Interaction steps as described here are repeated a fixed number of times ($k \cdot L \cdot L \cdot n$, where $k > 1$ is a parameter; the rest of this product equals the number of nodules in the model).

Choosing new symbionts

A new host or a host with an empty nodule (resulting from rejection) develops a new nodule and chooses new symbionts. Symbionts present themselves to the host as long as there is an empty slot in the nodule (i.e., as long as the number of symbionts in the nodule is less than *m*). Only symbionts available within the search range of the focal host are considered. A symbiont is accepted based on its initial offer (a_S) and the acceptance level of the host. The probability of accepting the symbiont is $[1 + \exp((\alpha - P_{S_{i,j},2})/\kappa_A)]^{-1}$, where κ_A is the slope of this function at its inflection point and measures how imperfectly the host perceives the initial offer of a symbiont.

Work plan

We will increase the complexity of the model gradually. The first version will model one-to-one interactions ($m = 1$ and $n = 1$). This is a direct extension of the Doebeli & Knowlton (1998) model to include partner choice and partner fidelity. Then we allow more symbionts per nodule, while keeping the number of nodules equal to 1. Finally, both parameters (*n* and *m*) will be set to exceed 1. The search range of hosts (*s*) is initially set to 1, i.e., hosts search for symbionts only in their immediate vicinity. Later on, we will increase this search range and also allow it to evolve.

Relevance and link to EEP's research plan

Pairwise cooperative interactions have been a subject of EEP research already for a long time. As this model focuses on pairwise cooperative interactions between individuals from different species, involving complex and dynamic interaction topologies, it will extend this previous research toward the investigation of real-life interaction network models and hopefully shed light on new effects that help maintaining cooperation.

Expected output and publications

We envisage at least one coauthored publication coming out of this summer project. The for-mulation of the problem is general, and we could eventually investigate other, related questions, which could result in further publications in the future.

References

Boza, G. and Scheuring, I. (2004). Environmental heterogeneity and the evolution of mutualism. Ecological Complexity, 1: 329-339.

Bull, J.J. and Rice, W.R. (1991). Distinguishing mechanisms for the evolution of co-operation. Journal of Theoretical Biology, 149: 63-74.

Doebeli, M. and Knowlton, N. (1998). The evolution of interspecific mutualism. Pro-ceedings of the National Academy of Sciences of the USA, 95: 8676-8680.

Hoeksema, J.D. and Kummel, M. (2003). Ecological persistence of the plant-mycorrhizal mutualism: a hypothesis from species coexistence theory. American Naturalist, 162: S40-S50.

Nowak, M.A. and May, R.M. (1992). Evolutionary games and spatial chaos. Nature, 359: 826-829.

Schwartz, M.W. and Hoeksema, J.D. (1998). Specialization and resource trade: bio-logical markets as a model of mutualism. Ecology, 79: 1029-1038.

Simms, E.L. and Taylor, D.L. (2002). Partner choice in nitrogen-fixation mutualism of legumes and rhizobia. Integrative and Comparative Biology, 42: 369-380.

West, S.A., Kiers, E.T., Simms, E.L. and Denison, R.F. (2002). Sanctions and mutual-ism stability: why do rhizobia fix nitrogen? Proceedings of the Royal Society of London, Series B, 269: 685-694.

Deriving harvest control rules for fisheries management

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Goal

To understand the interplay between fisheries management objectives, their translation into utility components, and the derivation of harvest control rules through utility maximization based on simulating stochastic fish population dynamics.

Background and motivation

As fish stocks continue to face substantially higher fishing levels, the need to manage fishing activity becomes direr. Most of the word's countries have access to fish resources and there are many different political and legal systems that dictate and restrict fishing activity. New strategies for the management of marine fisheries, including the development and evaluation of management procedures and harvest control rules (HCRs) are currently important research topics for many countries (Cochrane et al. 1998, Butterworth and Punt 1999, Cadrin 1999, Geromont et al. 1999, Ibaibarriaga et al. 2005, Lillegård et al. 2005). Fisheries management in Europe has traditionally focused on short-term projections for setting quotas according to conservation measures (Kelly 2006). Today, many fisheries managers and international advisory institutions (e.g., the International Council for the Exploration of the Sea, ICES) aim at more strategic, long-term fisheries management. This is partly in response to the call for ecosystem-based management. The scientific challenge is to understand how such management strategies may work.

Hilborn (2007) emphasizes that fisheries management needs clear objectives in order to be evaluated. In fisheries, the setting of such objectives will usually involve the resource's stakeholders (Baelde 2005, Paramor et al. 2005). However, due to the nature of multiple and conflicting objectives in fisheries (Horwood and Griffith 1992, Cochrane et al. 1998, Hilborn 2007) such as high yield vs. conservation, fisheries management objectives have often remained unclear (Horwood and Griffith 1992, ICES 2007).

One way to clarify different objectives in fisheries is through the use of utility functions. These can help to quantify and rank different biological, social, or economic objectives (Quinn and Deriso 1999). The optimizing of a utility function enables the objective derivation of a HCR. Economic discounting theory provides a formal way to prioritize long- or short-term objectives by using high discounting rates for short-term utility ("race to fish") or low discounting rates for long-term utility ("fishing for the future").

Because there is no "one size fits all" management strategy for fisheries (Caddy and Seijo 2005), a need arises to understand basic patterns of HCR derivation and implementation. Therefore, our approach in this study is a generic one using a simple population model. Stochasticity of populations causes qualitative changes in predictions relative to deterministic models (Lande et al. 1994, 1995, 2003) and therefore

will be included in our approach. Especially for long-term advice, stochastic considerations should be used in designing management procedures or rules (Kelly 2006).

Research questions

Current deficiencies in fisheries management within the EU are the lack of a formal framework for drafting and ranking specific stakeholder objectives, in conjunction with the lack of a transparent and communicable approach to management. The aim for this research is therefore to work towards the development of such a framework, following a perspective outlined by Hilborn (2007).

To achieve this, I will derive HCRs that reflect the trade-offs between different objectives of fisheries management (i.e., yield, profit, biological conservation, and employment). Once such HCRs are derived through numerical optimization based on simulating stochastic fish population dynamics, I will explore how they may be simplified by relying on fewer input and output variables. Such simplified HCRs facilitate communication and support a higher level of transparency.

This work is to be done in a broad setting using models representing generic fish stocks to produce a general foundation for HCR theory. This project will ultimately create concrete HCRs for a simulated fishery according to specific, pre-defined objectives based on the weighing of different stakeholder preferences. The objective-derived HCRs will then be applied and updated in the stochastic population model to finally assess its performance in relation to the original objectives.

Through this study, I will illustrate a formal route towards deriving appropriate management regimes with focus on compatible management goals to promote stakeholder consensus, incentives, and success in fishery management.

Methods and work plan

Following Heino (1998), I will use an age-structured population model. The simulated population is represented by $N_a(t)$, where N is the number of individuals at time t and a represents age classes where $a = 0, 1, \ldots, a_{max}$. Individuals that reach a_{max} die. Natural mortality rate M and recruitment to the fishery are age-class-specific. The effects of different recruitment regimes (Zheng 1995, Barrowman and Myers 2000), growth patterns, and HCRs can thus be explored. Stochasticity will be implemented in recruitment functions and in the application of HCRs to mimic variations in environment and fishing. The stock will be harvested instantaneously once a year according to the HCRs derived and updated annually.

Following Hilborn (2007), several utility components, corresponding to specific objectives, will be used: (1) yield, (2) employment, (3) profit, and (4) ecosystem preservation. Current values for these utility components will be extracted from the numerical model based on, respectively, (1) annual yield, (2) fishing effort, (3) difference between revenue and cost, and (4) risk of the fish population dropping below a pre-defined minimum level B_{lim} of biomass. These utility components are then translated into the same currency using appropriate weights, yielding total current utility. The choice of weights reflects different stakeholder preferences. Total utility is then calculated through time averaging with suitable discounting. I will use fishing mortality and minimum catch size regulation as action options that serve as input to the model determined by a HCR. The resulting numerical output from the model will affect the utility, which will then be maximized by altering the management actions, and thus the HCR, accordingly.

Relevance and link to EEP's research plan

One of the main research areas for the Evolution and Ecology Program at IIASA is fisheries-induced changes in exploited fish stocks. In this context, a comprehensive but basic understanding of how different management priorities affect fish stocks is needed. This research aims at quantifying the biological effects of different types of fisheries management regimes in a generic setting. The implications of different harvest regimes have serious biological and policy-relevant effects, which relate directly to the EEP's research plan and my own PhD thesis work.

Expected output and publications

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

References

Baelde, P. (2005). Interactions between the implementation of marine protected areas and right-based fisheries management in Australia. Fisheries Management and Ecology, 12: 9-18.

Barrowman, N.J. and Myers, R.A. (2000). Still more spawner-recruitment curves: the hockey stick and its generalizations. Canadian Journal of Fisheries and Aquatic Sciences, 57: 665-676.

Butterworth, D.S. and Punt, A.E. (1999). Experiences in the evaluation and implementation of management procedures. ICES Journal of Marine Science, 56: 985-998.

Caddy, J.F. and Seijo, J.C. (2005). This is more difficult than we thought! The responsibility of scientists, managers and stakeholders to mitigate the unsustainability of marine fisheries. Philosophical Transactions of the Royal Society of London, Series B, 360: 59-75.

Cadrin, S.X. (1999). A precautionary approach to fishery control rules based on surplus production modeling. Proceedings, 5th NMFS NSAW. NOAA Tech. Memo. NMFS-F/SPO-40.

Cochrane, K.L., Butterworth, D.S., De Oliveira, J.A.A. and Roel, B.A. (1998). Management procedures in a fishery based on highly variable stocks and with conflicting objectives: experiences in the South African pelagic fishery. Reviews in Fish Biology and Fisheries, 8: 177-214.

Engen, S., Lande, R. and Sæther, B.E. (1997). Harvesting strategies for fluctuating populations based on uncertain population estimates. Journal of Theoretical Biology, 186: 201-212.

Geromont, H.F., De Oliveira, J.A.A., Johnston, S.J. and Cunningham, C.L. (1999). Development and application of management procedures for fisheries in southern Africa. ICES Journal of Marine Science, 56: 952-966.

Heino, M. (1998). Management of evolving fish stocks. Canadian Journal of Fisheries and Aquatic Sciences, 55: 1971-1982.

Hilborn, R. (2007). Defining success in fisheries and conflicts in objectives. Marine Policy, 31: 153-158.

Horwood, J. and Griffith, D. de G. (1992). Management strategies and objectives for fisheries. Privately published.

Ibaibarriaga, L., Uriarte, A. and Roel, B. (2005). More on harvest control rules for the Bay of Biscay anchovy. Working document to the WGMHSA, pp. 11, Vigo, Spain.

ICES (2007). Report of the Study Group on Management Strategies (SGMAS). ICES SGMAS Report 2007.

Kelly, C. (2006). Modelling marine fish and fisheries dynamics: a new paradigm. In: Codling, E.A. and Kelly, C.J. (eds.) Reports from the FSS mini-symposia 2005-2005.

Lande, R., Engen, S. and Sæther, B.E. (1994). Optimal harvesting, economic discounting and extinction risk in fluctuating populations. Nature, 372: 3.

Lande, R., Engen, S. and Sæther, B.E. (1995). Optimal harvesting of fluctuating populations with a risk of extinction. American Naturalist, 145: 728-745.

Lande, R, Engen, S. and Sæther, B.E. (2003). Stochastic Population Dynamics in Ecology and Conservation. Oxford University Press.

Lillegård, M., Engen, S., Sæther, B.E. and Toresen, R. (2005). Harvesting strategies for Norwegian spring-spawning herring. Oikos, 110: 267-577.

Paramor, O.A.L., Hatchard, J.L., Mikalsen, K.H., Gray, T.S., Scott, C.L. and Frid, C.L.J. (2005). Involving fishers in the development of a fisheries ecosystem plan. ICES CM 2005/V:32.

Peterman, R.M. (2004). Possible solutions to some challenges facing fisheries scientists and managers. ICES Journal of Marine Science, 61: 1331–1343.

Quinn, T.J. and Deriso, R.B. (1999). Quantitative Fish Dynamics. Oxford University Press.

Zheng, J. (1995). Herring stock-recruitment relationships and recruitment patterns in the North Atlantic and Northeast Pacific oceans. Fisheries Research, 26: 257-277.

Probabilistic maturation reaction norms of sockeye salmon spawning populations of Bristol Bay, Alaska

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Goal

To estimate probabilistic maturation reaction norms (PMRNs) for length and age at maturation of locally adapted sockeye salmon spawning populations of the Wood River system, Bristol Bay, Alaska.

Background and motivation

Humans can influence life history traits of domesticated and wild animals through selective processes. Fishing is often deliberately size-selective for economic and biological reasons (Walters and Martell 2004). Size-selective fishing mortality is often associated with directional selection and changes in life history traits such as age and size at maturity (Law and Grey 1989, Policansky 1991). Short term and sustainable fishery yields can fluctuate due to life history evolution in harvested populations. Therefore, the evolution of age and size at maturity, phenotypic traits associated with yield, are of particular interest when assessing the effects of fishery selectivity (Law 1979, 2000).

While it is undeniable that age and size at maturity are shaped by environmental factors (Bigler et al. 1996, Pyper and Peterman 1999), numerous studies on wild and experimental fish populations have demonstrated that size-selective exploitation can affect these life history traits (Ricker 1981, 1995, Conover and Munch 2002, Walsh 2003, Olsen et al. 2004, Munch et al. 2005). Still, the selective effects of fishing and phenotypic changes it can cause have not been considered a great deal in fisheries management (Hamon et al. 2000, Law 2000). Specifically, less research has been conducted on evolutionary and fishery management implications of size-selective harvest for semelparous species.

Quantitative genetics and reaction norms are used to analyze the phenotypic and genetic variation that conditions the response to selection (Stearns 1992). Norms of reaction show the ranges of potential phenotypes, such as different ages and sizes at maturity, that a given genotype could develop if an individual is exposed to different environmental conditions (Stearns and Koella 1986). The probabilistic maturation reaction norm of a genotype or population describes the phenotypic maturation schedule of individuals, stocks, or species and is defined by the probabilities of becoming mature in the next season as a function of an individual's size and age. Across populations or within populations across time, differences in age and size at maturity associated with variation in growth and mortality may represent plastic responses to the environment if they follow the same reaction norm. Variation in age and size at maturity can be interpreted as a plastic response if the variability in growth rates is mainly due to environmental determinants (Heino et al. 2002a, Heino et al. 2002b, Hutchings 2004). Selection, due to many causes, may act on age and size at maturation and cause the reaction norm of an individual or population to shift in position (Stearns and Koella 1986, Heino et al. 2002b) or change shape (Haugen 2000).

It is important to characterize the maturation reaction norms in various populations. With this information, one can better understand variability in phenotypic traits, such as age and size at maturity, between populations of a given species that exhibit life history differences. Research has shown that in some cases human-induced selection, for example due to fishing, can change the shape or position of maturation reaction norms. A study on northern cod, which were heavily harvested in the 1970s and 80s and who suffered major stock collapses in the early 1990s, is a prime example of this. As harvest mortality on female northern cod increased throughout the 1980s and early 90s, the maturation reaction norm shifted continually toward smaller sizes and younger ages (Olsen et al. 2004). Research has also shown that even with low fishing pressure on Newfoundland stocks of American plaice, their maturation reaction norms have shifted towards maturation at younger age and smaller sizes (Barot et al. 2005). In these examples, and in others, alterations of the maturation reaction norms suggest that changes in age and size at maturation resulted not only from phenotypic plasticity due to variations in growth rate but from underlying genetic, and thus evolutionary, changes. Maturation reaction norms may help to disentangle phenotypic plasticity associated with different growth and mortality conditions from genetic effects that influence maturation as a result of reaction norm evolution (Heino et al. 2002a, Heino et al. 2002b). Thus, they may reveal changes in maturation schedules associated with size-selective fishing. From a management perspective, it is important to understand if life history trait changes over time, specifically in age and size at maturity, are genetic changes or plastic phenotypic responses (Morita et al. 2005), as genetic changes may have more long-term consequences.

While PMRNs have been developed for a number of iteroparous fish species, little work has been done understanding reaction norms for semelparous species, such as Pacific salmon. Bristol Bay, Alaska has some of the most diverse and abundant sockeye salmon (*Oncorhynchus nerka*) populations in the world. The Wood River system of the Nushagak fishing district is home to dozens of genetically and ecologically distinct sockeye spawning populations. Spawning sites include streams, rivers, and beaches, and fish are locally adapted to their site. We possess a great deal of data on life history traits of individual spawning populations so can examine if these populations differ in their PMRNs. An economically important commercial gillnet fishery has exerted strong, size-selective fishing pressure on these salmon since 1884. Fishery catch and escapement data and spawning ground data on age and size at maturity have been collected yearly since 1946. Additionally, the management of the Bristol Bay sockeye salmon fishery has varied over time but has been well documented (Link et al. 2003, Hilborn 2006).

Research questions

For this proposed study, I plan to calculate PMRNs for age and size at maturation of different Wood River system sockeye salmon spawning populations from the 1960s through the present. With these PMRNs, in the future I can understand changes in life history traits over time and will evaluate if the fishery selection has the potential to cause life history evolution. I can also use the reaction norms to later create an eco-genetic model of the effects of different size-selective harvest regimes.

Methods and work plan

To calculate PMRNs, I will use data collected on the Nushagak district and Wood River spawning ground sockeye salmon populations. Daily counts of the numbers of salmon caught in the Nushagak district and escaping into the 3 main freshwater sys-

tems are available yearly since 1946. In addition, age, sex, and length measurements from samples of the catch and escapement have been taken yearly. Count, age, sex, and length data from many of the spawning populations of sockeye salmon within the Wood River system are available during many, though not all, years since the 1940s. Finally, we have a great deal of information on past fishery management practices over time (Link et al. 2003, Hilborn 2006).

To calculate PMRNs of age and size at maturation for the spawning populations within the Wood River system, I will use the methods described by Heino et al. (2002a, 2002b) and Morita et al. (2005). Approximately 10 spawning populations, from the three main habitat types (streams, rivers, and beaches), with long-term data available, and with consistently large population sizes, will be chosen for assessment. Because semelparous species spawn only once before their death, it is easy to determine first-time spawners. We also have age and size data from yearly time intervals, consistent with the methods described by Heino et al. (2002a, 2002b).

In the Wood River system, juvenile sockeye salmon from all spawning populations rear for 1-2 years in 4 main nursery lakes. Environmental conditions are similar in these lakes (Burgner et al. 1969). Little is known about growth of fish from the different spawning populations, as genetic or other markers have not been developed to identify individual fish or populations. Thus, growth and mortality conditions are assumed to be similar for fish from all populations. After completion of rearing in the nursery lakes, sockeye migrate to the ocean, where they put on 99% of their body weight. In this stage little if anything is known about different growth and mortality conditions of fish from different spawning populations, so the same growth and mortality conditions will also be assumed for all fish. After completion of their ocean growth phase, sockeye salmon home to where they were born to spawn and die. As they are migrating back into freshwater, Bristol Bay sockeye are exposed to a heavy commercial gillnet fishery, which takes up to 80% of the run. This fishery is size-selective, and imposes greater mortality on some individual fish and populations due to their size. For example, large fish spawning in rivers and beaches may be more heavily exploited during some years than are small fish who can escape through the gillnets (Kendall et al. in prep.). Therefore, adult mortality of the different sockeye spawning populations can differ at this point.

To determine PMRNs, representative samples of both maturing and immature fish are required (Heino et al. 2002b). Because we only sample mature sockeye salmon that are returning to the Wood River system to spawn, we must reconstruct unobserved size distributions of immature fish. With our present data, we can calculate length- and age-based maturity ogives for the different Wood River sockeye spawning populations. The reconstruction procedure is outlined by Heino et al. (2002b) and includes one initialization step followed by a cycle of three steps. This reconstruction method requires the assumption of a growth model for immature fish. In this study a length-linear juvenile growth model will be used.

Another way to reconstruct the fork length of immature fish is that described by Morita et al. (2005), which uses a back-calculation method based on otolith measurements using a biological intercept method (Campana 1990). Otoliths are currently being measured from two Wood River spawning populations, and hopefully more populations and those from additional years will be examined in the near future. This data will also help to corroborate the findings of the growth model used to reconstruct immature sockeye lengths at age. Morita et al. (2005) describe a similar way to that of Heino et al. (2002b) to calculate the probability of a fish maturing. They used their results to examine the rule of age and size at maturity.

Given the mature and the immature reconstructed length at age data and maturity ogives for the Wood River system, PMRNs for length and age at maturation will be calculated.

Relevance and link to EEP's research plan

This research will estimate PMRNs for locally adapted populations of a major commercial fish and thus falls under EEP's research focus on evolutionary fisheries management. My research project will also expand the scope of EEP's research to fish of the Pacific Ocean and with a semelparous life history, and set up the opportunity to create an eco-genetic model for these fish.

Expected output and publications

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

References

Barot, S., Heino, M., Morgan, M.J. and Dieckmann, U. (2005). Maturation of Newfoundland American plaice (*Hippoglossoides platessoides*): long-term trends in maturation reaction norms despite low fishing mortality? ICES Journal of Marine Science, 62: 56-64.

Bigler, B.S., Welch, D.W. and Helle, J.H. (1996). A review of size trends among North Pacific salmon (*Oncorhynchus* spp.). Canadian Journal of Fisheries and Aquatic Sciences, 53: 455-465.

Burgner, R.L., DiCostanzo, C.J., Ellis, R.J., Harry, G.Y.J., Hartman, W.L., Kerns, O.E.J., Mathisen, O.A. and Royce, W.F. (1969). Biological studies and estimates of optimum escapements of sockeye salmon in the major river systems in southwestern Alaska. Fishery Bulletin, 67: 405-459.

Campana, S.E. (1990). How reliable are growth back-calculations based on otoliths? Canadian Journal of Fisheries and Aquatic Sciences, 47: 2219-2227.

Conover, D.O. and Munch, S.B. (2002). Sustaining fisheries yields over evolutionary time scales. Science, 297: 94-96.

Hamon, T.R., Foote, C.J., Hilborn, R. and Rogers, D.E. (2000). Selection on morphology of spawning wild sockeye salmon by a gill-net fishery. Transactions of the American Fisheries Society, 129: 1300-1315.

Haugen, T.O. (2000). Growth and survival effects on maturation patterns in populations of grayling with recent common ancestors. Oikos, 90: 107-118.

Heino, M., Dieckmann, U. and Godø, O.R. (2002a). Measuring probabilistic reaction norms for age and size at maturation. Evolution, 56: 669-678.

Heino, M., Dieckmann, U. and Godø, O.R. (2002b). Estimating reaction norms for age and size at maturation with reconstructed immature size distributions: a new technique illustrated by application to Northeast Arctic cod. ICES Journal of Marine Science, 59: 562-575.

Hilborn, R. (2006). Fisheries success and failure: the case of the Bristol Bay salmon fishery. Bulletin of Marine Science, 78: 487-498.

Hutchings, J.A. (2004). Norms of reaction and phenotypic plasticity. In: Hendry, A.P. and Stearns, S.C. (eds.) Salmonid life histories. Evolution illuminated: salmon and their relatives. Oxford University Press, pp. 154-174.

Law, R. (1979). Optimal life histories under age-specific predation. American Naturalist, 114: 399-417.

Law, R. (2000). Fishing, selection, and phenotypic evolution. ICES Journal of Marine Science, 57: 659-668.

Law, R., and Grey, D.R. (1989). Evolution of yields from populations with age-specific cropping. Evolutionary Ecology, 3: 343-359.

Link, M.R., Hartley, M.L., Miller, S.A., Waldrop, B., Wilen, J. and Barnett, J. (2003). An analysis of options to restructure the Bristol Bay salmon fishery. Bristol Bay Economic Development Corporation, Dillingham, AK.

Morita, K., Morita, S.H., Fukuwaka, M. and Matsuda, H. (2005). Rule of age and size at maturity of chum salmon (*Oncorhynchus keta*): implications of recent trends among *Oncorhynchus* spp. Canadian Journal of Fisheries and Aquatic Sciences, 62: 2752-2759.

Munch, S.B., Walsh, M.R. and Conover, D.O. (2005). Harvest selection, genetic correlations, and evolutionary changes in recruitment: one less thing to worry about? Canadian Journal of Fisheries and Aquatic Sciences, 62: 802-810.

Olsen, E.M., Heino, M., Lilly, G.R., Morgan, M.J., Brattey, J., Ernande, B. and Dieckmann, U. (2004). Maturation trends indicative of rapid evolution preceded the collapse of northern cod. Nature, 428: 932-935.

Policansky, D. (1991). Fishing as a cause of evolution in fishes. In: Stokes, T.K. McGlade, J.M. and Law, R. (eds.) The exploitation of evolving resources. Springer-Verlag, pp. 2-18.

Pyper, B.J. and Peterman, R.M. (1999). Relationship among adult body length, abundance, and ocean temperature for British Columbia and Alaska sockeye salmon (*Oncorhynchus nerka*), 1967-1997. Canadian Journal of Fisheries and Aquatic Sciences, 56: 1716-1720.

Ricker, W.E. (1981). Changes in the average size and average age of Pacific salmon. Canadian Journal of Fisheries and Aquatic Sciences, 38: 1636-1656.

Ricker, W.E. (1995). Trends in the average size of Pacific salmon in Canadian catches. In: Beamish, R.J. (ed.) Climate change and northern fish populations. National Research Council of Canada, Ottawa, pp. 593-602.

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

Stearns, S.C. and Koella, J.C. (1986). The evolution of phenotypic plasticity in life-history traits: predictions of reaction norms for age and size at maturity. Evolution, 40: 893-913.

Walsh, M.R. (2003). Evolution in response to size-selective mortality: changes in correlated characters among captive populations of the Atlantic silverside (*Menidia menidia*). Master of Science. Stony Brook University, Stony Brook, NY.

Walters, C.J. and Martell, S.J.D. (2004). Fisheries ecology and management. Princeton University Press.

Fisheries-induced evolution and sexual dimorphism in North Sea plaice

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Goal

To develop a multi-trait individual-based eco-genetic model for studying fisheries-induced evolution in North Sea plaice as documented by empirical data over the last century, with particular consideration of sex-specific mortality regimes and life-history responses.

Background and motivation

Fisheries-induced life history evolution

Selective exploitation of fish stocks is increasingly recognized as driving the evolution of life history traits (Stokes et al., 1993). Higher mortality in general, and positively size-selective mortality in particular, cause an organism's current reproduction to become relatively more important than its future reproduction (Heino and Kaitala, 1999). This may result in slower growth rates, maturation at younger ages and smaller sizes, and a higher relative reproductive investment (Roff, 1983). Accordingly, size-selective harvesting has been shown to be associated with changes in growth and maturation (Sinclair et al., 2002; Grift et al., 2003; Conover et al., 2005; Olsen et al., 2005). However, measuring life history trait combinations of individual animals in the field is notoriously difficult, as one would ideally have to follow individuals throughout their life, and also since changes in life history traits are often confounded by phenotypic plasticity due to environmental variation.

Since life history changes due to size-selective fishing typically go along with a reduction of sustainable yield (Law and Grey, 1989; Heino and Godø, 2002), it is of interest to adopt management strategies to let fish stocks with evolved life history traits recover, or at least to prevent further life history changes. Individual-based eco-genetic models provide a powerful tool for understanding and analyzing the evolution of life-history traits, their correlation structure, and the effects of different harvesting strategies.

North Sea plaice

Plaice are sexually dimorphic: females grow faster, become mature at larger sizes and older ages, and allocate more energy to reproduction than males (Rijnsdorp and Ibelings, 1989). Growth rates are expected to be dependent on population density (Beverton, 1964), and changes in the productivity of the ecosystem might also play a role (Rijnsdorp and Van Beek, 1991). From the early 1900s to the mid-1980s female length and age at maturation had decreased by 10–16% and 30–35%, respectively, whereas male length and age at maturation had decreased by 35% and 50–60%, respectively (Rijnsdorp, 1989). Although changes in fecundity might partly reflect changes in the trade-off between egg size and egg number, the hypothesis of a fisheries-induced increase in reproductive investment in adult females (smaller than 50cm) seems empirically supported (Rijnsdorp, 1991).

North Sea plaice has been exploited substantially already since the late 19th century (Rijnsdorp and Millner, 1996). Landing statistics collected by ICES since 1906 show that annual plaice landings varied around 50,000t annually until the mid-1950s, after which landings peaked at 150,000t in the 1980s and since then decreased to the present 55,000t (ICES, 2006). Commercial landings have been extensively sampled since 1957. While mortality rates for males and females are similar during the growing season from April to December, they almost quadruple for males, but just about double for females, during the spawning season from January to March (Rijnsdorp, 1993). This is in accordance with the finding that males spend much more time on the heavily exploited spawning grounds than females (Rijnsdorp, 1989).

Hypotheses on sexual dimorphism

Female fish usually have a high advantage of increased body size, since egg viability and total fecundity typically increase with maternal size (Trippel and Neil, 2004). Selection on male size is also driven by female preference, by male-male competition for females, or by sperm competition for eggs (Parker, 1993; Ball and Parker, 1996). If male-male competition and sperm competition are very weak, small or even dwarf males are predicted to arise evolutionarily (Parker, 1992). Selection then also favors early maturation to increase the reproductive lifespan.

If males are small, it seems at first sight paradoxical that their surplus energy resulting from a smaller cost of reproduction as compared to females is not invested into somatic growth. This apparent paradox might be resolved by stipulating a lower growth efficiency in males (Henderson et al., 2003) or by assuming male investment into a behavioral trait related to reproduction. Since male North Sea plaice stay longer on the spawning ground than females (Rijnsdorp, 1989), we might assume that for North Sea plaice this behavioral trait is described by the duration of staying on the spawning grounds. This duration is most likely positively correlated with the number of reproductive events and with the amount of sperm produced. Since male plaice are clearly smaller than females, the general theory No empirical evidence suggests that male-male competition is rather weak. But sperm competition might be important, since more sperm production associated with a longer stay on the spawning grounds will cause more fertilizations.

However, any sexual size dimorphism (SSD) is also affected by the ratios between sex-specific growth rates and mortalities (Parker, 1992). Since mortality in male plaice is highest during the spawning period (Rijnsdorp, 1993), it seems likely that the considered behavioral trait is associated with higher mortality rates due to a higher exposure to fishing gear and predators. The selection imposed by sperm competition, favoring larger size, is therefore counterbalanced by the selection imposed by higher mortality, favoring smaller size. We assume that this trade-off acting on the male reproductive behavior mainly determines the observed SSD of plaice.

If positively size-selective mortality in a size-dimorphic population increases, one would expect larger evolutionary responses in the larger sex. Apparently, in the case of North Sea plaice, the opposite has happened: changes in the onset of maturation are dramatically larger in males than in females (Rijnsdorp, 1989). This might be explained by the fact that male plaice experience a steeper increase of mortality rates on the spawning grounds, and are thus more affected by fishing mortality.

By considering a male behavioral trait measuring the duration males spend on the spawning grounds, we will try to capture two trade-offs: longer stays on the spawning grounds imply a time cost (resulting in higher mortality), as well as an energy cost (resulting in diminished surplus energy, and thus potentially in reduced growth).

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Table 1: Summary of observations related to SSD in the North Sea plaice fishery, of causes that may underlie these observations, and of approaches to how the latter could be accounted for in a model.

Observation	Presumed causes	Modeling approach
Males experience higher natural and fishing mortality	Males are more exposed to predators and fishing gear due to their spawning activity	Natural and fishing mortality in the model will differ between the sexes
Males stay longer on the spawning grounds	Selection for more time spent on the spawning grounds, since reproductive success is positively correlated with this duration	Male reproductive investment in the model will include investment into gonads and male reproductive behavior
Males are smaller at age	Stronger selection for early maturation, and thus indirectly for reduced growth, due to higher mortality and lower energetic costs of reproduction; direct selection for reduced growth because of higher mortality and larger investment into spawning activity	Model will incorporate selection for early maturation and for lower growth rate due to higher mortality associated with male reproductive behavior; energy lost on male reproductive behavior will slow down growth
Males mature earlier	Stronger selection for early maturation due to higher mortality and lower energetic costs of reproduction	Model will incorporate selection for early maturation, smaller gonads, and smaller body size based on assuming time and energy costs associated with male reproductive behavior
Males show a stronger response to size-selective harvesting	Steeper increase of male mortality rates on the spawning grounds due to their spawning activity	Model will incorporate separate mortalities for males and females on feeding and spawning grounds

In addition, also the trade-offs between gonadic investment and growth and between growth and survival will be considered. On this basis, we will attempt to test the following two hypotheses:

(1) Selection on male reproductive behavior – involving two trade-offs, between fecundity on the one hand and mortality and growth on the other – can explain the observed SSD in North Sea plaice.

(2) The higher exposure of males to fishing morality on the spawning grounds can explain their larger life history response to exploitation.

This test will be based on reconstructing the observations in the fishery with the help of an eco-genetic model for North Sea plaice. Table 1 summarizes the most striking observations concerning the SSD in North Sea plaice and suggests how these could be reflected in the model.

Research questions

Questions for devising an eco-genetic model for female plaice

- How do we set up an eco-genetic model to recover the observed life history of female plaice?

- Which adaptive traits should be considered?

- Can we recover the observed changes in female life history and the pace of evolution induced by size-selective harvesting?
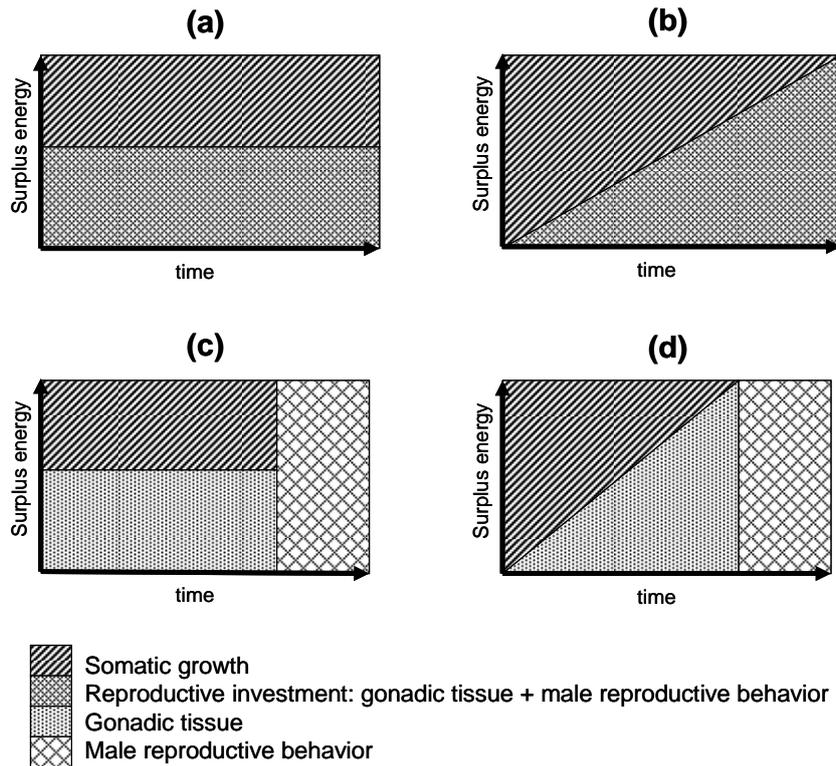
Figure 1: Possible patterns for the seasonal allocation of surplus energy to somatic growth and reproduction. Spawning occurs at the end of the shown time intervals. Surplus energy is assumed to be constant throughout the year. For females, only options (a) and (b) are considered, since reproductive investment in females solely consists of building gonadic tissue. For males, the reproductive investment in (a) and (b) has to be interpreted as the sum of energy used, in parallel, for gonadic tissue and male reproductive behavior. In (c) and (d), energy allocation to gonadic tissue and male reproductive behavior instead is sequential, and hence the behavioral reproductive investment can be disentangled from investment into gonadic tissue by allowing for a flexible date for the onset of this behavioral reproductive investment.

Questions for extending this model to capture the SSD

- How do we have to define, separately for each sex, adaptive traits, life-history parameters, and trade-offs, in order to recover the sexual size dimorphism?

- Can the trade-offs involved in male reproductive behavior, as described above, explain the observed SSD?

- Can we recover the observed changes in male life history and the pace of evolution induced by sex-specific and size-selective harvesting?

- Can we recover, in particular, the observed stronger effect of size-selective harvesting on males?

- What is the relative evolutionary importance of the time costs and the energy costs associated with male reproductive behavior?

- Can selection on one sex affect evolution in the other sex?

- Are fisheries-induced evolutionary responses in this population amplified by the SSD?

- Which management measures could be adopted to mitigate fisheries-induced evolution in sexually size-dimorphic populations such as North Sea plaice?

Methods and work plan

Eco-genetic model

To study the effect of size-selective harvesting in a sex-structured population, we will devise an individual-based eco-genetic model (Dunlop et al., 2007) for North Sea plaice. This model will include phenotypic plasticity in age and size at maturation and will allow somatic growth to be density-dependent. As described above, we will also include the trade-offs involved in the evolution of male reproductive behavior and thereby go beyond previous models of mortality-induced evolution (Roff, 1983; Martinez-Garmendia, 1998).

To model somatic growth, we will use a simplification of the integrated energy allocation model by West et al. (2001), in which growth is defined in terms of the rate of change in somatic weight w, $dw/dt = aw^{\alpha} - cw^{\gamma}$, where t is continuous time (or age), a scales the net energy intake, accounting for the costs of maintenance, c scales reproductive investment, and α and γ are the corresponding allometric exponents. Parameters a, c, and α, will be taken from empirical studies (Fonds et al., 1992; Mollet et al., in prep.), while γ is assumed to be 1. Reproductive investment for males will be interpreted to comprise both the investment into gonadic tissue (as measured by GSI) and the investment into reproductive behavior. We will assume a parallel allocation of energy into somatic and reproductive investment. Different options for the underlying partitioning are illustrated in Figure 1. A constant condition factor θ and shape parameter λ will be assumed to convert weight w to length l, $w = \theta l^{\lambda}$.

The transition from the juvenile to the adult part of the life cycle will be determined by a maturation reaction norm, predicting the phenotypically plastic response of age and size at maturation to environmental variation in somatic growth rates (Stearns and Koella, 1986; Ernande et al., 2004). A recently developed probabilistic extension models the probability to mature as a function of age and size (Heino et al., 2002; Barot et al., 2004). For the sake of simplicity, we will assume linear reaction norms described by their intercept b, slope m, and width e.

A quantitative genetic approach will be used to implement inheritance and express heritability in the evolving traits a, c, b, m, and e. Genetic variance will be represented by the distribution of trait values in the population (Van Noordwijk, 1989), whereas phenotypic variance resulting from environmental factors has to be assumed such that realistic values of heritability are obtained (Mousseau and Roff, 1987). The inheritance of quantitative traits in the offspring will be assumed to be equally determined by maternal and paternal trait values. In particular, the traits of each offspring will be drawn from a normal distribution with the mid-parental value as the mean. In sex-structured populations sex-specific traits will be considered.

Fecundity will be described by an allometric relation with respect to body size, while male reproductive success will depend, in addition, on assumptions made about the ecological implications of the duration males spend on the spawning grounds. Importantly, mating will not be assumed to be size-dependent, but random. The number of new individuals recruiting to the population at age 1 will be determined from a Beverton-Holt stock-recruitment function. Population dynamics will be based on annual time steps for growth, maturation, reproduction, and mortality.

Work plan

As a first step, we will try to recover the historical pattern of life history evolution in female plaice. The life history in the initial population will be matched to historical observations (Wallace, 1914).

As a second step, we will investigate simplified eco-genetic models for male plaice that (i) do not contain females explicitly and that (ii) do not describe male reproductive behavior through a separate adaptive trait (Figs. 1a and 1b). This implies assuming a constant fractional allocation of reproductive investment to male gonadic tissue and male reproductive behavior.

Time permitting, we might relax, as a third step, assumption (i) by analyzing sex-structured populations (as it might turn out that male and female life histories cannot be modeled independently from each other) and assumption (ii) by introducing a separate adaptive trait for male reproductive behavior (Figs. 1c and 1d).

Traits that might evolve in these models are thus the intrinsic growth rate (a), reaction norm parameters (b, m, and e), reproductive investment (c) and, if time permits, male reproductive behavior. Model predictions will be compared to empirical observations and to the result of previous studies, e.g., changes in a to a study by Rijnsdorp and Van Beek (1991), changes in b and m to a study by Grift et al. (2003), and changes in c to a study by Rijnsdorp et al. (2005). Empirical evidence for changes in male reproductive behavior might be obtained by analyzing changes in male mortality. In the longer term, also known changes in environmental conditions could be incorporated, like the absence of fishing during the world wars, the increasing fishing pressure in the early 1960s, or the high eco-system productivity in the 1960s.

Relevance and link to EEP's research plan

This project aims to evaluate the ecological and evolutionary effects of size-selective fishing in a sexually size-dimorphic population and is therefore directly linked to EEP's focus on evolutionary fisheries management. If observations on North Sea plaice can be reproduced, this could provide further evidence of fisheries-induced evolution and offer insights into the evolutionary origins and implications of sexual size dimorphisms. Studying fisheries-induced evolution in sex-structured population models that account for the trade-offs associated with male reproductive behavior is a novel contribution to existing applications of eco-genetic models.

Expected output and publications

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

References

Ball, M.A. and Parker, G.A. (1996). Sperm competition games: external fertilization and "adaptive" infertility. Journal of Theoretical Biology, 180: 141-150.

Barot, S., Heino, M., O'Brien, L. and Dieckmann, U. (2004). Estimating reaction norms for age and size at maturation when age at first reproduction is unknown. Evolutionary Ecology Research, 6: 659-678.

Beverton, R.J.H. (1964). Differential catchability of male and female plaice in the North Sea and its effect on estimates of stock abundance. Rapports et Proces verbaux des Réunions - Conseil permanent international pour l'Exploration de la Mer, 155: 103-112.

Conover, D.O., Arnott, S.A., Walsh, M.R. and Munch, S.B. (2005). Darwinian fishery science: lessons from the Atlantic silverside (*Menidia menidia*). Canadian Journal of Fisheries and Aquatic Sciences, 62: 730-737.

Dunlop, E.S., Shuter, B.J. and Dieckmann, U. (2007). Demographic and evolutionary consequences of selective mortality: predictions from an eco-genetic model of the smallmouth bass. Transactions of the American Fisheries Society, 136: 749-765.

Ernande, B., Dieckmann, U. and Heino, M. (2004). Adaptive changes in harvested populations: plasticity and evolution of age and size at maturation. Proceedings of the Royal Society of London, Series B, 271: 415-423.

Fonds, M., Cronie, R., Vethaak, A.D. and Van der Puyl, P. (1992). Metabolism, food consumption and growth of plaice (*Pleuronectes platessa*) and flounder (*Platichthys flesus*) in relation to fish size and temperature. Netherlands Journal of Sea Research, 29: 127-143.

Grift, R.E., Rijnsdorp, A.D., Barot, S., Heino, M. and Dieckmann, U. (2003). Fisheries-induced trends in reaction norms for maturation in North Sea plaice. Marine Ecology Progress Series, 257: 247-257.

Heino, M., Dieckmann, U. and Godø, O.R. (2002). Measuring probabilistic reaction norms for age and size at maturation. Evolution, 56: 669-678.

Heino, M. and Godø, O.R. (2002). Fisheries-induced selection pressures in the context of sustainable fisheries. Bulletin of Marine Science, 70: 639-656.

Heino, M. and Kaitala, V. (1999). Evolution of resource allocation between growth and reproduction in animals with indeterminate growth. Journal Evolutionary Biology, 12: 423-429.

Henderson, B.A., Collins, N., Morgan, G.E. and Vaillancourt, A. (2003). Sexual size dimorphism of walleye (*Stizostedion vitreum vitreum*). Canadian Journal of Fisheries and Aquatic Sciences, 60: 1345-1352.

ICES (2006). Report of the working group on the assessment of demersal stocks in the North Sea and Skagerrak. ICES CM 2006/ACFM:09.

Law, R. and Grey, D.R. (1989). Evolution of yields from populations with age-specific cropping. Evolutionary Ecology, 3: 343-359.

Martinez-Garmendia, J. (1998). Simulation analysis of evolutionary response of fish populations to size-selective harvesting with the use of an individual-based model. Ecological Modelling, 111: 37-60.

Mollet, F.M., Brunel, T., Ernande, B. and Rijnsdorp, A.D. Estimating onset of reproduction, reproductive investment and growth rate from individual growth trajectories, in preparation.

Mousseau, T.A. and Roff, D.A. (1987) Natural selection and the heritability of fitness components. Heredity, 59: 181-197.

Olsen, E.M., Lilly, G.R., Heino, M., Morgan, M.J., Brattey, J. and Dieckmann, U. (2005). Assessing changes in age and size at maturation in collapsing populations of Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences, 62: 811-823.

Parker, G.A. (1992). The evolution of sexual size dimorphism in fish. Journal of Fish Biology, 41: 1-20.

Parker, G.A. (1993). Sperm competition games - sperm size and sperm number under adult control. Proceedings of the Royal Society of London, Series B, 253: 245-254.

Rijnsdorp, A.D. (1991). Changes in fecundity of female North-Sea plaice (*Pleuronectes platessa* L) between 3 periods since 1900. ICES Journal of Marine Sciences, 48: 253-280.

Rijnsdorp, A.D (1993). Selection differentials in male and female North Sea plaice *Pleuronectes platessa* L. In: Stokes, T.K.A., McGlade, J. and Law, R. (eds.) The exploitation of evolving resources. Springer Verlag, pp. 19-36.

Rijnsdorp, A.D. (1989). Maturation of male and female North-Sea plaice (*Pleuronectes-Platessa* L). Journal Du Conseil, 46: 35-51.

Rijnsdorp, A.D., Grift, R.E. and Kraak, S.B.M. (2005). Fisheries-induced adaptive change in reproductive investment in North Sea plaice (*Pleuronectes platessa*)? Canadian Journal of Fisheries and Aquatic Sciences, 62: 833-843.

Rijnsdorp, A.D. and Ibelings, B. (1989). Sexual dimorphism in the energetics of reproduction and growth of North Sea plaice, *Pleuronectes-Platessa* L. Journal of Fish Biology, 35: 401-415.

Rijnsdorp, A.D. and Millner, R.S. (1996). Trends in population dynamics and exploitation of North Sea plaice (*Pleuronectes platessa* L) since the late 1800s. ICES Journal of Marine Sciences, 53: 1170-1184.

Rijnsdorp, A.D. and Van Beek, F.A. (1991). Changes in growth of plaice *Pleuronectes platessa* L and sole *Solea solea* (L) in the North Sea. Netherlands Journal of Sea Research, 27: 441-457.

Roff, D.A. (1983). An allocation model of growth and reproduction in fish. Canadian Journal of Fisheries and Aquatic Sciences, 40: 1395-1404.

Sinclair, A.F., Swain, D.P. and Hanson, J.M. (2002). Measuring changes in the direction and magnitude of size-selective mortality in a commercial fish population. Canadian Journal of Fisheries and Aquatic Sciences, 59: 361-371.

Stearns, S.C. and Koella, J.C. (1986). The evolution of phenotypic plasticity in life history traits - predictions of reaction norms for age and size at maturity. Evolution, 40: 893-913.

Stokes, T.K., McGlade, J.M. and Law, R. (1993). The exploitation of evolving resources. Springer-Verlag.

Trippel, E.A. and Neil, S.R.E. (2004). Maternal and seasonal differences in egg sizes and spawning activity of northwest Atlantic haddock (*Melanogrammus aeglefinus*) in relation to body size and condition. Canadian Journal of Fisheries and Aquatic Sciences, 61: 2097-2110.

Van Noordwijk, A.J. (1989). Reaction norms in genetic ecology - studies of the great tit exemplify the combination of ecophysiology and quantitative genetics. Bioscience, 39: 453-458.

Wallace, W. (1914). Report on age and growth and sexual maturity of the plaice in certain parts of the North Sea. Fisheries Investigation Series, 2: 79.

West, G.B., Brown, J.H., Enquist, B.J. (2001). A general model for ontogenetic growth. Nature, 413: 628-631

The influence of stock structure on fisheries-induced evolution in Icelandic cod

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Goal

To model component structure in a fish stock such as Icelandic cod and investigate its influence on fisheries-induced evolution.

Background and motivation

In recent years, evidence that fishing not only affects populations demographically but also changes their genetic composition has accumulated (Heino and Godø 2002). Fishing mortality is most often non-random: typically, gear is designed to select individuals that are larger, older or fastest-growing. Such selective fishing could lead to significant changes in life-history traits, which, if they are heritable, will lead to fishing-induced evolution (Law 2000; Heino and Godø 2002; Olsen et al. 2004). Changes in life-history traits, particularly in age and size at maturation, have been reported in a number of commercially exploited fish stocks (see reviews by Trippel 1995; Dieckmann and Heino 2007). Many studies have found fisheries-induced evolution to be a plausible explanation for observed trends towards earlier and smaller maturation in a number of stocks (Northeast Arctic cod: Heino et al. 2002b; Baltic cod: Vainikka et al. in prep; Atlantic cod: Barot et al. 2004; Olsen et al. 2004; Olsen et al. 2005; American plaice: Barot et al. 2005; North Sea plaice: Rijnsdorp 1993; Grift et al. 2003, 2007; North Sea sole: Mollet et al. 2006). Alternatively, changes in these life-history traits could be the result of phenotypic plasticity alone, for example, as a response to alterations in density-dependent growth rates with declining population abundance (Reznick 1990; Law 2000). Disentanglement of phenotypically plastic life-history responses to fishing from genetic responses has been made possible by application of the probabilistic reaction norm method developed by Heino et al. (2002a). Probabilistic maturation reaction norms are an extension of the original deterministic notion of maturation reaction norms (Stearns and Koella 1986) and describe the probability that immature individuals of a given age and size will mature during a given time interval (Heino et al. 2002a; Olsen et al. 2005). Fisheries-induced evolution is of concern to the sustainable management of fish stocks as it can result in lower sustainable yields (Law 2000; Conover and Munch 2002) and reduced stock stability (Olsen et al. 2004) as manifestations of the impact of life-history trait changes at the individual level, such as the influence of age and size at maturation on growth rate, fecundity and survival probability (Heino et al. 2002b). Furthermore, reversal of genetic change is likely to be slow (Law 2000).

Evidence of adaptive variation in northern temperate marine fish at spatial scales that are smaller than was previously thought has been documented in recent geographical comparisons of fitness-related traits (McIntyre and Hutchings 2003). For example, genetic differences in growth rate and feeding efficiency have been reported for populations of Northwest Atlantic cod (Purchase and Brown 2001), Atlantic halibut, and turbot (Imsland et al. 2000; Jonassen et al. 2000). A number of studies exploring small-scale structure of cod populations have provided evidence for the exis-

tence of adaptive variation and local populations (Ruzzante et al. 1999, 2000; Knutsen et al. 2003; McIntyre and Hutchings 2003; Salvanes et al. 2004; Neat et al. 2006; Jonsdóttir et al. 2006a,b; Pampoulie et al. 2006). The majority of fisheries assessments are based on modelling the dynamics of closed populations and assume homogeneous life-history characteristics. However, misleading results can be obtained if several closed populations, or a portion of a population, are the components actually modelled (NRC 1994). Failure to recognise or account for stock diversity can lead to erosion of spawning components, with known ecological consequences, but modelling structure in stock assessments is far from straightforward due to an inherent level of uncertainty concerning the actual configuration of the stock (Stephenson 1999; Begg and Marteinsdóttir 2002b).

Atlantic cod remains the most economically important fish stock in Iceland. Over the past 30 years, annual landings have varied from 180,000 to 470,000 tonnes, with an average catch of approximately 290,000 tonnes (MRI Iceland 2006). Preliminary investigations suggest that the age at maturation of the Icelandic cod stock has declined over the last few decades. Fishing mortality of the Icelandic cod stock is unevenly distributed on the Icelandic shelf. High levels of exploitation occur off the northwest and southwest coasts, corresponding to the main feeding and spawning grounds, respectively; these are also the areas where mature/spawning cod are most abundant. Conversely, cod on regional spawning grounds are exposed to relatively low exploitation, particularly in the north where the main nursery grounds are situated (Begg and Marteinsdóttir 2003). This provides relatively protected habitats for juvenile cod and thus ensures a supply of recruits for the main spawning component and stock as a whole (Begg and Marteinsdóttir 2003).

Recent studies have confirmed that in addition to the main spawning component off the southwest coast, smaller regional spawning components are significant sources of productivity and recruitment for the Icelandic cod stock (Begg and Marteinsdóttir 2000, 2002a,b; Marteinsdóttir et al. 2000a,b). Furthermore, life-history characteristics (e.g. somatic growth rates, age and size at maturity, and reproductive potential), condition and abundance of mature Icelandic cod have been found to exhibit spatial disparity (Marteinsdóttir and Begg 2002; Begg and Marteinsdóttir 2002a, 2003; Pétursdóttir et al. 2006; Pardoe et al. in prep). More recently, studies of otolith shape and chemistry and of genetic markers have provided evidence that the Icelandic cod stock is structured, with differentiation detected between cod from the north-eastern and south-western regions and also with depth (Jónsdóttir et al. 2006a,b; Pampoulie et al. 2006). Oceanic currents and environmental conditions are thought to have contributed to the spatial distribution and genetic composition of Icelandic cod (Begg and Marteinsdóttir 2002a; Pampoulie et al. 2006). Marteinsdóttir et al. (2000a) suggested that this population richness may be responsible for the relatively low recruitment fluctuation in this stock compared to most other cod stocks in the North Atlantic. The Icelandic cod stock is currently managed as a single homogenous unit but as evidence of stock structure accumulates, it seems it may be necessary to revise this management strategy (Begg and Marteinsdóttir 2002b; Jónsdóttir et al. 2006a,b; Pampoulie et al. 2006).

An investigation of the effect of stock structure on the rate, detection, and management of fisheries-induced evolution in commercially exploited fish stocks at risk of genetic change in life-history traits is an area that requires attention. In this project, my aim is to investigate the development and subsequent dynamics of structure in a stock such as Icelandic cod and its influence on fisheries-induced evolution, with additional consideration of the role of variable fishing pressure on individual stock com-

ponents. The development of an individual-based eco-genetic model (Dunlop et al. 2005a, 2007) will help tackle these research questions where empirical analysis would fail due to the limitations imposed by data availability.

Research questions

The questions that will be the focus of this research project are as follows:

- Are the observed life-history differences between cod in northern and southern Icelandic waters likely the result of genetic adaptation or are they a purely plastic response?

- What conditions are necessary to cause genetic divergence, as opposed to purely phenotypic differences, between stocks inhabiting different environments?

- How does stock structure influence the magnitude and rate of, and recovery from, fisheries-induced evolution in a stock exposed to selective harvesting?

- What effect does differential fishing pressure on the subunits of a structured stock have on fisheries-induced evolution?

- What does stock structure mean for the detection and management of fisheries-induced evolution?

Methods and work plan

To study stock structure and its influence on fisheries-induced evolution of probabilistic maturation reaction norms (PMRNs) (Heino et al. 2002a), I will develop a model that builds upon the existing individual-based eco-genetic model of Dunlop et al. (2005a, 2007 and in prep). Where possible, the model will be parameterized for the Icelandic cod stock. The model will be based on a 'southern' and 'northern' environment, which will differ in temperature and fishing mortality. Such differences will likely emerge as component specific biological processes, such as faster growth rates and earlier maturation in the southern environment. Individuals can be born in either environment and, accordingly, are referred to as belonging to the southern or northern population or stock component. Three types of migration will likely be included in the model to reflect the general life cycle of Icelandic cod:

- Juvenile migration - after birth juveniles in the southern population will mostly migrate to the northern environment.

- Spawning migration/Natal homing - once mature, individuals will migrate to one of the two environments to spawn. This will occur on an annual basis. The probability of migration will depend on the degree of natal homing, which will be modified between simulations.

- Adult migration - post-spawning, adults will stay in their current environment or migrate to the other. This will occur on an annual basis. The probability of migration will depend on the degree of adult migration, which will be modified between simulations.

Evolution of the following traits will be examined: reproductive investment, growth capacity, and the width, slope, and intercept of linear PMRNs. Model simulations will run on discrete, one-year time steps. The model will include a trade-off between growth and reproduction, implemented using the bi-phasic growth model of Lester et al. (2004), so that prior to maturation growth will be assumed to be linear, but after maturation will follow the Von Bertalanffy growth model. The reduction of adult growth rates relative to juvenile growth rates represents reproductive investment (Roff

1983). Growth will be density-dependent with a decreasing, non-linear function relating growth rate to population biomass. There will also be a linear trade-off between growth capacity and survival. Growth rate will be influenced by temperature and based on relationships for Icelandic cod reported by Björnsson et al. (2001). Natural mortality will be stage-specific. Reproduction will occur randomly between pairs of mature individuals. Inheritance will be based on a constant-segregation kernel and fecundity will be a function of maternal body size. Offspring mortality will be density-dependent and modelled using the Ricker stock-recruitment relationship.

Harvesting will reflect the exploitation history of Icelandic cod, and the consequences of realistic management scenarios for fisheries-induced evolution will be investigated (time allowing). Increased complexity (i.e. increased parameterisation for the Icelandic cod stock, non-linear maturation reaction norms, variable food availability and influence of energy allocation/nutritional status on maturation) will be added to the model as time permits.

Relevance and link to EEP's research plan

This project aims to assess the influence of population structure and spatially variable exploitation pressure on the response of a commercially important stock such as Icelandic cod to fisheries-induced evolution. It is therefore directly linked to the evolutionary fisheries management project of the EEP. In addition, studying fisheries-induced evolution in genetically and spatially structured populations is a novel contribution to existing applications of eco-genetic models.

Expected output and publications

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

References

Barot, S., Heino, M., O'Brien, L. and Dieckmann, U. (2004b). Longterm trend in the maturation reaction norm of two cod stocks. Ecological Applications, 14: 1257–1271.

Barot, S., Heino, M., Morgan, M.J. and Dieckmann, U. (2005). Maturation of the Newfoundland American plaice (*Hippoglossoides platessoides*): long-term trends in maturation reaction norms despite low fishing mortality? ICES Journal of Marine Science, 62: 56–64.

Begg, G.A. and Marteinsdóttir, G. (2000). Spawning origins of pelagic juvenile cod *(Gadus morhua)* inferred from spatially explicit age distributions: potential influences on year-class strength and recruitment. Marine Ecology Progress Series, 202: 193–217.

Begg, G.A. and Marteinsdóttir, G. (2002a). Environmental and stock effects on spatial distribution and abundance of mature cod *Gadus morhua*. Marine Ecology Progress Series, 229: 245-262.

Begg, G.A. and Marteinsdóttir, G. (2002b). Environmental and stock effects on spawning origins and recruitment of cod *Gadus morhua*. Marine Ecology Progress Series, 229: 263-277.

Begg, G.A. and Marteinsdóttir, G. (2003). Spatial partitioning of relative fishing mortality and spawning stock biomass of Icelandic cod. Fisheries Research, 59: 343-362.

Björnsson, B., Steinarsson, A. and Oddgeirsson, M. (2001). Optimal temperature for growth and feed conversion of immature cod (*Gadus morhua* L.). ICES Journal of Marine Sciences, 58: 29-38.

Conover, D.O. and Munch, S.B. (2002). Sustaining fisheries yields over evolutionary time scales. Science, 297: 94–96.

Dieckmann, U. and Heino, M. (2007). Probabilistic maturation reaction norms: Their history, strengths, and limitations. Marine Ecology Progress Series, 335: 253-269.

Dunlop, E.S., Shuter, B.J. and Ridgway, M.S. (2005). Isolating the influence of growth rate on maturation patterns in the small-mouth bass (*Micropterus dolomieu*). Canadian Journal of Fisheries and Aquatic Sciences, 62: 844–853.

Dunlop, E.S., Shuter, B.J. and Dieckmann, U. (2007). The demographic and evolutionary consequences of selective mortality: Predictions from an eco-genetic model of the smallmouth bass. Transactions of the American Fisheries Society, in press.

Dunlop, E.S., Heino, M. and Dieckmann, U. Modeling contemporary life history evolution: Introducing the eco-genetic approach. In preparation.

Grift, R.E., Rijnsdorp, A.D., Barot, S., Heino, M. and Dieckmann, U. (2003). Fisheries-induced trends in reaction norms for maturation in North Sea plaice. Marine Ecology Progress Series, 257: 247-257.

Grift, R.E., Heino, M., Rijnsdorp, A.D., Kraak, S.B.M. and Dieckmann, U. (2007). Three-dimensional maturation reaction norms for North Sea plaice. Marine Ecology Progress Series, 334: 213-224.

Heino, M. and Godø, O.R. (2002). Fisheries-induced selection pressures in the context of sustainable fisheries. Bulletin of Marine Sciences, 70: 639–656.

Heino, M., Dieckmann, U. and Godø, O.R. (2002a). Measuring probabilistic reaction norms for age and size at maturation. Evolution, 56: 669–678.

Heino, M., Dieckmann, U. and Godø, O.R. (2002b). Estimating reaction norms for age and size at maturation with reconstructed immature size distributions: a new technique illustrated by application to Northeast Arctic cod. ICES Journal of Marine Sciences, 59: 562–575.

Imsland, A.K., Foss, A., Nævdal, G., Cross, T., Bonga, S.W., van Ham, E.H. and Stefansson, S.O. (2000). Counter gradient variation in growth and food conversion efficiency of juvenile turbot. Journal of Fish Biology, 57: 1216–1226.

Jonassen, T.M., Imsland, A.K., FitzGerald, R., Stefánsson, M.Ö., Bonga, S.W., van Ham, E., Nævdal, G. and Stefansson, S.O. (2000). Geographic variation in growth and food conversion efficiency of juvenile Atlantic halibut related to latitude. Journal of Fish Biology, 56: 279–294.

Jónsdóttir, I.G., Campana, S.E. and Marteinsdóttir, G. (2006a). Otolith shape and temporal stability of spawning groups of Icelandic cod (*Gadus morhua* L.). ICES Journal of Marine Science, 63: 1501-1512.

Jónsdóttir, I.G., Campana, S.E. and Marteinsdóttir, G. (2006b). Stock structure of Icelandic cod *Gadus morhua* L. based on otolith chemistry. Journal of Fish Biology, 69(Supp C): 136-150.

Knutsen, H., Jorde, P.E., André, C. and Stenseth, N.C. (2003). Fine-scaled geographical population structuring in highly mobile marine species: the Atlantic cod. Molecular Ecology, 12: 385-394.

Law, R. (2000). Fishing, selection, and phenotypic evolution. ICES Journal of Marine Sciences, 57: 659–668.

Lester, N.P., Shuter, B.J. and Abrams, P.A. (2004). Interpreting the von Bertalanffy model of somatic growth in fish: the cost of reproduction. Proceedings of the Royal Society of London, Series B, 271: 1625-1631.

Marine Research Institute, Reykjavik, Iceland. (2006). Status of marine stocks in Icelandic waters 2005/2006. Prospects for the Quota Year 2006/2007.

Marteinsdóttir, G. and Begg, G.A. (2002). Essential relationships incorporating the influence of age, size and condition on variables required for estimation of reproductive potential in Atlantic cod *Gadus morhua.* Marine Ecology Progress Series, 235: 235–256.

Marteinsdóttir, G., Gudmundsdóttir, A., Thorsteinsson, V. and Stefánsson, G. (2000a). Spatial variation in abundance, size composition and viable egg production of spawning cod *(Gadus morhua* L.) in Icelandic waters. ICES Journal of Marine Science, 57: 824–830.

Marteinsdóttir, G., Gunnarsson, B. and Suthers, I.M. (2000b). Spatial variation in hatch date distributions and origin of pelagic juvenile cod in Icelandic waters. ICES Journal of Marine Science, 57: 1182–1195.

McIntyre, T.M. and Hutchings, J.A. (2003). Small-scale temporal and spatial variation in Atlantic cod (*Gadus morhua*) life history. Canadian Journal of Fisheries and Aquatic Sciences, 60: 1111–1121.

Mollet, F.M., Kraak, S.B.M. and Rijnsdorp, A.D. (2006). Fisheries-induced evolutionary changes in maturation reaction norms in North Sea sole (*Solea solea*). ICES CM 2006/H: 14.

Neat, F.C., Wright, P.J., Zuur, A.F., Gibb, I.M., Gibb, F.M., Tulett, D., Righton, D.A. and Turner, R.J. (2006). Residency and depth movements of a coastal group of Atlantic cod (*Gadus morhua* L.). Marine Biology, 148: 643-654.

NRC (National Research Council). (1994). An assessment of Atlantic bluefin tuna. National Academy Press, Washington, DC.

Olsen, E.M., Heino, M., Lilly, G.R., Morgan, M.J., Brattey, J., Ernande, B. and Dieckmann, U. (2004). Maturation trends indicative of rapid evolution preceded the collapse of northern cod. Nature, 428: 932–935.

Olsen, E.M., Lilly, G.R., Heino, M., Morgan, M.J., Brattey, J. and Dieckmann, U. (2005). Assessing changes in age and size at maturation in collapsing populations of Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences, 62: 811:823.

Pampoulie, C., Ruzzante, D.E., Chosson, V., Jörundsdóttir, T.D., Taylor, L., Thorsteinsson, V., Daníelsdóttir, A.K. and Marteinsdóttir, G. (2006). The genetic structure of Atlantic cod (*Gadus morhua*) around Iceland: insight from microsatellites, the *Pan* I locus, and tagging experiments. Canadian Journal of Fisheries and Aquatic Sciences, 63: 2660-2674.

Pardoe, H.E., Thordarson, G. and Marteinsdóttir G. Spatial and temporal trends in condition of Atlantic cod (*Gadus morhua* L.) on the Icelandic shelf. In preparation.

Petursdóttir, G., Begg, G.A. and Marteinsdóttir, G. (2006). Discrimination between Icelandic cod (*Gadus morhua* L.) populations from adjacent spawning areas based on otolith growth and shape. Fisheries Research, 80: 182-189.

Purchase, C.F. and Brown, J.A. (2001). Stock-specific changes in growth rates, food conversion efficiencies, and energy allocation in response to temperature change in juvenile Atlantic cod. Journal of Fish Biology, 58: 36–52.

Reznick, D.N., Bryga, H. and Endler, J.A. (1990). Experimentally induced life-history evolution in a natural population. Nature, 346: 357–359.

Rijnsdorp, A.D. (1993). Fisheries as a large-scale experiment on life-history evolution: disentangling phenotypic and genetic effects in changes in maturation and reproduction of North Sea plaice, *Pleuronectes platessa* L. Oecologia, 96: 391–401.

Roff, D.A. (1983). An allocation model of growth and reproduction in fish. Canadian Journal of Fisheries and Aquatic Sciences, 40: 1395-1404.

Ruzzante, D.E., Taggart, C.T. and Cook, D. (1999). A review of the evidence for genetic structure of cod (*Gadus morhua*) in the Northwest Atlantic and population affinities of larval cod off Newfoundland and the Gulf of St Lawrence. Fisheries Research, 43: 79-97.

Ruzzante, D.E., Wroblewski, J.S., Taggart, C.T., Smedbol, R.K., Cook, D. and Goddaard, S.V. (2000). Bay-scale population structure in coastal Atlantic cod in Labrador and Newfoundland, Canada. Journal of Fish Biology, 56: 431-447.

Salvanes, A.G.V., Skjaeraasen, J.E. and Nilsen, T. (2004). Subpopulations of coastal cod with different behaviour and life history strategies. Marine Ecology Progress Series, 267: 241-251.

Stearns, S.C. and Koella, J.C. (1986). The evolution of phenotypic plasticity in life-history traits - predictions of reaction norms for age and size at maturity. Evolution, 40: 893-913.

Stephenson, R.L. (1999). Stock complexity in fisheries management: a perspective of emerging issues related to population sub-units. Fisheries Research, 43: 247–249.

Trippel, E.A. (1995). Age at maturity as a stress indicator in fisheries. Bioscience, 45: 759–771.

Vainikka, A., Gårdmark, A., Bland, B. and Hjelm, J. Decreased growth and size at maturation in the eastern Baltic cod, *Gadus morhua* – do maturation reaction norms suggest correlation or causality? In preparation.

The evolution of social norms for renewable resource exploitation

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Goal

To develop a model in which social norms evolve that regulate harvesting of a renewable resource.

Background and motivation

This research is motivated by the observation that a lot of renewable resources are severely depleted, while others are conserved very well. Many scientists, inspired by Hardin (1968), have argued that privatization of common-pool resources is the only way to overcome the so-called "tragedy of the commons". This view has been contradicted in numerous case studies that revealed how government interventions may deteriorate the situation (Somanathan 1991). In fact, neither government intervention nor the property-rights regime alone can explain why certain resources are managed better than others. It seems that local participation is an important factor for success. Hence, some governments are transferring the control of resources back to local communities. The overall results of this policy are mixed (Knox and Meinzen-Dick 2001).

All of those approaches suffer from the assumption that the institutional setting is exogenous. Instead, institutions often evolve together with the resource (Ostrom 1990). The outcome of such a process is difficult to understand and predict, since both the institutions and the state of the resource change over time. Successful policy design is therefore only possible if the different complexities at the resource level and at the community level are understood and taken into account (Baland and Platteau 1996). Concerning dynamics at the community level, a lot of confusion arose due to unclear terminology and fundamentally different theoretical presumptions (Bowles and Gintis 2002). This intellectual ambiguity mostly results from the fact that observed collective behavior is not just the aggregation of individual actions (Coleman 1990). Instead, individuals act differently in a certain group, since imitation and social norms influence choices. When individuals are not entirely sure about appropriate behavior, as a shortcut they may just do what everyone else or a particularly competent individual is doing. When the overall uncertainty is high, this mechanism may lead to herd behavior. This is particularly visible in situations such as riots, escape panics, or financial crashes, but also in fashions or fads (Noelle-Neumann 1974; Granovetter 1978; Dornbusch et al. 2000; Gladwell 2000; Bettencourt 2002; Scheffer et al. 2003). Imitation models often borrow mechanisms that come from the field of epidemiology. These mechanisms are by their nature deterministic and therefore silent about the question why a certain type of behavior evolves in the first place. This brings us to the second mechanism: The evolution of social norms.

Very much like imitation, social norms can be interpreted as a shortcut that helps individuals make the right choices when information is not perfect (Cialdini 2001). A social norm is defined as a customary rule of behavior that is self-reinforcing (Young 2003). It is sustained as individuals fear external sanctions, like punishment or disapproval, or feel internally obliged to follow the norm (Kendal et al. 2006). Norms do of

course not emerge randomly, but evolve for a reason. Coleman (1990, p. 241) notes that there must be a certain "demand" for a norm, i.e., the norm may help solving a coordination or externality problem. This point has been made earlier by Arrow (1971), but is not undisputable since certain norms seem to make everybody worse off (Elster 1989). On the other hand, many norms that may look futile now may have been appropriate at the time they evolved. It is important to make two remarks at this point. Firstly, none of the explanations are mutually exclusive. It is very likely that imitation and social norms influence behavior at the same time. Second, these explanations are not necessarily at odds with the concept of rational, profit-maximizing agents. Especially in situations in which information is sparse and uncertainty is high, heuristics may offer a decent outcome, since the alternative would not be a well considered move, but a random guess.

Research questions

The main purpose of this project is to develop a model that sheds light on the following questions:

1. How do social norms for renewable resource harvesting emerge?

2. What determines the sustainability and resilience of an established system of social norms?

The first question can only be answered by taking environmental and social feedback effects explicitly into account. While those feedback effects may lead to countless different outcomes, they are not necessarily unpredictable, because the underlying mechanisms are most likely stable. Therefore, it is an important first step to develop a model in which these general environmental and social feedback effects are defined. Including local differences by adding specific factors that may be environmental, social, or economic, will help revealing why different environmental conditions lead to different norms. Factors that may be of interest are temporal and spatial variability of a resource, or economic dependence on the resource. The second question is especially interesting for policy makers, who try to strengthen a system of local social norms. Factors of interest could be the influx of new agents or changing economic outside options.

Methods and work plan

Will the real model for social norms please stand up?

While there is broad consensus on the importance of social norms for explaining human behavior, science has reached anything but consensus on how to model them. Very often a norm is simply defined as an equilibrium of a dynamic game (e.g., Sethi and Somanathan 1996). While this may be true in some cases, this definition is very broad, as it does not satisfy what Coleman called demand for norms. This confusion is not surprising, since norms operate both at the individual level and at the population level. In this micro-macro transition, aptly described in Coleman (1990, pp. 244), norms are part of a feedback process, as individual actions shape the norm, which in return influences individual choices.

While this is verbally compelling, it is hard to implement in a framework based on evolutionary game theory. First of all, typical models of evolutionary game theory require an a priori defined set of competing strategies, such as cooperation and defection, which is of course a simplification, since an extraction level is in fact continuous. This shortcoming is, however, not the largest problem. Standard models of evolution-

ary game theory cannot distinguish dynamics at the individual and at the population level. It is impossible to say whether there are indeed two competing norms or if all agents follow the same strategy and defect with a certain probability, since both situations would lead to the same result. This is a general degeneracy of matrix games, as pointed out by (Dieckmann and Metz 2006). Besides, a framework based on unconditional strategies does not allow for institutional change, such as a higher tendency to cooperate if the resource is threatened with extinction (Sethi and Somanathan 1996).

In other models, a certain norm, e.g. inequity aversion, is introduced in the utility (payoff) function of an individual (e.g., Falk et al. 2000; López-Pérez 2006). While these models explain human behavior quite well and do not sacrifice the concept of utility maximizing agents, they are theoretically cumbersome as any norm has to be introduced on an ad-hoc basis. Besides, optimizing agents base their decisions on their objective functions and on the constraints they have. Some authors argue that norms are rather a constraint than an objective (Baland and Platteau 1996, Ch. 6).

Social norms as function-valued traits

We have seen that simple models of evolutionary game theory lose much of their beauty since they cannot separate actions from norms. Another class of models assumes that agents may sacrifice a norm for other objectives or goods. While this is true, it is theoretically ill-defined, since a norm is treated as a commodity or as a constraint, while it is more: It is a certain code of how individuals should behave in certain situations (Akerlof 2007). Therefore it is neither a commodity, nor an action as such, but some kind of rule that translates information into action. While economists have reached and realized this point often, they stop here, as they run out of models. Biologists, on the other hand, deal with this kind of problems very often and have an arsenal of tailor-made tools to analyze them.

The translation rule implied by a social norm is akin to a reaction norm of classical biology, which, for a given genotype, describes the pattern of phenotypic expression across a range of environmental conditions. In the particular case we wish to analyze, agents will choose a certain extraction level. This choice is based on observable information and the social norm, where the social norm is the mediator between action and information. Such reaction norms, or, more general, function-valued traits, will face selective pressures (Dieckmann et al. 2006). The same holds for social norms. It is then examined whether an existing norm, hold by everyone, could be replaced by a different norm. If a new norm will have a higher chance of being adopted than the existing one, the new norm will replace it. In its simplest form, this approach is based on the assumption that the resource dynamics inside the community is at equilibrium when a slightly different norm tries to "invade". Invasion occurs as a result of slight adjustments in the social norms adopted by agents or because new agents arrive from outside the community. The resultant dynamics will be analyzed with concepts that come from the field of adaptive dynamics (Dieckmann and Law 1996; Metz et al. 1996; Geritz et al. 1998).

The translation from information into action

In our planned model, three sources of information serve as input variables:

1. *Resource status;* which reflects the demand for the norm. If it is in the common interest to reduce harvesting effort and if there is a certain need or urgency, an agent may be more willing to do so. As an easy start, we will assume that a resource will grow according to a logistic growth function. A straightforward extension would be to assume an Allee effect. If this effect is strong, the resource will

go extinct when falling below a certain threshold level. If it is weak, the population will remain viable, but will grow at a lower rate. Further extensions would be to include environmental stochasticity, or a growth function that allow catastrophic regime shifts (Scheffer et al. 2001).

2. *Monetary payoffs;* which reflect net profits of different choices. A very basic starting point would be to assume that the profits (π) depend on the effort level (*e*), which has a certain cost (*w*), while the harvest (*h*) delivers a certain revenue determined by the price (*p*): $\pi = p*h - w*e$ and $h = q*e*x$, where x is the resource stock and q is an efficiency coefficient. It is convenient to assume that *w*, *p* and *q* are exogenous. The linear harvesting function may be too simple for certain resources, for instance, in fisheries interfering nets and queuing vessels may reduce efficiency. Besides, larger fish stocks may lead to decreasing marginal harvest rates, as nets may become congested. A straightforward possibility to account for both would be the use of the following function: $h = f(E)*q*e*x^{\alpha}$, where α < 1 and *f(E)* is the aggregate effort of all agents that takes values between 0 ((for *E* = ∞) and 1 (for *E* = 0). The harvesting function could also include stochastic effects due to exogenous shocks, such as weather effects. This may be important if agents require a certain subsistence level of income, leaving no other option than excessive harvesting. This may not be the case if cooperation will reduce current risk and variability, since the chance to fall below the subsistence level is then reduced (Swallow 1995). In a similar vein, agents may be more inclined to reduce harvesting if the resource acts as an insurance (Baland and Francois 2005). Furthermore, outside options may incline the agent to harvest excessively (Tarui 2007).

3. *Past actions of other users;* since this determines which behavior is appropriate. Individuals want to avoid being the one sucker that has reduced efforts, while no one else has, but people also want to avoid anti-social behavior when everyone else is cooperative. Evolution of social norms is closely related to conformity (Bernheim 1994), since non-conformity may lead to punishment or loss of social status that reduce an individual's profit. A simple functional form to start with would be to consider the average or the modal effort level of all agents.

Based on these input variables, the agent chooses an appropriate effort level. "Appropriate" in the sense that it is consistent with the social norm the agent holds. While the resource dynamics and harvesting dynamics take place continuously, the updating of the social norms take place in discrete steps. This distinction is due to the assumption that agents may change their behavior frequently, whereas the underlying social norms or opinions change only slowly.

The transmission of social norms

The question whether a resident social norm is replaced by an invading norm depends on the fitness of the resident and the invader. Fitness is usually interpreted as the number of expected offspring, or more precisely, as the long-term per capita growth rate in a given environment – but different definitions and measures are used as well (Metz 2006). In the particular case we plan to analyze, the mechanisms underlying the definition of fitness are less clear, since we are not dealing with reproduction, but with human behavior.

Two transmission mechanisms are prominent: (i) payoff-based transmission that favors the norm that yields the highest payoff, and (ii) conformity-based transmission that copies the most frequent behavior (Henrich and Boyd 2001). Both mechanisms can be combined in a straightforward way, by assuming that the probability of social

norm s_i to be imitated is given by $p(s_i) = \pi_i^\lambda / \sum_{j=1}^{n} \pi_j^\lambda$, where the parameter λ can take any value in the range $(0, \infty)$. If λ is set to zero, the probability of imitation will be equal to the relative frequency with which strategies are represented among agents $i = 1, \ldots, n$. If λ approaches ∞, only the most successful norm will be imitated. For the use of a similar function in a different context, see Egas et al. (2005). The model could be extended by assuming that imitation is not only based on profits, but also based on social appreciation.

Work plan

It will be desirable to start not too complicated, since this project combines theories from different fields and parsimony may induce understanding. One appropriate framework will be an agent-based model; another will be the canonical equation of adaptive dynamics. Instead of using continuous actions, one could also start with binary ones, simply indicating whether or not to exploit the resource. The same could be assumed for the three input variables in the sense that below a certain threshold the agent switches behavior (Posch et al. 1999). This may facilitate interpretation and analysis. This would leave two possibilities for each of the three input variables, resulting in eight different situations an agent could face. The three threshold levels would evolve over time, together with the eight extraction levels the social norm prescribes for the eight different situations. This setup would thus result in models incorporating 3 + 8 = 11 continuous evolving traits.

Relevance and link to EEP's research plan

This research is very close to EEP's project Evolution of Cooperation and, moreover, uses tools developed in EEP's project Foundations of Adaptive Dynamics. Earlier work at IIASA has shown that this synergy can be particularly fruitful. Adaptive dynamics is a relative new concept and is therefore still unfamiliar to most scientists outside theoretical biology. Particularly the economic science is more and more interested in using concepts such as evolution, coevolution, and adaptation, in order to explain economic changes and human behavior. Therefore, it may very well be possible to make an impact there.

Expected output and publications

This work will be part of my PhD thesis and is intended for publication in an international scientific journal.

References

Akerlof, G.A. (2007). The Missing Motivation in Macroeconomics. The American Economic Review, 97: 5-36.

Arrow, K.J. (1971). Political and Economic Evaluation of Social Effects and Externalities. In: Intriligator, M.D. (ed.) Frontiers of Quantitative Economics. North-Holland Publications, pp. 3-25.

Baland, J.M. and Francois, P. (2005). Commons as insurance and the welfare impact of privatization. Journal of Public Economics, 89: 211-231.

Baland, J.M. and Platteau, J.P. (1996). Halting degradation of natural resources, Clarendon Press.

Bernheim, B.D. (1994). A Theory of Conformity. The Journal of Political Economy, 102: 841-877.

Bettencourt, L.M.A. (2002). From boom to bust and back again: the complex dynamics of trends and fashions. Arxiv preprint cond-mat/0212267.

Bowles, S. and Gintis, H. (2002). Social Capital and Community Governance. The Economic Journal, 112: 419.

Cialdini, R.B. (2001). Influence: science and practice, Allyn and Bacon.

Coleman, J.S. (1990). Foundations of Social Theory. Belknap Press.

Dieckmann, U., Heino, M. and Parvinen, K. (2006). The adaptive dynamics of function-valued traits. Journal of Theoretical Biology, 241: 370-389.

Dieckmann, U. and Law, R. (1996). The dynamical theory of coevolution: A derivation from stochastic ecological processes. Journal of Mathematical Biology, 34: 579-612.

Dieckmann, U. and Metz, J.A.J. (2006). Surprising evolutionary predictions from enhanced ecological realism. Theoretical Population Biology, 69: 263-281.

Dornbusch, R., Park, Y.C. and Claessens, S. (2000). Contagion: Understanding How It Spreads. The World Bank Research Observer, 15: 177.

Egas, M., Sabelis, M.W. and Dieckmann, U. (2005). Evolution of specialization and ecological character displacement of herbivores along a gradient of plant quality. Evolution, 59: 507-520.

Elster, J. (1989). Social Norms and Economic Theory. The Journal of Economic Perspectives, 3: 99.

Falk, A., Fehr, E. and Fischbacher, U.R.S. (2000). Appropriating the Commons-A Theoretical Explanation, Working paper No. 55, Institute for Empirical research in Economics, University of Zurich.

Geritz, S.A.H., Kisdi, E., Meszena, G. and Metz, J.A.J. (1998). Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. Evolutionary Ecology, 12: 35-57.

Gladwell, M. (2000). The Tipping Point: How Little Things Can Make a Big Difference. Little, Brown and Company.

Granovetter, M. (1978). Threshold Models of Collective Behavior. American Journal of Sociology, 83: 1420.

Hardin, G. (1968). The Tragedy of the Commons. Science, 162: 1243-1248.

Henrich, J. and Boyd, R. (2001). Why people punish defectors - Weak conformist transmission can stabilize costly enforcement of norms in cooperative dilemmas. Journal of Theoretical Biology, 208: 79-89.

Kendal, J., Feldman, M.W. and Aoki, K. (2006). Cultural coevolution of norm adoption and enforcement when punishers are rewarded or non-punishers are punished. Theoretical Population Biology, 70: 10-25.

Knox, A. and Meinzen-Dick, R.S. (2001). Collective Action, Property Rights, and Devolution of Natural Resource Management: Exchange of Knowledge and Implications for Policy, CGIAR Systemwide Program on Property Rights and Collective Action, International Food Policy Research Institute, Washington DC.

López-Pérez, R. (2006). Introducing Social Norms in Game Theory, Working paper No. 292, Institute for Empirical research in Economics, University of Zurich.

Metz, J.A.J. (2006). Fitness. IIASA Interim Report IR-06-061. International Institute for Applied Systems Analysis, Laxenburg, Austria.

Metz, J.A.J., Geritz, S.A.H., Meszéna, G., Jacobs, F.J.A. and van Heerwaarden, J.S. (1996). Adaptive dynamics: A geometrical study of the consequences of nearly faithful reproduction. In: van Strien, S.J., Verduyn Lunel, S.M. (eds.) Stochastic and Spatial Structures of Dynamical Systems. Proceedings of the Royal Dutch Academy of Science (KNAW Verhandelingen), Amsterdam, pp. 183-231.

Noelle-Neumann, E. (1974). The spiral of silence: A theory of public opinion. Journal of Communication, 24: 43–51.

Ostrom, E. (1990). Governing the Commons: The Evolution of Institutions for Collective Action. Cambridge University Press.

Posch, M., Pichler, A. and Sigmund, K. (1999). The efficiency of adapting aspiration levels. Proceedings of the Royal Society of London, Series B, 266: 1427-1435.

Scheffer, M., Carpenter, S., Foley, J.A., Folke, C. and Walker, B. (2001). Catastrophic shifts in ecosystems. Nature, 413: 591-596.

Scheffer, M., Westley, F. and Brock, W. (2003). Slow Response of Societies to New Problems: Causes and Costs. Ecosystems, 6: 493-502.

Sethi, R. and Somanathan, E. (1996). The Evolution of Social Norms in Common Property Resource Use. The American Economic Review, 86: 766-788.

Somanathan, E. (1991). Deforestation, Property Rights and Incentives in Central Himalaya. Economic and Political Weekly, 26: 37.

Swallow, B.M. (1995). Mobile Flows, Storage, and Self-Organized Institutions for Governing Common-Pool Resources: Comment. Land Economics, 71: 537-538.

Tarui, N. (2007). Inequality and Outside Options in Common-Property Resource Use. Journal of Development Economics, 83: 214-239.

Young, H.P. (2003). The power of norms. In: Hammerstein, P. (ed.) Genetic and Cultural Evolution of Cooperation. MIT Press, pp. 389–400.

The evolution of food-web diversity based on body size and niche traits

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Goal

To explore conditions under which long-term phenotypic evolution of body size and of a trait representing the continuum of alternative ecological niches leads to the emergence of diverse food webs with several trophic levels.

Background and motivation

The concept of ecological niche, which characterizes the function of an organism within an ecosystem, is of fundamental importance in ecology. It is also closely linked to the coexistence of species through the principle of competitive exclusion: this cornerstone of population ecology states that two species cannot coexist if they compete for common resources within a single niche. An important question in ecology is thus to understand how similar two ecological niches can be while still allowing species to coexist.

MacArthur and Levins (1967) first approached this question quantitatively, and their pioneering study has been followed by several others (see, e.g., Meszéna et al. 2006). These studies consider the possibility of packing given species within an abstract niche space, and thus cannot explain how different species coexist when allowed to evolve freely. In fact, as observed by Abrams (1983), evolutionarily realized differences are likely to be much larger than what one would predict from considering species packing alone.

Several physiological and biological traits that may be important determinants of a species' ecological niche have been identified; foremost among these is body size. However, only a few attempts have been made to date to theoretically explore how evolution of such traits may lead to diverse food webs. An exception is a recent study by Brännström et al. (in preparation; see also Loeuille and Loreau 2005) that introduces an evolutionary food web model based on considering the body size of individual species as their evolving trait. Although this model is capable of producing food webs with three to four trophic levels, the resulting food webs always exhibit a certain regularity, with typically equal spacing in body size on a logarithmic scale. Thus, this model cannot yet explain the coexistence of ecologically different species with approximately the same body size.

To overcome this limitation, one can incorporate, in addition to body size, an evolving "niche trait" to distinguish, in a simplified manner, the continuum of possible ecological roles species with the same body size can assume. The ability of a predator to forage on a prey, as well as the interference competition between species, would then be determined both by relative difference in body size and by distance in niche space.

Research questions

The key questions that will be addressed in this project concern the evolutionary dynamics of food web models under the combined effect of a body-size trait and a niche trait. More specifically, we will examine

1. How the niche trait, when combined with the body-size trait, contributes to adaptive radiations between ecologically different species, and

2. How the diversity of a food web is created and maintained in such a setting.

In particular, we will explore how evolved diversity depends on the dimension of the niche trait.

Methods and work plan

The evolutionary food web model we will investigate characterizes a species entirely through its trait value(s). These determine the intrinsic mortality rate, but also intraspecific and interspecific interaction coefficients that represent exploitation and interference competition. Mathematically, this is described by mappings from trait value(s) to interaction coefficients.

In particular, we will consider the intrinsic mortality rate $m(x)$ of a species with body size x, the rate $a(x,y)$ at which a species with body size x exploits a species with body size y, and the mortality rate $c(x,y)$ arising from interference competition between a species with body size x and one with body size y. A niche trait can then be represented by a point in one- or two-dimensional Euclidean space: it affects the strength of interactions such that when two species have niche traits far apart they do not interact. Mathematically, this can be described by $f(|n_1-n_2|)a(x,y)$ and $f(|n_1-n_2|)c(x,y)$, where f is a declining but positive function and n_1 and n_2 are the niche traits of species 1 and 2, respectively, using Gaussian functions for $a(x,y)$ and $c(x,y)$ (Brännström et al., in preparation).

Once the mapping from traits to intrinsic mortality and to the two interaction coefficients has been defined, we will employ adaptive dynamics techniques to investigate how these trait values change under gradual evolution. Three processes are of interest here: gradual evolution, extinction, and evolutionary branching (with the latter implying speciation, or adaptive radiation, in asexual organisms). Gradual evolution is described by the canonical equation of adaptive dynamics (Dieckmann and Law 1996). Extinctions can be detected by checking when the density of a species falls below a prescribed threshold. Detecting evolutionary branching requires careful geometric consideration, but, once detected, we can introduce a new species simply by adding an additional equation for describing the evolutionary emergence of the new species in the vicinity of the branching point.

By relying on these simplified descriptions, the evolutionary process in our approach will be analyzed under the assumption of small mutational steps. Adopting the canonical equation of adaptive dynamics in the case with one-dimensional niche trait values, we will have three equations for each species, one Lotka-Volterra equation describing the species' density and two canonical equations describing gradual evolution of its body size and niche trait. When the density of a species drops below a certain threshold, the equations representing the corresponding species will be removed. Near evolutionary branching points, we will introduce a new species with similar trait values so that it may diverge from its ancestor. Although criteria for evolutionary branching get more complex in higher-dimensional trait spaces, the above description is readily extended to niche traits with two or more dimensions. Along with analytical techniques, we will employ suitable numerical simulations using either MATLAB or C/C++.

Relevance and link to EEP's research plan

Exploration of food web evolution based on body size is one of the ongoing topics of research of in the EEP Program. The insights expected from this summer project will be valuable for understanding evolving biodiversity, and will potentially also be applicable to evolutionary fisheries management.

Expected output and publications

We expect that the project will result in one or more coauthored publications in peer-reviewed international scientific journals.

References

Abrams, P.A. (1983). The theory of limiting similarity. Annual Review of Ecology and Systematics, 14: 359-376.

Brännström, Å., Loeuille, N., Loreau, M. and Dieckmann, U. Metabolic scaling, competition and predation induces repeated adaptive radiation, in preparation.

Loeuille, N. and Loreau, M. (2005). Evolutionary emergence of size-structured food webs. Proceedings of the National Academy of Sciences of the USA, 102: 5761-5766.

Meszéna, G., Gyllenberg, M., Pásztor, L. and Metz, J.A.J. (2006). Competitive exclusion and limiting similarity: a unified theory. Theoretical Population Biology 69: 68-87.

MacArthur, R. and Levins, R. (1967). The limiting similarity, convergence, and divergence of coexisting species. American Naturalist, 101: 377-385.