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Probabilistic maturation reaction norms for age and size at maturation of chum salmon in Korea

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Goal

To estimate probabilistic maturation reaction norms (PMRNs) for age and size at maturation of chum salmon in South Korea.

Background and motivation

It has long been realized that the proportion of mature fish at any given age and size affects a stock's population dynamics and thus influences the potential yield that can be extracted from the stock. It is thus important to disentangle the environmental and evolutionary effects that influence this proportion over the long run. Individual fish typically follow different growth trajectories and their maturation is influenced by these, so that growth-related phenotypic plasticity in maturation and the evolution of maturation schedules often occur together. Evolution of maturation schedules is expected to result from fishing, especially when such fishing is size-selective, since all fish species are genetically adapted to ancestral environmental conditions that are strongly altered by modern fishing. Researches on fisheries-induced evolutionary responses in maturation schedules have suggested that these schedules have often shifted towards smaller sizes and younger ages, an effect that should be taken into account for the effective management of current fisheries (Olsen et al. 2004; Barot et al. 2005).

Probabilistic maturation reaction norms (PMRNs) characterize maturation schedules by describing the age- and size-dependent probability of maturation during one season. Their estimation thus helps to separate the fundamental biological processes of maturation, growth, and survival. Whereas the average age and size at maturation observed in a population is significantly affected by all three of these processes, PMRNs describe maturation probabilities conditional on an individual having grown to, and survived until, a given age and size, thus enabling a closer inspection of the maturation process itself. In other words, PMRNs reveal the confounding effects that variations in growth and survival have on maturation (Kraak 2007). Specifically, changes over time in a PMRN could be interpreted as being suggestive of evolutionary or genetic changes, often driven by changes in environmental conditions including the extra mortalities imposed by fishing. For example, studies on Northeast Arctic cod show that long-term shifts in PMRNs are accompanied by maturation changes due to phenotypic plasticity in response to short-term environmental fluctuations, e.g., in feeding conditions (Jørgensen 1990; Heino et al. 2002b).

Chum salmon are semelparous fish in the North Pacific, spawning in freshwater and maturing once during their life time. Bigler et al. (1996) proposed that chum salmon have more than doubled during the past 20 years due to favorable ocean con-

ditions, population management policies, and artificial enhancement programs, while the size at maturation of chum salmon has decreased dramatically. Recently, Ishida et al. (2002) reported that chum salmon and sockeye salmon showed significant decreasing trends in body size at ocean age 3 and older ages between the mid-1970s and the late 1990s in the central Bering Sea. In addition, Morita et al. (2001) found that sea surface salinity was significantly associated with the growth of chum salmon in the North Pacific, potentially causing the decrease in size at maturation and the increase in age at maturation observed in Japanese chum salmon (Morita et al. 2005).

The Namdae River, located on the east coast of Korea, constitutes the southern boundary of the natural range of chum salmon in the North Pacific. Although age at maturation in Korean chum salmon can vary between 2 to 5 years, most individuals (ca. 90%) matured at ages 3 or 4. The average age at maturation was 3.7 years in the 1980s and 1990s. The mean age at maturation ranged from 3.3-3.5 years between 1984 and 1987, and then increased to 3.7-4.1 years in the 1990s (Seo et al. 2006).

Research questions

In this project, I will calculate PMRNs for age and size at maturation from Korean chum salmon data collected in the Namdae River. Specifically, I will focus on the following questions:

- How did the mean age and size at maturation of chum salmon change from 1984 to 1998?
- What are the mean growth trajectories of chum salmon at sea and how did these change during the study period?
- What are the mean survival probabilities of chum salmon at sea and how did these change during the study period?
- What are the stock biomasses of chum salmon at sea and how did these change during the study period? Can we estimate relationships between stock biomass at sea and growth increments or survival probabilities at sea?
- What is the shape of PMRNs in chum salmon and how did the PMRNs change during the study period? In particular, has the PMRN of chum salmon a negative or positive slope?
- How are the growth, survival, and maturation of chum salmon affected by various environmental factors, such as zooplankton biomass, sea surface temperature, and stock biomass?
- Can we detect evidence of fisheries-induced evolution on maturation in chum salmon?

My study will thus address not only environmental variability in life-history traits, but also compare maturation changes that may arise from fisheries-induced evolution with environmentally induced changes in age and size at maturation. Since commercial fishing of chum salmon occurs with gillnets near the coast (with corresponding catches being recorded since 1990), and since gillnets are highly size-selective, fisheries-induced selection pressures are expected to exist in this system. The estimation of PMRNs could make it possible to comprehend and predict the direct effects of varied

environmental factors and of size-selective fishing pressures on the life-history traits of chum salmon.

Methods and work plan

I will use data collected, through research surveys at salmon weirs in the Namdae River conducted by Korea's National Fisheries Research and Development Institute (NFRDI), from adult chum salmon returning to the east coast of Korea from late September to early December between 1984 and 1998 (the detailed surveys by NFRDI stopped in 1998). Although a total of 2,846 specimens were measured for fork-length, weight, sex, and age, this data only includes mature specimens sampled while they were ascending the Namdae River. To calculate PMRNs, representative samples of maturing and immature fish are required. Based on the techniques described by Heino et al. (2002a, 2002b), I will reconstruct the unobserved size distributions of immature salmon.

All 2,846 specimens of mature chum salmon were sampled with scale measurements. Since fish scales record a fish's growth history, we can estimate the growth trajectories of immature chum salmon individuals, and thus investigate their effects on the maturation process. For the potential improvement of the PMRN reconstruction, back-calculation of growth trajectories will be used to reconstruct the fork-lengths of immature fish during their stay at sea (Morita et al. 2005), based on scale-length and annulus-length measurements using a biological intercept method (Campana 1990). Korean chum salmon and Japanese chum salmon from the western gyre of the North Pacific appear to follow similar interannual variation in their growth increments (Bigler et al. 1996).

Effects of hatchery releases on wild stocks of chum salmon were reported by Kaeriyama (1998). While the increasing age and decreasing size at maturation in Korean chum salmon has been attributed to density-dependent competition with salmon released from hatcheries on the Japanese island of Hokkaido, little is actually known about density-dependent effects on marine survival and growth. Through this project, we could possibly estimate density-dependent growth rates at sea.

Relevance and link to EEP's research plan

This project aims to evaluate the evolutionary effects implied by harvesting in conjunction with varying environmental conditions by estimating probabilistic maturation reaction norms (PMRNs) for Korean anadromous chum salmon. This work is therefore directly linked to EEP's research project on *Evolutionary Fisheries Management*.

Expected output and publications

The research results will be published as one or more co-authored articles in scientific journals.

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Speciation through sexual selection in spatially heterogeneous environments

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Goal

To investigate how frequency-dependent local interactions can induce mating domains in spatially heterogeneous environments, thus causing speciation through sexual selection and the evolution of assortative mating.

Background and motivation

Speciation in sympatry has received considerable attention because, unlike for speciation in allopatry, the lack of population subdivision means that reproductive isolation must be achieved in the presence of persistent gene flow. One mechanism that is thought to be capable of creating reproductive isolation in sympatry is frequency-dependent disruptive selection combined with reinforcement through selection against maladapted hybrids. Such disruptive selection could act on an ecological trait, as in Dieckmann and Doebeli (1999), or on a sexually selected trait via divergent Fisherian runaway, as in Higashi et al. (1999). While it has been shown that species produced via frequency-dependent disruptive natural selection can stably coexist (Dieckmann and Doebeli 1999), it is not known whether sexual selection is capable of generating equivalently stable species. Even though ecologically heterogeneous environments are known to stabilize such species (Lande 1982; Payne and Krakauer 1997), corresponding studies are surprisingly few and leave open many questions that deserve to be explored. Furthermore, there are no theoretical studies so far examining sexual selection in heterogeneous environments that are neutral with respect to natural selection, such as environments that are heterogeneous in local carrying capacity and/or growth rates. Without such studies, it is difficult to assess the relative importance of sexual selection in speciation and the evolution of assortative mating.

Lande (1982) analyzed the joint evolution of geographic variation in female mating preferences and secondary sexual characters in males in an ecologically heterogeneous environment and found that sexual selection tended to enhance spatial population structure, to a larger extent than would be expected under natural selection alone. Payne and Krakauer (1997) suggested that Lande's model, as well as the non-spatial models presented by Kirkpatrick (1982) and Seger (1985), always result in eventually homogeneous populations when applied to ecologically homogeneous environments with constant diffusion. They then showed that, if diffusion was not constant, but dependent on local conditions, spatially structured populations could emerge even in the absence of environmental heterogeneity. In particular, they showed that when the dispersal of males was inversely proportional to their mating success, spatially heterogeneous populations and assortative mating could evolve, resulting in segregated mating domains individually characterized by the co-occurrence of mutually compatible mat-

ing traits. However, while this was not explicitly stated in their paper, it turns out that the spatial population structures reported by Payne and Krakauer (1997) were in fact only transitory, and only applied before one mating domain eventually replaced all others. The authors also showed that, in the presence of an ecological gradient, population structure became more pronounced. It has since been shown that mating-dependent dispersal is not the only mechanism capable of leading to such evolutionary outcomes (Dieckmann 2004).

A number of important questions emerge from these results, the primary one being: How do the spatial dynamics of mating traits affect long-term population structure and the evolution of assortative mating when situated in spatially heterogeneous environments? In other words, How much environmental heterogeneity is required for stably maintaining mating domains in which different mutually compatible combinations of mating traits prevail and across which hybridization will be rare? A number of follow-up questions are discussed below.

Research questions

The focus of this research project will be to investigate how frequency-dependent local interactions between different mating types (Payne and Krakauer 1997; Dieckmann 2004) can induce spatial structure and the evolution of assortative mating in spatially heterogeneous environments. More specifically, we will try to answer the following questions:

- How do environments implying spatial heterogeneity in the local amplitudes of carrying capacities and/or growth rates affect the emergence and persistence of mating domains under frequency-dependent local effects on mobility (Payne and Krakauer 1997)?
- How do environments requiring local adaptation, such as those in Lande (1982), affect the emergence and persistence of mating domains?
- How do results extend to frequency-dependent local effects on fecundity and mortality (Dieckmann 2004)?
- How do results differ when temporal variations in environmental heterogeneity are considered?
- How do results differ when the considered environments are two-dimensional instead of one-dimensional?

It may also be worthwhile investigating environments in which there is an ecological advantage of rarity. This will tend to discourage the evolution of assortative mating, and thus compete with the selection created by the aforementioned mechanisms.

Methods and work plan

We will focus on developing and investigating stochastic individual-based models and may, time permitting, eventually examine the possibility of approximating these through deterministic continuum models.

We will begin by extending an existing individual-based model (Doebeli and Dieckmann 2003) with the first aim of reproducing the main results reported by Payne and Krakauer (1997). In particular, we will show that in homogeneous environments the negative dependence of dispersal in males on their mating success can be a suffi-

ciently strong force to generate mating domains. We will then show that these spatial structures do not persist over evolutionary time, as one mating domain eventually replaces all others. Next, we will show how environments (i) implying spatial heterogeneity in the local amplitudes of carrying capacities and/or growth rates or (ii) requiring local adaptation stabilize otherwise transient mating domains. Following ideas presented in Dieckmann (2004) we will also investigate the effects of frequency-dependent mortality and frequency-dependent fecundity.

After exploring spatial environmental structures described by linear gradients, we will examine more complex heterogeneities. For example, Lande (1982) considered three spatial environmental structures that could be investigated: a one-step, a two-step (comprising of a one-step up and a one-step down), and an environment periodically changing in space.

It will be important to compare results in one-dimensional space with those in two dimensions, since it has been suggested that, in the absence of spatial environmental structure, mating domains deteriorate more quickly in two dimensions than in one (Dieckmann, unpublished). This effect results from domain boundaries encroaching on convex domains; a phenomenon that naturally cannot occur in a single spatial dimension.

We will also investigate temporal variation, both on its own and in combination with spatial heterogeneity. This could be done in one of two ways, both of which are likely to provide interesting results. First, spatial patches could experience some probability of extinction during each generation. Re-colonization would then occur via dispersal. This will increase the overall level of stochasticity in the model, and will likely reduce the persistence of mating domains. Alternatively, the spatial environmental structure could fluctuate in time, so that, for example, a patch could gradually oscillate between having high or low carrying capacity, or between favoring one local adaptation or another. It is not clear a priori how such variation will affect results.

We plan to consider two mechanisms of assortative mating, in order to be consistent with previous models. In the “fixed relative-preference” mating scheme, a female with preference strength a , is a times more likely to mate with a male bearing the desired trait than with a male not bearing that trait (Kirkpatrick 1982). A more general approach is the “best of N ” scheme, in which a female surveys N males before choosing a mate. Again she is a times more likely to choose a male with the desired trait (Seger 1985). In one extreme, for $N = 1$, the “best of N ” scheme corresponds to random mating, whereas in the other extreme, when N approaches the size of the whole population, the “best of N ” and the “fixed relative-preference” schemes become equivalent. Possible extensions here include considering the evolution of a , or male and female mating traits that are coded for by multiple loci and that are thus subject to segregation and recombination. The latter has been suggested by Bridle et al. (2000) as a worthwhile extension of the model in Payne and Krakauer (1997).

Our tentative plan is to further investigate interesting results from the individual-based models with the help of an approximate analytical continuum model. However, without such results having yet been assembled and the feasibility of such approximations having been scrutinized, it is not realistic to speculate about the details of such a model.

Relevance and link to EEP's research plan

This project is an extension of work that was developed at IIASA. I will be using the adaptive dynamics framework to extend the individual-based models developed in Doebeli and Dieckmann (2003). This project will thus make contributions to EEP's research project on *Adaptive Dynamics Theory*. Furthermore, our model will contribute to EEP's research project on *Evolving Biodiversity* by investigating the conditions under which ecologically similar species may or may not arise and coexist over evolutionary time.

Expected output and publications

This work will be a part of my PhD thesis and is intended for publication as a co-authored article in an international scientific journal.

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Modeling coregonid fish diversification along a vertical gradient in water temperature

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Goal

To develop an adaptive dynamics model for understanding the ecological diversification of coregonid fish along an environmental gradient in depth and water temperature.

Background and motivation

Ecology of speciation

The theory of adaptive speciation and radiation suggests that macro-evolutionary phenomena of diversification are ultimately the outcome of micro-evolutionary processes driven by natural selection (Orr & Smith 1998; Coyne & Orr 2004; Dieckmann et al. 2004). Hence, phenotypic and ecological diversity are likely to imply divergent or disruptive natural selection arising from differential resource use, competitive intraspecific interaction, and ecological opportunity. Competitive interactions involving the exploitation of different resources or habitats, between individuals and populations within the same geographical area, are thus of major importance for understanding the origin of biological diversity. In addition, the geographical conditions underlying speciation processes have long been the focus of debate. However, mechanisms of ecologically based sympatric, parapatric, and allopatric speciation appear to be similar, with disruptive or divergent natural selection as the driving force of diversification and the evolution of reproductive isolation as a consequence of selection on traits between environments (Schluter 1996, 2000). The process of ecologically based speciation of sexual populations within the same geographical area does not only necessitate the emergence of reproductive isolation during diversification, but also requires the ability of the incipient species to coexist stably (Coyne & Orr 2004; Gavrilets 2004). Hence, it is often the same ecological conditions that produce disruptive natural selection, cause adaptive speciation through the gradual evolution of reproductive isolation, and enable the coexistence of closely related species in sympatry.

Speciation models

The theory of adaptive dynamics (Dieckmann & Law 1996; Geritz et al. 1998) is recognized by many as ‘the’ mathematical tool for the study of adaptive evolution. It lies at the basis of theoretical models investigating ecology-based processes of evolutionary diversification (Doebeli & Dieckmann 2005). For one-dimensional traits slowly mutating in small steps, the theory states that the frequency-dependent selection of an asexually reproducing population proceeds in the direction of a local fitness gradient until an evolutionarily ‘singular’ strategy is reached, where selection pressures cease. The singular strategy is either evolutionarily stable, implying an evolutionary outcome

with a single morph, or an ‘evolutionary branching’ point, leading to the evolutionary divergence of two morphs. In most existing models of sympatric adaptive speciation (Dieckmann et al. 2004), ecological specialization through resource partitioning is the key driver of diversification. Besides models assuming discrete or patchy environments (Meszena et al. 1997; Day 2000), models have been developed for describing the evolution of reproductive isolation along continuous environmental gradients in asexual (Mizera & Meszena 2003) as well as sexual populations (Doebeli & Dieckmann 2003).

One conclusion from advances in adaptive speciation theory is that sympatric and/or parapatric speciation is theoretically plausible and may thus be a common process in nature. However, theoretical speciation models are not easily evaluated in terms of ecological plausibility and may lack ecological realism in their assumptions about system properties. Empirically motivated and data-based speciation models including ecologically derived quantitative assumptions are therefore needed for evaluating the importance of these processes in nature. One of the best model systems for studying adaptive diversification are northern freshwater fish occupying postglacial environments, in which several taxa have generated species and ecological diversity in a manner consistent with the theory of adaptive speciation (Schluter 1996, 2000). There is increasing evidence that ecological opportunity in species-poor postglacial lakes in combination with high intraspecific competition within the ancestral population promotes adaptive divergence in fishes (e.g., Hudson et al. 2007). Biotic and abiotic environmental factors in these systems are potential causes of diversification. Their characteristics determine the strength of selection acting on phenotypic evolution and thus ultimately determine the potential for speciation.

Study system

In the deep oligotrophic postglacial Lake Stechlin in Germany, two planktivorous coregonid fish species co-occur within the pelagic area: common vendace, *Coregonus albula* (L.), and endemic dwarf-sized Fontane cisco, *Coregonus fontanae* (Schulz & Freyhof). The two species are easily distinguished by their differential spawning times and exhibit distinct morphological characteristics (Schulz & Freyhof 2003). The sympatric evolution of this species pair has been suggested based on mtDNA and microsatellite analyses (Schulz et al. 2006). Both species perform regular diel vertical migrations, but differ in their average night-time population depths, with Fontane cisco being found a few meters deeper in the water column than vendace throughout the year (Helland et al. 2007; Mehner et al. 2007). This difference in depth distribution is associated with a difference in mean experienced water temperature, which declines continuously with depth (Mehner et al. 2005). Despite the depth segregation, diet compositions of the species are rather similar, with a clear dominance of planktonic food (Helland et al. 2008). Hence, exploitative competition between the two species can be assumed to be high, whereas mechanisms reducing competition (and thus potentially driving divergence) are unrelated to diet. One mechanism promoting ecological divergence between the species is a difference in temperature-specific metabolic costs (Ohlberger et al. 2008), which directly influences the competitive abilities of the two populations. Also the temperature preferences of the two species differ according to their slight vertical segregation. These thermal preferences further correspond to temperatures of minimal net costs of swimming, highlighting temperature as the pre-

dominant environmental factor shaping the divergence between the species (Ohlberger et al., submitted).

Lake Stechlin features typical characteristics of newly colonized postglacial systems: intraspecific competition for food resources is high due to the low productivity of the lake, and ecological opportunity is high due to the weak interspecific competition with planktivores from other taxa and due to the low risk of predation by higher trophic levels. This setting offers the unique opportunity to investigate whether these system characteristics, in conjunction with adaptation in the metabolic temperature optimum, allow for ecological diversification and eventual parapatric/sympatric speciation along the environmental gradient given by water temperature. If proven plausible, this would add new insights into the theory of adaptive speciation, support the prevalence of speciation along environmental gradients in natural systems, and highlight the importance of temperature in shaping processes of ecological and evolutionary diversification.

Research questions

The main question for this study is whether a lake's temperature-depth gradient is prone to induce the adaptive speciation of fish populations in sympatry/parapatry through microhabitat adaptation and segregation along the gradient.

In particular, I will address the following two research questions:

- Are the ecological mechanisms associated with the metabolic temperature optimum, treated as the single adaptive trait in the evolutionary model, sufficient to induce evolutionary branching of the ancestral population along the temperature-depth gradient?
- Does evolutionary branching occur under the assumptions and parameter estimates inferred from observational and experimental data?

Two further research questions will be addressed if time allows:

- Is size structure necessary for evolutionary branching to occur, or is a second adaptive trait needed (such as size at maturation or a trait determining maintenance costs)?
- Does evolutionary branching occur in an extended model of sexual populations under the assumption of assortatively mating individuals?

Methods and work plan

Based on the observational and experimental knowledge about the Lake Stechlin coregonids, we will design a model for their evolutionary diversification along the lake's temperature-depth gradient. First, we will specify the basic equations to describe the system (see below) and implement these into the simulation software. After this implementation, and based on a preliminary estimation of parameter values, the model will be analyzed numerically using adaptive dynamics techniques and direct numerical simulations. Finally, a sensitivity analysis will deepen our understanding of the model's behavior and enable its refinement as needed. For simulation and analysis, we will use the MATLAB computing environment. We will begin with a fairly simple model and gradually increase its complexity as time allows. Specifically, we will start with a single adaptive trait and asexual reproduction with mutation. If necessary and

possible, we will include size structure and/or extend the model to sexual reproduction with recombination and assortative mating.

Model description

The starting point for our simple initial model is a hypothetical ancestral population with a potential for divergence in the quantitative adaptive trait given by its metabolic temperature optimum T_i . For the evolutionary dynamics, we assume asexual reproduction, a low mutation probability μ , and a small standard deviation σ of mutation steps, so that evolution follows the canonical equation of adaptive dynamics (Dieckmann & Law 1996) in conjunction with fitness-based conditions for evolutionary branching (Geritz et al. 1998), as specified in detail below. The population dynamics are deterministic and structured with regard to depth x , with $0 < x < x_{\max}$. The foraging rate $r_i(x)$ of a morph i is assumed to drop with temperature $T(x)$ on both sides around T_i . Exploitative competition for a single unstructured resource, considered as the predominant cause of competition in our system, is logistic and occurs at each depth. The rate density at which resources become available is given by a depth-dependent carrying capacity density $K(x)$. Since temperature, food density, and light intensity continuously decrease with depth $K(x)$ and prey catchability $c(x)$ decline monotonically with depth. Gain in the biomass density $B_i(x)$ of morph i at depth x , which includes fecundity, is proportional to prey catchability, foraging rate, and the logistic competition factor. Biomass loss, which includes mortality, arises from maintenance costs $m(T)$, which monotonically decrease with temperature. Therefore, the per capita growth rates $f_i(x)$, in terms of biomass, are given by the difference between per capita resource intake rates and per capita maintenance costs. We further assume the rapid redistribution of individuals along the depth gradient following foraging dynamics, which can be chosen gradually between being random and optimal by varying a parameter α . Individuals keep adjusting their depth according to their per capita growth rate. We further define the number of morphs n , the morph index i , with $i = 1, \dots, n$ for residents and $i = 0$ for a rare mutant, and the average biomass b_i of an individual of morph i . For the evolutionary dynamics we define the invasion fitness of a morph f_i , its first derivative (or selection gradient) g_i , and its second derivative h_i . Derivatives of the invasion fitness are taken with respect to the mutant trait value and are evaluated at the trait value of the corresponding resident.

Basic equations

Biomass of morph i : $B_i = \int_0^{x_{\max}} B_i(x) dx$.

Invasion fitness of morph i : $B_i^{-1} \int_0^{x_{\max}} f_i(x) B_i(x) dx$.

Resource intake rate density of all morphs competing at depth x : $I(x) = c(x) \sum_{i=1}^n r_i(x) B_i(x)$.

Per capita growth rate of morph i at depth x : $c(x) r_i(x) [1 - I(x) / K(x)] - m(T(x))$.

Foraging dynamics (fastest timescale)

$B_i(x) = B_i f_i^\alpha(x) / \int_0^{x_{\max}} f_i^\alpha(x') dx'$.

Population dynamics (fast timescale)

$\frac{d}{dt} B_i = f_i B_i$.

Gradual evolutionary dynamics (slow timescale)

$\frac{d}{dt} T_i = \frac{1}{2} \mu \sigma^2 \frac{B_i}{b_i} g_i$.

Evolutionary branching dynamics (slowest timescale)

If $h_i > 0$ and $|g_i| < \frac{1}{2}\sigma h_i$, then $n \rightarrow n+1$, $T_n \rightarrow T_i + \sigma \operatorname{sgn} g_i$, $B_n \rightarrow \frac{1}{2}B_i$, and $B_i \rightarrow \frac{1}{2}B_i$.

Relevance and link to EEP's research plan

This project aims at enhancing the understanding of ecological diversification and speciation along an environmental gradient by frequency-dependent disruptive natural selection arising from competitive intraspecific interaction and ecological opportunity. It therefore intends to provide new insights into causes of adaptive diversification within a contiguous spatial area and may advance the understanding of impacts of environmental change on ecosystems in dependence on their evolutionary history and ecological characteristics. The proposed research plan combines aspects of the *Evolving Biodiversity* and *Adaptive Dynamics Theory* research projects of the EEP. It further bridges between theoretical and empirical as well as biological and mathematical approaches by integrating experimental and observational knowledge into the described modeling approach.

Expected output and publications

This work will be included in my Ph.D. thesis and is intended for publication as a co-authored research article in an international scientific journal.

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Mitigating fisheries-induced evolution in lacustrine brook charr in southern Quebec

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Goal

To develop a comprehensive fisheries management policy that mitigates fisheries-induced evolution in lacustrine brook charr populations in southern Quebec.

Background and motivation

Size-selective mortality due to fishing can impose strong selection on harvested fish populations, causing evolutionary changes in key life-history traits such as size at maturation (e.g., Swain et al. 2007). Understanding and predicting harvest-induced evolutionary change is crucial for the long-term maintenance of sustainable fisheries (e.g., Jørgensen et al. 2007). In this project, I will investigate optimal management strategies for an evolutionarily sustainable fishery of the lacustrine brook charr (*Salvelinus fontinalis*) in southern Canada. Brook charr inhabit a series of lakes, some of which are harvested, while some are not (Magnan et al. 2005). This provides an ideal model system for investigating harvest-induced evolutionary changes and developing management strategies that mitigate such changes. Using data collected over the years on brook charr ecology by the Research Group on Aquatic Ecosystems at l'Université du Québec à Trois-Rivières, I parameterized an eco-genetic model (akin to the approach of Dunlop et al., submitted) with the aim of investigating the effects of harvesting on life-history variation in brook charr populations. The important next step will be to elucidate optimal management strategies for the brook charr populations.

Research questions

The goal of this research project is to develop a comprehensive fisheries management policy to slow down or reverse ongoing and past evolutionary change due to harvesting practices, and to minimize the risk of future change by improving these practices. More specifically, we will address the following questions:

- How can fisheries managers manage fishing effort to minimize future evolutionary change in brook charr populations?
- How does the translocation of individuals with late-maturing genes from unharvested to harvested lakes curtail ongoing evolutionary change in the latter?
- How can these two strategies be effectively combined?

Methods and work plan

Akin the approach of Dunlop et al. (submitted), the eco-genetic model for this project will follow an individual-based implementation (e.g., DeAngelis and Mooij 2005).

Ecological model

I will consider a population of brook charr that inhabit a single lake with a single dynamic resource (e.g., zoobenthos). While the charr are modeled individually, the resource is not, and in each lake the resource density grows according to a logistic growth curve in the absence of charr predation. The charr consume the resource, and thus grow in both weight and length. Somatic growth is density-dependent, and thus slows down when resource availability is low. A proportion of mature individuals reproduce once a year, depending on whether they consumed enough food during the year to allocate energy reserves to gonadal mass. Brook charr are iteroparous, and reproduce two to three times after they mature. An individual's size at maturation is a function of both genetic and environmental effects. Following the approach described in Dunlop et al. (submitted), I will assume that maturation is governed by a probabilistic maturation reaction norm (PMRN; Heino et al. 2002), describing the weight- and age-specific probabilities of maturation in a given season. At the beginning of a given mating season, the probability that an individual of age a , sex g , and size w_a is mature is given by $p_m = [1 + \exp(-(w_{a,g} - w_{p50,a,g})/d)]^{-1}$, where $w_{p50,a,g} = i_g + as_g$ describes the PMRN midpoint (i.e., the weight at which 50% maturation probability is reached) at age a for sex g , and d is a constant that describes how steeply p_m changes around the midpoint. The quantities i_g and s_g are sex-specific evolving traits (see below). Sex is assigned randomly at birth. All individuals suffer a size-specific risk of fishing mortality and natural mortality, with the latter representing both density-independent mortality (e.g., predation by aquatic birds such as cormorants) and density-dependent starvation mortality.

Genetic model

Each individual charr carries a diploid genome. An individual's evolving trait values are determined by the additive effect of between 1 and 25 autosomal loci. All loci are weighed equally, with the initial allelic values at each locus for the evolving traits i_g and s_g being drawn randomly between 0 and M_i/n or M_s/n , respectively, where n is the number of loci. All loci are freely recombining, although the number of loci can be interpreted as characterizing tight linkage groups. To assess the effects of neutral processes such as genetic drift on the evolving populations each locus will have a neutral counterpart that has the same initial allelic value and is subject to the same mutation rate, but plays no part in determining the individual's phenotype, and thus does not affect fitness. Time permitting, I will also examine the sensitivity of the model's predictions to the genetic architecture of the evolving traits determining the PMRN: in particular, I will consider the effects of epistasis and dominance (e.g., Roff 1997). Mature males and females are paired up at random, with individual males being able to pair up with more than one female during the mating season (e.g., Thériault et al. 2006). Prior to reproduction, each parent produces a haploid gamete that contains, at random, half the parental alleles. With a small mutation probability (ca. 10^{-6}), the allelic value at a locus changes by a random amount drawn from a normal distribution with zero mean and a standard deviation that is proportional to M_i/n or M_s/n , with allelic values being bounded from below by 0. The gametes of each parent fuse to determine the genotype of the offspring. This approach follows the model of Strand et al. (2002) and the individual-based implementation of van Doorn

and Dieckmann (2007). For the sake of simplicity, I will assume that life-history traits other than size at maturation (such as offspring size, maternal investment in gonadal mass, and rates of somatic growth) are not subject to evolutionary change.

Model analysis

I will run the model for 2000 years to allow populations to attain their demographic and evolutionary equilibrium. Subsequently, I will compare the predicted evolving traits i_g and s_g to those observed in the field (e.g., Hendry 2003). This allows a direct comparison of the predictions of the eco-genetic model in the absence of harvesting to values observed in nature, thereby providing a measure of the model's capacity to mirror the system's ecological and evolutionary processes. Afterwards, I will run the model for a further 50 years with a given harvesting strategy. I will also run the model for entire 2250 years without harvesting in order to characterize its baseline behavior.

The first management policy I will investigate is based on harvesting that optimizes annual fishing effort. This is the level of fishing effort that maximizes the number and size of individuals harvested each year, while minimizing the risk of harvest-induced evolutionary change. Since increasing fishing yield is bound to increase harvest-induced evolutionary change, the goals of this policy imply a trade-off. I will employ a genetic algorithm (e.g., Taylor and Hastings 2004) to determine the optimal harvest strategy that strikes the best balance between these competing objectives. Considering a 50-year time frame, I will examine 100,000 harvest strategies initially sampled from a multivariate uniform distribution. Each harvest strategy is characterized by five parameters, $\{\alpha, \beta, a, b, c\}$. The first two parameters determine the size-dependence of harvesting. Specifically, selectivity at weight w is assumed to be proportional to $p_f = [1 + \exp(\alpha + \beta w)]^{-1}$. The last three parameters determine the density-dependence of harvesting. In particular, the total allowable catch in year t is assumed to be given by $Y_t = a + bH_t + cH_t^2$ (Eikeset et al., in preparation), where $H_t = \sum_i w_{i,t} p_{f,i,t}$ is the harvestable biomass in year t , with the sum extending over all fish i . The fishing season is assumed to lie between the growing season and the mating season. The annual probability of a fish at weight w to get harvested is thus given by $p_f Y_t / H_t$. This probabilistic treatment implies sampling variation in annual catches Y_t .

At the end of each simulation for a harvest strategy, I will calculate the strategies success as $Y/(1 + \delta/\delta_0)$, where $Y = \sum_t Y_t$ is the biomass of fish captured over all years, δ is the average relative amount of evolutionary change the evolving traits, and δ_0 determines the sensitivity of this success measure to changes in δ . Thus, when there is no evolutionary change, so that $\delta = 0$, a strategy's success is measured by its cumulative yield, while evolutionary change amounting to $\delta = \delta_0$ implies that the strategy's success is halved. I will then rank the harvesting strategies according to their success to determine the 100 best strategies, and generate 100,000 permutations of these 100 best strategies with free "recombination" between the five parameters determining the strategies. I will iterate this process until no better harvesting strategy can be generated.

Time permitting, I will use this modeling framework to examine a second management policy that involves the translocation of individuals with larger-maturing genes from unharvested to harvested lakes. I will subject the harvested lake to the optimal harvesting strategy determined from the analysis described above. I will then

begin to analyze translocations from a single unharvested lake into a harvested lake. While gene flow between populations mitigates the potential for local evolutionary divergence, conserving genetic resources requires minimizing the amount of artificial genetic contamination. I will use the eco-genetic model to determine (i) the degree to which translocations allow brook charr populations to recover intra-population allelic diversity at the loci controlling for maturation probability, should such diversity have been lost to harvesting, and (ii) the degree to which translocations promote genetic homogenization across populations at loci for traits other than the maturation probability. This policy once again implies two competing objectives. As before, I will utilize a genetic algorithm, now to optimize a strategy's success $h/(1 + \delta/\delta_0)$, where h is a measure of genetic homogeneity (such as F_{st}) between the two lakes at neutral loci.

Relevance and link to EEP's research plan

Characterizing and predicting the extent of fisheries-induced adaptive change is a main goal for the research project on *Evolutionary Fisheries Management* of the Evolution and Ecology Program at IIASA. Linking existing theoretical approaches to data is crucial if we are to generate comparative predictions on the evolutionary effects of different fishery-management strategies. This work aims to develop a general framework that can be readily be used by stakeholders and other policy-makers to design a wide range of strategies that manage the risk of fisheries-induced adaptive change.

Expected output and publications

I anticipate the results of this work to be presented as co-authored research articles. They will also be used as a chapter in my PhD dissertation.

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Evolution of conditional dispersal in structured populations

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Goal

To investigate the influence of population structure, both self-generated and environmentally imposed, on the evolution of conditional dispersal in asexual and sexual populations.

Background and motivation

Dispersal is a topic of paramount importance in theoretical ecology (Dieckmann et al. 1999; Levin et al. 2003) influencing species abundances and distributions, population dynamics, genetic diversity, and the evolution of reproductive isolation. While dispersal is costly, theoretical investigations have demonstrated its selective advantage in numerous situations, e.g., to avoid kin competition (Lambin 2001) and inbreeding (Perrin 2001), and to escape local catastrophes in temporally or spatially varying environments (Kun & Scheuring 1997). The majority of these theoretical models assume *unconditional* dispersal (e.g., Travis & Dytham 1998), such that dispersal is characterized by a single global variable, typically defined as the dispersal rate or as the dispersal probability during a generation. While unconditional dispersal may occur in some cases, there is ample empirical evidence that dispersal is *conditional* in many species (see, e.g., references in Travis et al. 1999). In particular, the probability of an individual emigrating from its current patch may be contingent upon local conditions.

Recently, there has been a growing interest in the development of theoretical models of the evolution of conditional dispersal (e.g., Janosi & Scheuring 1997; Travis et al. 1999; Kun & Scheuring 2006; Bach et al. 2007), wherein an individual's probability of emigration is characterized as a function of local conditions, such as the local density of conspecifics or the local availability of acceptable mates. The functional form of this conditional dependence has often been assumed *a priori*, such that only a few parameters controlling the shape of the function were allowed to evolve. For example, Travis et al. (1999) assumed a linear density-dependent dispersal strategy and allowed its slope and intercept to evolve, whereas Bach et al. (2007) assumed a sigmoidal density-dependent dispersal strategy and allowed its steepness and half-saturation density to evolve. While prescribing a particular functional form for the dispersal function may be appropriate in some cases, it can severely limit the search space of available functions, and may therefore systematically bias the search for an evolutionary stable dispersal strategy. Kun and Scheuring (2006) recently investigated a more general, three-parameter density-dependent dispersal strategy, which could capture numerous qualitatively different shapes (including linear and sigmoidal). However, even in this case, the evolving function, which in principle is infinite-dimensional, has been reduced to a three-dimensional vector-valued trait, and such low-dimensional parameterizations are known to lead to spurious outcomes in certain

situations (Dieckmann et al. 2006). In contrast, *function-valued traits* characterize phenotypic variation along a continuum, and naturally allow for the evolution of arbitrary functional relationships (Dieckmann et al. 2006). Representing conditional dispersal as a function-valued trait may therefore avoid some of the aforementioned biases and allow for the full exploration of the space of possible functional forms. Surprisingly, the formulation of conditional dispersal as a function-valued trait has yet to be undertaken.

Dispersal models typically treat space either (i) as being continuous in two dimensions with local interactions and dispersal or (ii) as a metapopulation of discrete and internally well-mixed populations coupled by dispersal. Environmental variability is often introduced as random noise with spatial heterogeneity. In contrast to random environmental variation, gradual environmental gradients along continuous spatial dimensions have also proven to be an interesting avenue of investigation (Doebeli & Dieckmann 2003; Leimar et al. 2008); e.g., environmental gradients have been shown to facilitate the evolution of reproductive isolation under parapatric conditions close to sympatry (Doebeli & Dieckmann 2003). As previous studies have demonstrated that random environmental variability plays an influential role in the evolution of conditional dispersal mechanisms, gradual environmental gradients may be expected to affect the evolution of conditional dispersal and, thus, the eventual functional form of the evolving dispersal strategy.

When studying dispersal in metapopulations, it is often assumed that the involved populations are arranged on a regular graph, typically a two-dimensional lattice with periodic boundary conditions (e.g., Travis & Dytham 1998; Travis et al. 1999; Kun & Scheuring 2006; Bach et al. 2007). However, this assumption of topological regularity is an oversimplification when populations are embedded in heterogeneous interaction networks. In particular, some populations will often be more highly connected than others. In related contexts, such as epidemiology and evolutionary game theory, the inclusion of heterogeneous interaction networks has been shown to dramatically impact ecology and evolution. For example, scale-free network structures (Barabási & Albert 1999) promote the evolution of cooperation in the graph-based prisoner's dilemma (Santos & Pacheco 2005), and hierarchical metapopulation structures promote the emergence of multiscale resurgent epidemics in the classical susceptible-infectious-recovered model of disease spread (Watts et al. 2005). In the context of conditional dispersal, the inclusion of such complex population structures has yet to be investigated.

Research questions

With this project, and its potential continuation after the summer, we plan to address a succession of research questions:

- Does the representation of the conditional dispersal rate as a function-valued trait lead to the evolution of dispersal functions not found in previous studies?
- When populations are self-structuring in continuous and homogeneous habitats, is evolution still expected to lead to density-dependent dispersal that is low below a threshold density and high above it?

- How is the evolution of conditional dispersal affected by local adaptation along environmental gradients?
- How does the evolution of conditional dispersal reconcile the mutually conflicting goals of escaping the local crowding by conspecifics and the local scarcity of acceptable mates?
- How do topological properties of complex metapopulation structures, such as assortativity and hierarchical organization, affect the evolution of conditional dispersal?

Methods and work plan

Work plan

The main steps in this project are as follows:

- First, we will develop an evolutionary model of conditional dispersal in a two-dimensional continuous and homogeneous habitat. Conditional dispersal will be described as a function-valued trait based on the local density of conspecifics. To avoid the confounding effects of sexual reproduction, we will initially assume that individuals reproduce, and thus inherit their phenotypic traits, asexually.
- Second, we will include an environmental gradient along which individuals can exhibit local adaptation. Conditional dispersal will be based on local environmental quality, which in turn is affected by local carrying capacity and the local density of phenotypically similar conspecifics.

Time permitting, we will extend this model as follows:

- We will include sexual reproduction and assortative mating, with conditional dispersal being based on local environmental quality and the density of acceptable mates.
- We will investigate the impact of various topological properties of metapopulation structures on the evolution of conditional dispersal.

Evolving traits

The dispersal strategy of an individual will be represented as a function-valued trait (Dieckmann et al. 2006), describing its dispersal rate (or, alternatively, its dispersal distance) in response to one or more arguments. Initially, this function will be contingent upon just a single argument: the local ratio of competition pressure to carrying capacity. Subsequently, a second argument may be included: the local density of acceptable mates.

In the presence of an environmental gradient, an individual will be assumed to possess another evolving trait determining to which location along the gradient it is best adapted (Doebeli & Dieckmann 2003).

Population structures

In the first part of this project, we will assume that individuals are located in a two-dimensional continuous habitat, in which the phenotype-dependence of carrying capacity changes along an environmental gradient (Doebeli & Dieckmann 2003). We will assume periodic boundary conditions, and in order to avoid an abrupt discontinuity in the environmental gradient at the boundaries, we will employ a smooth gradient that peaks at the center of the spatial domain and implies identical environmental con-

ditions at its two ends. Such a gradient could be described by e.g., a sinusoidal function.

Subsequently, metapopulation structure will be represented as a graph $G = (V, E)$, where V is the set of vertices, denoting individual populations, and E is the set of edges, denoting possible dispersal routes between them. For example, an individual situated in population $i \in V$ may disperse to population $j \in V$ if $(i, j) \in E$. When investigating irregular population structures, we plan to explore random graphs with varying degrees of assortativity and hierarchical metapopulation models:

- A random graph consists of N vertices, such that an edge is formed between each vertex with some probability p . Assortativity r is informally defined as the affinity with which vertices of similar degree (number of neighbors) connect to one another (see Newman 2002 for a formal definition). In *assortative* graphs ($r > 0$) vertices of similar degree are more likely to be connected to one another, whereas in *disassortative* graphs ($r < 0$) vertices of dissimilar degree are more likely to be connected to one another. The assortativity of graphs will be tuned using the method provided by Payne & Eppstein (2008).
- A hierarchical metapopulation structure, as described by Watts et al. (2005), is defined as follows. Populations are hierarchically organized on a tree, such that the probability that population i is connected to population j is given by $p_{ij} \propto \exp(-x_{ij} / \zeta)$, where x_{ij} is the distance (i.e., the number of edges along the tree) between population i and population j , and ζ is a parameter that determines the attenuation of connection probability with distance.
- Other complex metapopulation structures of practical interest could also be investigated, such as small-world (Watts & Strogatz 1998) and scale-free (Barabási & Albert 1999) graphs. Further, other relevant topological properties (such as community structure; Newman 2006) could be systematically investigated. Moreover, directed graphs could be considered, in which dispersal routes can be traversed in only one direction.

Population dynamics

Population dynamics will follow those described by Doebeli & Dieckmann (2003). An asynchronous, individual-based stochastic model will be developed in which time is continuous and generations overlap. The initial population will consist of a single, randomly chosen ancestral phenotype. Individuals will be assigned birth, death, and dispersal rates; the time lapse between these events will be drawn from an exponential distribution with a mean equal to the inverse of the sum of the event rates of all individuals. Individuals will be chosen to take part in the selected event probabilistically, in proportion to their corresponding rates. Birth and death events will be handled as by Doebeli & Dieckmann (2003). For birth under asexual reproduction, the offspring will undergo mutation with some small probability; otherwise, the offspring will inherit the parental phenotype faithfully. For birth under sexual reproduction, the offspring phenotype will be drawn from a normal distribution around the mid-parental phenotype. Under sexual reproduction, we will assume a fixed degree of assortative mating, with the mating probability between two local-adaptation phenotypes being given by a normal distribution. Initially, Gaussian competition kernels will be assumed, but the sensitivity of our results to this assumption will be tested by investigating leptokurtic competition kernels as well.

Relevance and link to EEP's research plan

This work contributes to two of the research projects of the Evolution and Ecology Program at IIASA. Specifically, investigating the interplay between population structure and conditional dispersal is relevant to EEP's projects on *Adaptive Dynamics Theory* and *Evolving Biodiversity*. As discussed in EEP's research plan, advancing general insights into spatially structured evolutionary processes (Task 1.1) and developing and applying new techniques for simplifying spatial complexity (Task 1.2) are major goals of the program. By gaining an understanding of the important influence of population structure on the evolution of conditional dispersal, the proposed research has the potential to contribute to both of these goals.

Expected output and publications

The results of this research will be communicated through co-authored publications in international scientific journals, and may be included in my Ph.D. dissertation.

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Coevolution of cooperation and volunteering in public goods games

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Goal

To investigate the coevolution of cooperative investment and volunteering in general public goods games with nonlinear payoff functions.

Background and motivation

In modern societies, individuals often have a large degree of freedom and anonymity. This allows individuals to get away not only with free-riding on the efforts of others, but also with opting out from participating in cooperative enterprises altogether. An enduring conundrum in the biological and social sciences is how cooperation can emerge and be maintained in the presence of free-riders. The nature of this conundrum is illustrated by the well-known public goods game (PGG; Kargel and Roth 1995), in which groups of cooperators outperform groups of defectors, whereas defectors always outperform cooperators in any mixed group (Dawes 1980). When the PGG is played once, defection is the rational choice, but many theoretical and experimental investigations have identified supportive mechanisms such as reciprocal interactions (e.g., Axelrod and Hamilton 1981; Nowak and Sigmund 1993), spatial structure (e.g., Nowak and May 1992; Killingback et al. 1999), and reputation (e.g., Nowak and Sigmund 1998; Wedekind and Milinski 2000) under which cooperation is nonetheless sustained.

Voluntary participation is another possible mechanism that may allow cooperation to be sustained in the presence of free-riders. However, despite this being one of the most natural options that can be justified *a priori* even under complete anonymity, it has so far been considered in only a handful of studies (e.g., Hauert et al. 2002a, 2002b, 2007; Semmann et al. 2002). These studies investigated a classical PGG in which individuals could cooperate, defect, or opt not to participate in the game altogether, instead relying on a small but fixed payoff. The evolutionary dynamics of these three pure strategies can resemble the “rock-scissors-paper” cycle known from evolutionary game theory, and thus prevent populations from ending up with 100% defection. Moreover, the freedom of opting out from the game can pave the way for the emergence and establishment of cooperative behavior based on the punishment of defectors (Hauert et al. 2007).

While supportive mechanisms such as voluntary participation can explain why a significant number of cooperators may be present in a population, they do not explain how the pure strategies under consideration emerged in the first place. Doebeli et al. (2004), exploring this question for the related ‘snow drift’ game, showed that two pure strategies corresponding to cooperation and defection readily emerge as a consequence of gradual evolution of a continuously varying cooperative investment.

In a similar spirit, rather than assuming *a priori* the existence of discrete behavioral strategies, in this project we will consider individuals with continuously varying

and gradually evolving cooperative investments and participation rates (Sasaki et al. 2007), leading to a new model, describing a continuous voluntary PGG. Furthermore, following Doebeli et al. (2004) and Brännström et al. (in preparation), we will consider nonlinear payoff functions, which naturally leads to a more general and, as yet, largely unexplored class of PGGs. This will not only allow us to explore the coevolution of cooperation and volunteering from a broader perspective, but is also likely to shed new light on processes of two-dimensional evolutionary branching that are attracting increasing attention (e.g., Vukics et al. 2003; Ito and Dieckmann 2007).

Research questions

The main purpose of this project is to study two-dimensional evolutionary dynamics in the continuous voluntary PGG with a general nonlinear payoff function, instead of the traditional linear form.

Our specific research questions are as follows:

- What are the effects of nonlinear payoff functions on the fitness landscape emerging from the continuous voluntary PGG, and on the evolutionary stability of its singular strategies?
- What kind of evolutionary diversification happens in the vicinity of the singular strategies? Is there a possibility of trimorphic evolutionary branching, gradually leading to the three pure strategies that have been assumed *a priori* in previous studies?
- What plausible mechanisms give rise to nonlinear payoff functions? Can these be integrated as special cases in an overarching mathematical framework?

Methods and work plan

In the continuous voluntary PGG that we consider in this project, each individual has a strategy consisting of two continuously varying trait values, (c, w) , where c represents the level of cooperative investment a participating individual offers in the game, while w measures the willingness to participate in the game. The model considers a large and well-mixed population of constant size, whose members live on a small but fixed income. At the beginning of each game, $N > 2$ individuals $i = 1, \dots, N$ are randomly selected and offered the option of participating in the game. To this, each individual agrees with probability $p_i = p(w_i, \bar{w})$, where \bar{w} denotes the average participation willingness in the population. After a group of k participants has thus been formed, each participant invests an amount c_i ($1 \leq i \leq k$) towards a public good. The population's benefit from this public good is denoted by $B(c_1 + \dots + c_k)$ and hence depends on the group's total cooperative investment. This benefit is then shared equally among all k participants. Specifically, each participant's payoff is determined as a net benefit, obtained by subtracting his or her cost, $C(c_i)$, from his or her benefit, $B(c_1 + \dots + c_k)/k$. In the traditional linear case, it is assumed that $B(c_1 + \dots + c_k) = r(c_1 + \dots + c_k)$ and that $C(c_i) = c_i$. The payoff of nonparticipants is fixed at σ and is independent of the outcomes of the game. If there is only one participant, we assume that this single player has to act as a nonparticipant and therefore receives the payoff σ .

We will use adaptive dynamics techniques (Dieckmann and Law 1996; Geritz et al. 1998) to analyze the evolution of the two-dimensional continuous strategy (c, w) . For this purpose we will consider the invasion fitness $S(y, x)$ of a rare mutant with strategy $y = (c_y, w_y)$ in a monomorphic resident population with strategy $x = (c_x, w_x)$. The growth rate of the mutant will be proportional to $S(y, x)$ and the evolution will be governed by the canonical equation of adaptive dynamics (Dieckmann and Law 1996). Assuming replicator dynamics, we have that $S(y, x) = P(y, x) - P(x, x)$, where $P(y, x)$ and $P(x, x)$ denote the expected payoff of a mutant within the resident population and the average payoff in the resident population, respectively. This yields

$$P(y, x) = p_y g(y, x) + (1 - p_y) \sigma,$$

where $p_y = p(w_y, w_x)$, while $g(y, x)$ denotes the expected payoff of the mutant participating in the game. Then, $g(y, x)$ is given by

$$g(y, x) = (1 - p_x)^{N-1} \sigma + \sum_{k=2}^N \binom{N-1}{k-1} (1 - p_x)^{N-k} p_x^{k-1} \left[\frac{B((k-1)c_x + c_y)}{k} - C(c_y) \right],$$

where the first term denotes the expected payoff if there is no co-player, the second term the expected payoff if there is at least one co-player, and the square bracket the net payoff to the mutant in a group of $k-1$ resident players ($k > 1$). Regardless of specifications of the functions $p(\dots)$, $B(\dots)$, and $C(\dots)$, we obtain a Taylor expansion of $S(y, x)$ around the resident strategy as

$$S(y, x) = a_{10}(x)(c_y - c_x) + a_{01}(x)(w_y - w_x) + \underbrace{\sum_{i,j=1}^{\infty} a_{ij}(x)(c_y - c_x)^i (w_y - w_x)^j}_{(A)},$$

with coefficients

$$a_{10}(x) = p_x \left. \frac{\partial g}{\partial c_y} \right|_{y=x}, \quad a_{01}(x) = (g(x, x) - \sigma) \left. \frac{\partial p_y}{\partial w_y} \right|_{y=x}, \quad \text{and} \quad a_{ij}(x) = \left(\frac{\partial^i g}{\partial c_y^i} \frac{\partial^j p_y}{\partial w_y^j} \right)_{y=x}$$

for $i, j \geq 1$.

We will first explore what general insights we can obtain without as yet specifying in detail any of the functions above. Note that when all the functions are linear with respect to the mutant strategy, the higher-order terms (A) above are reduced to $a_{11}(x)(c_y - c_x)(w_y - w_x)$, so that $S(y, x)$ is described by a hyperbolic paraboloid.

Second, we will consider a simple nonlinear functional form for the benefit derived from the group's total investment as $B((k-1)c_x + c_y) = r[(k-1)c_x + c_y]^a$, while keeping $C(c_y) = c_y$ and $p_y = p(w_y, w_x) = w_y$ linear. The exponent a determines the degree of nonlinearity and, in particular, whether the marginal common benefit increases ($a > 1$) or decreases ($a < 1$) with the group's total cooperative investment. In the parameter space (N, r, a) , we will explore the evolutionarily singular strategies x^* of the game's adaptive dynamics, given by a vanishing selection gradient, $D(x^*) = \partial S(y, x^*) / \partial y|_{y=x^*} = 0$. Then, if an evolutionarily singular strategy exists, we will apply standard stability analysis by calculating the Jacobian $J(x^*) = \partial D(x) / \partial x|_{x=x^*}$. For convergence stable strategies, which are characterized by a dominant eigenvalue of $J(x^*)$ that has a negative real part, we will then investigate whether there exist directions through x^* along which $S(y, x^*)$ is minimized at x^* , which would imply a lack of local evolutionary stability and thus a potential for evolutionary branching at x^* (Geritz et al. 1998).

Regarding the third research question mentioned above, we will consider simple and plausible mechanisms that may introduce nonlinearities in costs and participation probabilities, such as switching costs, costs for deviating from the majority, and a bias of participation towards the population's mean. The nonlinear functional forms arising from these considerations will be analyzed in the same spirit as the special case described above. Drawing from the insights derived from the specific explorations, we will finally try to integrate all special cases into a comprehensive mathematical framework.

Time permitting, we will complement the mathematical and numerical analysis of the canonical equation with an individual-based model, in which many simplifying assumptions, such as rare and small mutational steps and monomorphic resident populations, are readily relaxed.

Relevance and link to EEP's research plan

This project directly contributes to EEP's research project on the *Evolution of Cooperation*, which has recently highlighted the importance of voluntary participation (Hauert et al. 2002a, 2002b). The project will use adaptive dynamics techniques that have largely been developed by researchers associated with EEP's research project on *Adaptive Dynamics Theory*. The project is expected to increase our understanding of conditions under which cooperation can evolve, and may, moreover, provide an improved theoretical basis for studying the emergence of costly punishment (Hauert et al. 2007).

Expected output and publications

The research is intended for publication as a coauthored article in an international scientific journal and will form an essential part of my PhD thesis.

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