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**Eight Research Projects**

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# **Analysing the Potential for Genetic Change in Pike Populations Exploited by Recreational Fisheries**

Robert Arlinghaus

*Leibniz Institute for Freshwater Ecology and Inland Fisheries,  
Berlin, Germany*

## **Goal**

To analyze the possibility for recreational fishing to induce genetic changes in exploited fish populations, and thereby to increase awareness of such potential among stakeholders and stimulate increased research effort and long-term monitoring of fish populations exploited by angling fisheries.

## **Background and motivation**

As a result of selective (i.e. non-random) mortality, exploitation of wild living resources can directly or indirectly act as an (often overlooked) evolutionary force (Stokes et al. 1993; Law 2000; Palumbi 2001; Ratner and Lande 2001; Heino and Godø 2002; Coltman et al. 2003; Ernande et al. 2003). Fishing-induced selection has been identified as having the potential to alter the genetic architecture of fish populations, leading to changes in stock properties such as long-term yield and demographic traits such as size and age at maturation or growth rate (Ricker 1981; Law & Grey 1989; Heino 1998; Conover & Munch 2002). Although much of the available evidence of a potential evolutionary effect is still inconclusive, it seems necessary to include its implications in sustainable fisheries management strategies (Law 2000; Heino & Godø 2002). This, *inter alia*, results from the precautionary approach to fisheries management and the internationally binding Convention on Biodiversity that demand that fishing effects should be reversible, and not irreversibly alter biodiversity of evolving natural resources, neither at the level of species nor communities.

Until now, empirical and theoretical research on potential adaptive change induced by fishing has mostly focused on commercial exploitation in the marine environment or in anadromous fish (see Borisov 1979; Ricker 1981; Policansky 1993; Law 2000; Heino and Godø 2002 and references therein). In industrialized countries of the temperate regions, recreational fisheries (angling) systems constitute important socio-ecological systems that involve millions of people exploiting thousands of different freshwater fish stocks (Arlinghaus et al. 2002). As a result, substantial social and economic benefits are generated (Arlinghaus 2004a, 2004b). But the ecological and evolutionary impacts of angling fisheries are less well understood. Furthermore, the systems' behavior and management has not been studied thoroughly, and most research on recreational fisheries appears parochial, with a strong national orientation and relatively small frames of reference in terms of theory, concepts, models, and empirical bases (Aas 2002).

As ecological processes and anthropogenic impacts of fisheries can only be understood at a more regional or local level, recreational fisheries systems provide an alternative to analyze fishing-induced genetic changes and natural resource-people interactions. As such, the development of predictable models in recreational fisheries

would increase our understanding of the interplay between social and ecological systems and expand the awareness of potential fishing-induced genetic change to the angling environment, particularly in freshwater ecosystems. Some features of angling practices such as the release of caught fish are unique in recreational fisheries, which limit the transfer of management systems and research results from commercial to recreational fisheries (Arlinghaus et al. 2002). In addition to direct angling mortality and despite high rates of catch-and-release angling in many recreational fisheries (Policansky 2002), substantial hooking mortality (Munoeke & Childress 1994) or sublethal physiological and fitness alterations (Cooke et al. 2002) may occur in recreational fisheries, leading to opportunities for angling selection to operate even without physical harvest. Therefore, as regards recreational fisheries specific models have to be developed or established ones tuned and predictions have to be tested empirically.

One might be tempted to assume that angling impacts are less severe than commercial impacts. However, this assumption is flawed under conditions of high angling effort, hence impact, which is particularly strong near metropolitan centers or in areas with limited angling waters available (Post et al. 2002; McPhee et al. 2003). Angling mortality as fishing mortality in general is strongly size-dependent, which is the result of the typical higher interest of anglers in larger fish (Arlinghaus 2004a, 2004b) and the fact that most recreational fisheries are managed based on some variants of size and bag limits (Arlinghaus et al. 2002). Typically, minimum-size limits are applied that allow for harvest of species that have spawned at least once in a lifetime. Minimum sizes are usually set to ensure that (most of) the population has reached maturity and has spawned before being allowed to be harvested by anglers. Consequently, annual exploitation rates of popular angler species such as pike (*Esox lucius*) were found to be 2 to 9 times larger in large pike (> 50 cm) above the minimum size as compared to smaller individuals (< 50 cm) (Pierce et al. 1995). Comparatively low effort of 1.24 angler-hours/ha already removed 50% of the annual adult pike production in small lakes in the United States (Mosindy et al. 1987). In rainbow trout (*Oncorhynchus mykiss*) fisheries in Canada, Cox and Walters (2002) reported maximum exploitation rates of between 0.21 and 0.81%. In these lakes, critical angling effort was found to be in the low range of observed angling effort, which indicates that population overfishing may be possible. Recently, Post et al. (2002) found evidence of fish population collapses in four high profile recreational fisheries in Canada. Altogether, it has been suggested that selective angling mortality can be one of the most important variables in structuring freshwater fish populations (Beard & Essington 2000), typically reducing the mean age and size of the exploited population (Goedde and Coble 1981; Olsen and Cunningham 1989). However, it is important to note that there are also many examples of recreational fisheries where angling effort on adult fish is rather low and negative effects may be negligible (e.g., Beard et al. 2003 for walleye *Sander vitreum* fisheries in Wisconsin). Thus, the evolutionary effects of angling are not likely to impact every fishery.

The current call for an “evolutionarily enlightened management” (Ashley et al. 2003) demands in-depth studies in recreational fisheries, as life-history evolution may take place on contemporary (i.e. less than a few hundred generations, sometimes only decades) time scales under heavy exploitation (Conover and Munch 2002; Haugen and Vøllestad 2001; Koskinen et al. 2002; Stockwell et al. 2003). There are important

specificities of recreational fisheries that such an analysis of potentially angling-induced genetic change has to take into account:

1. Harvesting goals (e.g. escapement of a certain abundance of fish to reproduce, or quota systems) are rarely in place in recreational fisheries. There is almost no monitoring and no long-term data sets are available.
2. Angler predominantly target and remove top predators of the food webs such as pike, largemouth bass (*Micropterus salmonides*), walleye, or salmonids. Top predators encompass species that itself suffer from comparatively low predation pressure (e.g. predation by other piscivores) but are often dependent on the density of their prey. Larger mature individuals of these species that have survived bottlenecks in juvenile stages should be the fittest in the given environment.
3. Selectivity among mature animals above minimum size limit may be low (Mosindy et al. 1987; Raat 1991; Cox 2000). That is, a certain proportion of individuals of the whole (mature) stock is harvested each year with positively density-dependent mortality. Literature data on “moderate” exploitation (e.g. 20-80% of stock harvested per year) is available and should be taken for simulation.
4. Exceptions to the statement above are trophy fisheries, where only the largest fish are taken home and other fish are released. Hooking mortality in catch-and-release of smaller fish (smaller than trophy size, which is situational and dependent on the angler’s perception) may become important.
5. In recreational fisheries, there is probably no selective exploitation in spatially different spawning grounds to select for late maturation as proposed by Heino (1998) for cod (*Gadus morhua*). Thus, catching immature fish will always occur, although presumably at lower rates as compared to mature fish.
6. Immature fish are usually caught and released (legal requirement), although illegal harvest has been documented (Gigliotti and Taylor 1990; Sullivan 2002). Here, hooking mortality and non-compliance mortality is crucial and may be important for evolutionary change in maturation that is supposed to be lower if immature individuals are mostly below the size limit (Ernande et al. 2003). Literature data on hooking mortality and non-compliance mortality rates for some species is available.
7. In recreational fisheries, bycatch is usually negligible or returned alive to the water.
8. Catch-and-release makes fish harder to catch due to learning or change in behavior (Raat 1985).
9. Angling catchability (i.e. the proportion of stock vulnerable to angling) can be either negatively density-dependent (lake trout, Shuter et al. 1998) or density-independent (e.g., walleye, Hansen et al. 2000).

10. Due to high mobility and efficiency of anglers, it is assumed that the whole stock of fish is vulnerable to anglers. However, some fish may be temporarily not vulnerable, e.g. satiated fish (Cox and Walters 2002).
11. Mortality of mature (e.g. above minimum size) individuals in recreational fisheries may lead to high abundances and productivity of smaller fish not desired by anglers (Pierce et al. 1995). Thus, although individual growth rates of smaller fish may increase due to increased prey abundance or decrease due to competition or reduced size-at-maturation, the productivity of the whole stock may be stable, but mean size in the population will decrease. Potential new resources available due to reduced density will be consumed by the smaller variety of the same species or by other species. Higher abundances of smaller fish will reduce economic benefits and induce angler dissatisfaction. Anglers may ultimately leave the fishery or respond by enhanced stocking, thus confounding the detection of fish stock declines. Biomass of desired size classes will be greatly reduced in the long-term. Some fish species such as pike show signs of self-regulation via cannibalism.
12. Angling vulnerability was found to be a heritable trait in largemouth bass ( $h^2 = 0.34$ , Phillip et al., unpublished manuscript). Relative to other traits that are known to be heritable, angling vulnerability appears to have one of the higher heritabilities. The response to selection increased with each generation, and was found to be correlated with a cumulative selection differential reflecting the increased magnitude of difference between highly vulnerable and less vulnerable fish with each successive generation. Highly vulnerable and less vulnerable bass differed in important fitness traits (Cooke, unpublished manuscript). Angling vulnerability covaried with factors including higher metabolic rates, reduced metabolic scope and increased parental care activity. However, growth rates of highly vulnerable and less vulnerable fish were not different. Angling may lead to “mortality of the fittest” if highly vulnerable fish are selectively removed.

## Research questions

In my summer project I plan to focus on the following questions:

1. Under the conditions encountered in most angling fisheries (explained above), is genetic change for younger age-at-maturation, smaller size-at-maturation, increased reproductive effort, or reduced growth rate conceivable?
2. Which of the traits mentioned above experience the strongest selection differentials in fish populations typically exploited by anglers? The fish species chosen for a case study will be pike (*Esox lucius* L.) which is highly demanded by many anglers in the temperate regions (e.g., Arlinghaus and Mehner 2004).

## **Methods and work plan**

The approach used in this project is twofold.

First, a detailed model of the population dynamics of pike will be constructed that integrates the functional relationships between selected adaptive traits and the population demography as a whole given certain (natural and fishing) mortality rates in a particular pike fishery. Deterministic matrix population models for structured populations will be used (Caswell 2001). The advantage of this approach is that matrix models are relatively easy to construct. They classify a population into discrete stages (e.g. age or length classes) and project abundance in these stages in discrete time. All individuals within a stage are treated as identical, which may or may not be a useful simplification. In the first analysis an age-structured population model will be constructed. The matrix population model will be parameterized for northern pike as one of the most important recreational fish populations in Central Europe (Arlinghaus 2004b) and parts of North America (Pierce et al. 1995). Biological information on pike is available and will be used for the model (Raaf 1988; Craig 1996). After constructing the population matrix, the model will be iterated until a certain equilibrium level is achieved, i.e. population characteristics do not change or fluctuate any more. This stationary case determines the age distribution of the resident population, and thus determines the environment in which the evolution in response to fishing impact takes place.

In the second step, reproduction ratios ( $R_0$ ; describing the expected number of offspring produced by a female over her life span) will be calculated for variants of the trait under consideration (e.g. age-at-maturation). In other words, as age-at-maturation is varied in the original matrix population model,  $R_0$  in dependence of the trait and the distribution of the trait in the population (frequency-dependant selection) can be calculated. This information is used to estimate the selection differentials for the different traits by weighting the distribution of the different trait values with  $R_0$  for that given trait value and subtracting from it the mean trait value in the resident population. The outcome of this deterministic simulation can thus provide qualitative insights into the dynamics of selected traits that were previously found to be adaptive under commercial exploitation and are now considered under conditions of angling.

Concerning the planned time schedule, the first month should be devoted to building the matrix population model and compiling literature data. In the second month, simulations should be run, while the third month should be devoted for report preparation and result presentation.

## **Relevance and link to ADN's research plan**

This project links directly to ADN's research focus on *Fisheries-Induced Adaptive Change*.

## **Expected output and publications**

This work is intended for publication as a co-authored research article. Either a modeling paper should be prepared or an essay be written.

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# Metapopulation Dynamics of Sexual and Parthenogenetic Hermaphrodites

Ružica Bruvo

*Institute of Animal Evolution and Ecology,  
University of Münster, Germany*

## Goal

To understand the factors that enable the coexistence of sexual and asexual hermaphrodites in metapopulations with limited dispersal and partial interbreeding.

## Background and motivation

That clonality is rare in nature represents a well known yet unresolved paradox: due to differences in intrinsic growth rates, sexual populations producing both males and females should be rapidly outcompeted by their asexual counterparts (Maynard Smith, 1978). Main advantage to recombination is likely to stem from creating variability, which results in an increased ability of sex to fight parasites and/or to purge deleterious mutations (“Red Queen” and “mutational” hypotheses; (Hamilton *et al.*, 1990; Kondrashov, 1993). Acting separately, the effects from parasites and deleterious mutations are often insufficient to overcome the reproductive advantages of asexuality. Yet synergism between these two forces can largely expand the parameter space under which sex is maintained (Howard and Lively, 1994, 1998, 2003; West *et al.*, 1999). Importantly, spatial population structure was shown to provide a crucial advantage to sex in face of an accumulation of deleterious mutations (Peck *et al.*, 1999) and parasite pressures (Keeling and Rand, 1995).

Most of the theory, however, deals with comparing pure sexual versus asexual populations that do not directly interact and are otherwise equal, which is fairly rare in nature. Many clonal forms have various levels of hidden recombination, and some can partially interbreed with their coexisting sexual counterparts (Simon *et al.*, 2003). In hermaphrodites, the switch to parthenogenesis is often accompanied by an incomplete loss of male function, resulting in more complex dynamics and different costs to sex than in gonochorist systems (Mogie, 1996; Joshi and Moody, 1998; Britton and Mogie, 2001).

In the freshwater planarian *Schmidtea polychroa*, sexuals and parthenogens are both hermaphroditic, and share the same morphology and habitat preference. They differ in ploidy levels, sexuals being diploid and parthenogens polyploid. Parthenogens mate, but use the received sperm only to trigger egg development, so their progeny is essentially clonal. Parthenogens have highly reduced allocation to male function (Weinzierl *et al.*, 1998) and higher fecundity (Weinzierl *et al.*, 1999). They can sire offspring to sexuals, which occasionally leads to the origin of new parthenogenetic lineages (Benazzi Lentati, 1970; Weinzierl *et al.*, 1999). Such a source of clonal variability is likely to accentuate the costs to sex (Peck and Waxman, 2000; D'Souza *et al.*, 2004). Importantly, the flatworm populations are highly structured, with patchy distribution along the shore and limited individual dispersal.

Previous studies suggest that costs to sex in mixed populations of *S. polychroa* may be partially counterbalanced by the decrease in fitness of asexuals due to deleterious mutation accumulation as well as parasite selection pressures (Storhas, 2000; Storhas *et al.*, 2000; Michiels *et al.*, 2001; Bruvo *et al.*, 2004). However, it remains unclear in what way the limited dispersal and metapopulation dynamics influence the coexistence of the two biotypes. In addition, the differences in genome size (ploidy levels) of the two biotypes are likely to play an important role, but have thus far not been addressed. Polyploidy can effectively mask the slightly deleterious mutations (Mable and Otto, 2001), allowing parthenogens to support higher mutation loads. Furthermore, polyploidy may be associated with an increased individual defence spectrum, leading to more intricate host-parasite interactions and potentially enhancing the advantage to asexuals.

## Research questions

This project will explore the influence of metapopulation structure on the dynamics of coexistence of sexual and asexual hermaphrodites. In contrast to the classical approaches, which assume no direct interaction between clonal and sexual forms (e.g., Hamilton *et al.*, 1990; Keeling and Rand, 1995; Howard and Lively, 1998; Peck *et al.*, 1999), I aim to study the system where both sexuals and parthenogens are hermaphroditic and parthenogenesis is sperm-dependent, such that the two forms can occasionally interbreed. Moreover, I intend to consider limited dispersal and spatially localized interactions between the two forms. The first focus will be on the following:

- Under what conditions can either of the reproductive biotypes invade the other?
- What conditions permit coexistence between the two biotypes?
- What is the role of the spatial population structure in permitting this coexistence, as compared to homogeneous populations?

The hypothesis is that under certain conditions, resulting primarily from metapopulation dynamics, the coexistence may be guaranteed even without the more traditional explanations that involve genetic deterioration (mutations) and environmental selective pressures (parasites).

In this initial phase, I aim to contrast only the two discrete reproductive modes (sex versus asex).

An additional approach would be to take account of the occasional sexual events and thus consider the possibility of an organism being in-between the two reproductive forms, i.e. to explore the continuous transition from one reproductive mode to another. Therefore, the question would be:

- What amount of sexuality (or asexuality) is adaptive in the spatially structured metapopulations?

Having explored this basic metapopulation framework, if the time permits, I plan to extend it to further study the effects of

- Accumulation of deleterious mutations,
- Parasite selection pressures, and

- Both forces acting in synergism.

At this point, an important novelty is to take account of the different ploidy levels in parthenogenetic and sexual forms; thus it will be interesting also to address the question:

- Is there an adaptive value of increased genome size linked to clonal reproduction?

## Methods and work plan

I will first use a simple metapopulation dynamics model to explore competition between interbreeding sexuals and parthenogens, taking into account spatial population structure. In this respect, in order to test the relevance of the spatial population structure, I aim to contrast the dynamics of the homogeneous population with that of the structured one.

To characterize sexual and parthenogenetic organisms, I will consider the planarian *S. polychroa* as a model system. Here, both sexual and parthenogenetic forms are obligately outcrossing hermaphrodites, and parthenogenesis is pseudogamous so reproduction always requires mating with another individual.

Parthenogens are characterized by:

- higher fecundity than sexuals: when mated to another parthenogen, they produce  $B_p$  offspring through their female function,  $B_p > B_s$  ( $B_s$  denotes offspring from matings between two sexuals);
- when mated to sexuals, parthenogens produce an even higher number of offspring than when mated to other parthenogens,  $B_{pm} > B_p$ ,
- parthenogens have lower sperm amount and quality, so their sexual mating partners get less offspring from mixed matings,  $B_{sm} < B_s$ .

In this way, altogether four different fecundity factors will be taken into account.

To characterize metapopulation dynamics and account for demographic and environmental stochasticity, I will use adaptive dynamics theory and develop a framework similar to the one described by Parvinen *et al.* (2003). Habitat consists of a finite number of patches. They are spatially distributed following a one-dimensional circular stepping stone model (e.g., Gandon and Rousset, 1999), which approximates the natural distribution of planarians along the lake shoreline. Patches are characterized by size and number of individuals of each reproductive mode. Reproduction takes place at random within the patches, and the number of offspring depends on the reproductive mode of the mother parent and her mating partner (see above). Local population growth is logistic and density-dependent. Individuals can migrate between the neighboring patches; once inside the disperser pool, they can also experience different mortality rates than within the breeding patches. Patches can also be made prone to stochastic loss (extinction of all individuals).

Based on this framework, I first aim to use a simulation approach and explore the dynamics of competition between the two reproductive strategies under the following parameters:

- female fecundity in sexuals versus parthenogens (see above);
- migration rates,

- size of local populations versus number of patches,
- dispersal risk (influenced by the distance between patches),
- carrying capacity of patches,
- initial frequencies of the two biotypes, and
- initial spatial distribution of the two biotypes.

Furthermore, if the time permits, I plan to extend this view and explore (i) the effects of an accumulation of deleterious mutations, and (ii) the effects of antagonistic coevolution with parasites, using the same metapopulation framework as described above.

To describe an accumulation of deleterious mutations, individual genomes can be characterized by a large number of unlinked loci (sites) (see e.g. Peck *et al.*, 1999). At each site, mutations occur randomly at rate  $\mu$  per generation. Mutations are slightly deleterious, and selection against them results in decreased viability. The novelty in this respect is to take account of the differences in ploidy levels of sexuals and parthenogens. Because sexuals have smaller genomes, mutations can accumulate at lower number of sites (alleles), but they are also more likely to be expressed and selected against. In sexuals, reproduction involves free recombination and mixing of parental genomes, and in parthenogens, offspring inherit the same genome as mother. Selection against deleterious mutations is expected to be more efficient in sexual offspring due to variation in their mutation loads.

Host-parasite dynamics can be introduced by defining host and parasite disease interaction loci (e.g., Howard and Lively, 1998; Agrawal and Lively, 2003). Parasite virulence alleles need to match host resistance alleles in order to infect. As part of each parasite generation, hosts are exposed to random parasites. Infected hosts have reduced survival, and parasites that do not infect die. Parasites reproduce faster, which allows them to adapt to host genotypes. Sexually produced offspring should display more diversity at resistance loci. Parthenogenetic offspring are genetically identical to their mothers, and so have a higher chance of meeting a parasite that will successfully infect. In particular, I intend to focus on the effects of limited host and/or parasite dispersal, which potentially result in local parasite adaptations and patchy distribution of infections.

Finally, synergism between the effects from deleterious mutation accumulation and parasite selective pressures can be addressed by allowing both forces to act simultaneously. This can be done in a way similar to the approach used by Howard and Lively (1998); the important novelty in this respect will be to focus on the effects of spatial population structure and interactions between the two reproductive forms.

## **Relevance and link to ADN's research plan**

This project will extend the present view of the evolution and maintenance of sex by taking account of the complex ecological interactions in hermaphrodite populations with spatial metapopulation structure. Adaptive Dynamics Theory will prove crucial for characterization of metapopulation dynamics in this system. Moreover, while the study of virulence has already been in focus of the Adaptive Dynamics Network (e.g. Dieckmann, 2002), this project opens up new applications of this theory by exploring the effects of host-parasite interactions in the context of the Red Queen hypothesis on the metapopulation level.

## Expected output and publications

The study envisaged here is expected to result in at least one jointly authored paper in an international scientific journal and will be integrated as one chapter into my PhD thesis.

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# **New Techniques for Estimating the Timing of Speciation from Molecular Data**

Yurji Bukin

*Limnological Institute, Siberian Branch of the  
Russian Academy of Science, Irkutsk, Russia*

## **Goal**

To examine the reliability of using pairwise differences between mtDNA sequences (and of other methods of molecular analysis) for inferring the timing of past speciation, using individual-based evolutionary models.

## **Background and motivation**

Today a host of different molecular data exists for many organisms. With the help of molecular data we can study gradual evolution, speciation, and others population processes. Even though different molecular methods exist for this purpose, there is a problem of assessing the reliability of existing techniques and of devising new techniques where necessary. In this study I will focus on methods based on pairwise differences between mtDNA sequences and compare these with alternative methods.

We use a numerical evolutionary model for the study of speciation processes. Modern computing greatly facilitates the investigation of such individual-based models. These models correspond more closely to natural populations of organisms than do other, simpler models. Simulating the molecular evolution of neutral “nucleotide” sequences in addition to that of selected characters gives us an opportunity of investigating the applicability and reliability of available phylogenetic techniques. The neutral sequences considered in our model are transferred to offspring via the maternal line, which is analogous to the transfer of mitochondrial DNA (mtDNA).

Phylogenetic evolutionary trees can be constructed using molecular sequences extracted at the end of simulation runs; these demonstrate the possibility of reconstructing evolutionary history. Numerical indicators can assess the genetic exchange between subpopulations. Also environmental change, resulting in changing population sizes, can be traced based on neutral molecular data (Strimmer and Pybus, 2001, Emerson et al., 2001). The individual-based model allows us to estimate the reliability of these and alternative methods (Semovski and Sherbacov, manuscript, Emerson et al., 2001). In addition, questions about the speed of molecular evolution can be addressed by studying the influence of model parameters on the speed of the ‘molecular clock.’

An important method of molecular analysis is based on the distribution of pairwise differences between mtDNA sequences. This technique has been used to study the timing of speciation events and of abrupt environmental changes. We have compared this method with alternative methods of molecular analysis (Semovski and Sherbacov, manuscript, Semovski et al., 2004, Semovski et al., 2003). We used parametric bootstrapping to estimate the statistic significance of observed differences in the distribution of pairwise DNA differences (Semovski et al., 2003).

This method may also allow detecting the effects of interspecific interactions on evolving neutral mtDNA sequences (Sankoff and Nadeau, 2000). In particular, the interaction between organisms of different species may be responsible for differences between the speeds of their molecular evolution. To explore these questions, and to provide a test bed for the comparison of alternative molecular methods, I will focus in this study on a model of predator-prey coevolution.

## Research questions

My study will address three interrelated sets of issues:

- I will compare the method based on the distribution of pairwise differences between mtDNA sequences with a method for reconstructing phylogenetic trees. In particular, I will assess their differential performance in estimating the timing of past speciation events. In addition, I will compare the reconstructed phylogenetic trees of evolution with the ‘real’ phylogenetic trees directly recorded in our numerical simulations.
- I will study the reliability of the method based on the distribution of pairwise differences between mtDNA sequences. In particular, we must understand when we may use this method safely and when its results are not to be trusted. In this context, spurious effects resulting from finite sample size have to be explored.
- I will study the influence of interspecific interactions on the speed of molecular evolution. This may suggest methods for recalibrating molecular clocks when studying coevolutionary dynamics.

## Methods and work plan

The first set of instruments for my work contains methods for reconstructing phylogenetic trees. There are established algorithms for inferring phylogenetic trees from DNA data.

The second instrument for my work is the distribution of pairwise differences between mtDNA sequences. I have devised a computer program to construct distributions of these differences. This program constructs the distribution and estimates its reliability. It can be applied to the output of individual-based evolutionary models.

The third instrument for my work is an individual-based model of predator-prey coevolution. The deterministic approximation of the population dynamics in this model is given by the following equations (Doebeli and Dieckmann, 2000),

$$\frac{dN_1(x)}{dt} = r_1 N_1(x) \left[ 1 - \int C_1(x-x') N_1(x') dx' / K_1(x) \right] - p N_1(x) \int C_2(y'-x) N_2(y') dy' ,$$

$$\frac{dN_2(y)}{dt} = r_2 N_2(y) [1 - N_2(y) / K_2] + pa N_2(y) \int C_2(x'-y) N_1(x') dx' ,$$

where  $N_1(x)$  and  $N_2(y)$  are the population sizes of prey and predator,  $x$  and  $y$  are their phenotypes,  $C_1$  defines competition between prey individuals, and  $C_2$  defines the ability of predators to harvest prey. The intraspecific competition in the prey population causes

its phenotypic divergence. Such divergence may cause the divergence of predators (Doebeli and Dieckmann, 2000). All individuals in my model possess ecologically neutral “nucleotide” sequences, as described in the preceding section.

First, I will investigate different evolutionary scenarios with the help of the individual-based model. I will then use the final DNA sequences extracted from the model to compare the method based on the distribution of pairwise differences between mtDNA sequences with other methods and to assess the reliability of the former. Molecular data collected throughout simulation runs will give me the possibility to study the speed of the molecular clock and to construct the ‘real’ phylogenetic trees.

## Relevance and link to ADN’s research plan

In this project we aim at building a framework for the study of speciation and coevolution based on selected and neutral molecular data. This will give us useful insights for studying these phenomena in natural populations. The planned program of research will extend previous studies carried out in the context of ADN’s research focus on *Adaptive Speciation*. In particular, the coevolutionary model studied here is based on the one proposed by Dieckmann and Doebeli (1999).

## Expected output and publications

This work will be the final part of my PhD thesis and is expected to be published in a jointly authored paper.

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# Maturation Reaction Norm Evolution in Smallmouth Bass Populations

Erin Dunlop

*Department of Zoology, University of Toronto,  
Toronto, Canada*

## Goal

To model and understand the evolution of maturation reaction norms in two recently diverged populations of smallmouth bass.

## Background and motivation

Patterns of divergence in introduced populations derived from a common source can provide valuable insights into the processes that create life history variation and that drove the formation of new species. In general, rapid divergence of life history traits can occur in populations that are spatially segregated and evolve differentially in response to selective forces in the new environment. In particular, such divergence can occur when fish populations are introduced into novel environments. Such introductions are common, often mediated or caused by humans (Pimentel et al. 2000). Recent studies have observed life history evolution in grayling (*Thymallus thymallus*) populations separated for less than a century (Haugen 2000, Haugen and Vollestad 2000, Haugen and Vollestad 2001, Koskinen et al. 2002). Other studies have shown adaptive divergence of life history traits within at most 30 generations in newly colonized chinook salmon (*Oncorhynchus tshawytscha*) populations (Quinn et al. 2001) and within 30-60 generations in translocated guppy (*Poecilia reticulata*) populations (Reznick et al. 1990). These types of studies provide a rare and important glimpse at the processes creating widespread life history variation across populations and the natural evolution of new populations.

For the proposed project, the divergence of two smallmouth bass (*Micropterus dolomieu*) populations will be modeled. The two populations were introduced in the early 1900's, from the same source population (Orendorff 1983). Smallmouth bass are littoral predators that inhabit freshwater lakes throughout North America and elsewhere throughout the world. They are ecologically important predators that often shape littoral fish communities (Jackson 2002) and are an economically important sport fish. Our two study populations are from Provoking Lake and Opeongo Lake, located in Algonquin Provincial Park, Canada. Studies completed in the 1980's (Orendorff 1983) and more recently, revealed that the Provoking population had a high population density and extremely slow-growing adults, whereas the Opeongo population had a lower population density and faster-growing adults. The sizes and ages at maturation also differ between the populations. Therefore, although the populations had the same source, at the present time their growth and maturation differ substantially. Preliminary research suggests that low availability of large-sized prey has contributed to the slow growth rates of the Provoking Lake population. Research also suggests that the Provoking Lake population has higher adult mortality (possibly due to low food availability) and lower predation on

young-of-the year (YOY) smallmouth bass (due to a lack of predatory species in the lake community) than the Opeongo Lake population. In the proposed study, a modeling approach will be used to determine if differences in YOY predation and adult mortality could have contributed to an evolutionary divergence between these populations.

Mortality has been shown to influence growth and maturation in several fish populations. In the experiments of Reznick and colleagues (i.e. Reznick et al. 1990) on guppies (*P. reticulata*), high ratios of adult to juvenile predation selected for younger ages and smaller sizes at maturation while high ratios of juvenile to adult predation selected for older ages and larger sizes at maturation. Thus, it is possible that differential mortality at particular life stages (i.e. YOY and adult stages) in the Provoking and Opeongo smallmouth bass populations has contributed to the divergence in growth and maturation.

One method of characterizing the growth and maturation of a population is through its maturation reaction norm. Growth rates can vary plastically in response to environmental conditions. The sizes and ages at maturation are not independent of each other and are bound to vary with growth rates in a plastic way. This range of growth rates and the subsequent range in size and age at maturation within a population determine its observable maturation reaction norm (Stearns and Koella 1986). In general, a reaction norm characterizes the phenotypes that a particular genotype expresses across a range of environmental conditions (Stearns and Koella 1986). The maturation reaction norm of a genotype or population is defined by the probabilities of becoming mature in the next season as a function of an individual's age and size. Across populations, or within populations through time, differences in the sizes and ages at maturation that are associated with differences in growth, may represent plastic responses to the environment because they follow the same reaction norm (Stearns and Koella 1986). Interpreting variation in age and size at maturity as a plastic response is justified if the underlying variation in growth rates is mainly environmentally determined (Heino et al. 2002). In addition, selection may act on the ages and sizes at maturation and cause the reaction norm of a population to shift away from its original position (Heino et al. 2002, Stearns and Koella 1986) or to change its shape (Haugen 2000).

There are a few interesting examples of how selection can influence the shape or position of maturation reaction norms. In a study on arctic grayling (*T. thymallus*) populations, as harvest mortality on adults increased, age at maturation became less plastic and the maturation reaction norm became more vertical (Haugen 2000). In a different study on North Sea plaice (*Pleuronectes platessa*), the maturation reaction norm shifted to smaller sizes at maturation in response to selective harvest (Grift et al. 2003). In both cases, changes in the position and shape of the maturation reaction norm suggested that changes in age and size at maturation were genetically determined, and not merely plastic responses to variations in growth rates. Estimating maturation reaction norms can therefore help disentangle the plastic effects of growth on the age and size at maturation from any genetic changes that may occur in the age and size at maturation as a result of reaction norm evolution (Heino et al. 2002). From a management perspective, it is important to determine if changes over time in a population are genetic adaptations or plastically based, as genetic changes are more difficult to reverse. Modeling maturation reaction norm dynamics in the Provoking and Opeongo smallmouth bass populations

should provide insight into the relative contribution of phenotypic plasticity and genetic adaptation to the observed divergence of life history traits.

Previous models of maturation reaction norm evolution have employed deterministic continuum dynamics at the population level (e.g. Ernande et al. 2004). This was justified because population abundances of the species modeled were large. Population abundances of smallmouth bass populations are considerably smaller than those of the commercial marine species modeled previously, motivating the use of individual-based models for this study system. Individual-based models are being used more frequently as they allow an intuitive approach for merging genetics and demography (i.e. Chambers 1993, Jager 2001). Using an individual-based model in this study will provide a powerful approach to modeling maturation reaction norm dynamics in the Provoking and Opeongo smallmouth bass populations.

## **Research questions**

For the proposed study, I plan on constructing a model to predict how variations in YOY and adult mortality between populations are expected to influence their maturation reaction norms. For this purpose, I will be modeling maturation reaction norm evolution under different levels (i.e. low, moderate, and high levels) of mortality on either YOY or adult smallmouth bass. This work will provide clues as to, (1) the possible cause of life history divergence between smallmouth bass populations, (2) how fish community composition influences introduction/invasion dynamics of populations, and (3) the speed at which evolution occurs in freshwater sport fish populations.

## **Methods and work plan**

I will construct an individual-based simulation model to predict maturation reaction norm evolution in response to selective forces in the environment of newly introduced populations. I will be using data collected on the Provoking and Opeongo Lake smallmouth bass populations to parameterize the model. Such data will come from an annual angler survey that has been conducted on Opeongo Lake since the 1930's (Shuter et al. 1987) and from detailed studies of growth and maturation conducted recently on both populations.

The model will incorporate the following components. The bi-phasic somatic growth model proposed by Lester et al. (2004) will be used to simulate growth. Growth will be linear before maturation and follow the Von Bertalanffy growth model after maturation. The reduction of adult growth rates relative to juvenile growth rates will represent reproductive investment (following an approach similar to that of Roff 1983). A density-dependent growth function will be used to define the empirical function between growth and population abundance (based on empirical data). Growth will be limited for adults in the Provoking population to mimic the absence of large-sized prey in the diet. Density-dependent natural mortality will also be incorporated into the model. Maturation reaction norms will be linear with a constant envelope and modeled with an evolving intercept and slope. To simulate introduction, individuals in the founding population will be yearlings with a pre-determined body size (based on the empirical body size distribution of yearlings). Simulations will run on a discrete, one-year time step for approximately 100 years with maturation, reproduction, growth, and death occurring annually. Predation on YOY bass and adult mortality will be manipulated to determine their influence on

maturation reaction norm dynamics. Different scenarios (i.e. low, medium, and high level of YOY/adult mortality) will be simulated to mimic introduction into Provoking and Opeongo Lakes. Increased complexity (i.e. dynamic maturation envelope, non-linear maturation reaction norm, dynamic growth reduction after maturation) will be added to the model as time permits.

## Relevance and link to ADN's research plan

This project models dynamics of maturation reaction norms in populations of a freshwater sport fish and is thus directly linked to ADN's research focus on Fisheries-Induced Adaptive Change.

## Expected output and publications

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

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# Conditions for Evolutionary Branching in Two-dimensional Trait Spaces

Hiroshi Ito

*Department of Systems and Sciences,  
University of Tokyo, Japan*

## Goal

To investigate the conditions for evolutionary branching in two-dimensional trait spaces without assuming infinitesimal mutation probabilities and step sizes.

## Background and motivation

Speciation by ecological interaction (Schluter 1994; Feder et al. 1997; Orr and Smith 1998) is one of the important processes underlying the generation of biodiversity. Recently, theoretical studies based on adaptive dynamics theory (Metz 1996; Dieckmann & Law 1996; Dieckmann 1997) have provided a general framework for understanding this phenomenon by introducing the concept of evolutionary branching in a trait space (Geritz et al. 1998; Dieckmann & Doebeli 1999; Doebeli and Dieckmann 2000). These studies proposed analytical conditions for branching at evolutionarily singular points (called evolutionary branching points) in one-dimensional trait spaces, under the assumption that both the mutation probability and the mutation step size are infinitesimally small. An asexual monomorphic population situated in the vicinity of a branching point can then be shown to first converge to that point and then to diverge into two subpopulations driven by frequency-dependent disruptive selection. Evolutionary branching points thus are convergence stable fitness minima.

In multidimensional trait spaces, the branching condition is still expected to be similar to that derived for one-dimensional trait spaces (Dieckmann 2000; Vukics et al. 2003; Egas and Dieckmann, submitted), since a population under the aforementioned infinitesimal assumptions experiences disruptive selection only if the fitness gradients in all directions vanish. This formal reasoning, however, implies a serious problem: evolutionary branching in a focused trait cannot occur if the population simultaneously experiences directional selection in any other trait that is not considered.

My previous research, and my recent investigations with Ulf Dieckmann, addressed the adaptive dynamics in two-dimensional trait space and showed that if either mutation probability or step are not infinitesimally small, evolutionary branching can still arise, if only the magnitude of the fitness gradient in the other trait is small enough relative to the curvature of the fitness valley at the branching point in the focal trait. There appears to exist a certain threshold for evolutionary branching under such conditions, which depends on the relationship among the fitness curvature in the focal direction, the fitness gradient, mutation probabilities, and mutational step sizes. Since both mutation probabilities and mutational step sizes are not infinitesimally small in real populations, and since such populations tend to evolve in multidimensional trait spaces, understanding that threshold is necessary for understanding the mechanism of evolutionary branching in real populations (Schliewen et al. 1994; Schluter 1994; Feder et al. 1997; Losos et al. 1998).

## Research questions

For simplicity, I will focus on two-dimensional trait spaces and on situations in which a population experiences frequency-dependent disruptive selection on one trait and directional selection on the other trait. In this system, I will try to determine the threshold condition for evolutionary branching.

## Methods and work plan

To understand the branching mechanism in detail, I will investigate branching conditions along an artificial two-dimensional fitness landscape for an asexual population. This landscape is constructed by combining two one-dimensional fitness landscapes. Evolution in the first trait is modeled according to a resource competition model in a one-dimensional trait space that brings about evolutionary branching (Dieckmann & Doebeli 1999). Evolution in the second trait simply follows a constant fitness gradient, which can prevent evolutionary branching in the first trait when mutation probabilities and mutational step sizes become too small.

For this project, I plan to utilize three alternative descriptions of the evolutionary process unfolding in asexual populations:

1. *Monomorphic and polymorphic stochastic model on artificial fitness landscape.*  
To analyze the effects of mutation probability and mutation step separately, I will calculate evolutionary dynamics based on the polymorphic stochastic model and on the monomorphic stochastic model introduced by Dieckmann & Law (1996). The purpose of these analyses is to approximate the branching threshold, based on the shape of the fitness landscape and on the mutation probabilities and steps.
2. *Individual based model on natural fitness landscape.*  
To examine the usefulness of the threshold condition thus obtained, I will apply it to two different individual-based models defined on two-dimensional trait spaces. These models were previously constructed in my PhD research project, and are based on resource competition and predator-prey interactions, respectively.
3. *Deterministic description of dynamics based on canonical equation.*  
I will also try to deterministically describe evolutionary dynamics including evolutionary branching in the resource competition model and the predator-prey model, based on the canonical equation of adaptive dynamics.

## Relevance and link to ADN's research plan

This project aims to bridge a gap between analytical predictions and numerical studies of evolutionary dynamics involving evolutionary branching, and thus directly links to ADN's research foci on *Adaptive Speciation* and on the *Foundations of Adaptive Dynamics*.

## Expected output and publications

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

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# Structure and Stability of Evolving Food Webs

Jacob Johansson

*Department of Theoretical Ecology,  
University of Lund, Sweden*

## Goal

To study how food webs are expected to change their structure, composition of interactions, and stability properties in the course of evolution.

## Background and motivation

The relationship between the diversity and stability of ecological systems has long been an issue for research and debate. Using theoretical evidence from food web models as well as verbal arguments several studies suggest that large complex communities will be more stable than small and simple ones, whereas other studies show the opposite (McKann 2000). Some models corroborating both views have been proposed (e.g. Wilmers et al. 2002) and recently it has been proposed that the presence of weak links in food webs is important for the stability of ecological systems (Janssen and Kokkoris 2003; McKann 2000).

Models of evolving food webs have also been used in order to understand patterns of speciation and extinction in the fossil record (e.g. Yoshida 2003). Some of these studies show fluctuating species diversity with periods of increasing diversity followed by extinction avalanches (Calderelli et al 1998), while others have resulted in more stable number of species over time (Drossel et al. 2001)

Evolution in food webs has been simulated as small random changes in the interaction coefficients themselves (Ginzburg 1988) or in abstract traits that map onto interactions (e.g. Calderelli et al 1998; Drossel et al. 2001; Yoshida 2003). Competitive communities (i.e. communities excluding predation), have also been modeled using evolution along fitness gradients in trait space (Rummel and Roughgarden 1983).

Using the theoretical framework of adaptive dynamics, novel techniques have been developed to model community evolution under ecological interactions such as competition and predation (Doebeli and Dieckmann 2000). Applying these techniques in order to simulate food web evolution could yield new insights into long-term diversity patterns and into the issue of stability of ecological systems.

## Research questions

In this project I will try to address questions such as the following:

- How do the interactions between species change in terms of their strength and distribution during the evolution of a food web? Do weak links evolutionarily appear as stabilizing factors?

- How will food web structure change in the evolving community? Will food chains be long or short? Will community stability increase or decrease? Will genetic similarity between species correspond to ecological and functional similarity?
- How do speciation and extinction events affect the structure of the evolving community and its stability properties?
- Does speciation rate change during evolution? Can we expect cascade extinctions? Will the food web evolve towards a fixed community (an ESS solution)?

## Methods and work plan

To address these questions, adaptive dynamics theory is a suitable tool, since it is a general approach that ties evolution and ecology together and requires relatively few assumptions.

Each species will be characterized by  $L$  different traits. The traits of a species  $i$  will be modeled as vectors  $\mathbf{u}_i = (u_{i1}, \dots, u_{iL})$  with elements containing continuous values between 0 and 1, as a generalization of the model of Calderelli et al. (1998). The interaction coefficients  $\alpha_{ij}$  between two species  $i$  and  $j$  will be functions of a ‘score’ defined as

$$S_{ij} = \mathbf{u}_i \mathbf{M} \mathbf{u}_j^T = \sum_{pq} u_{ip} u_{jq} M_{pq}$$

where  $\mathbf{M}$  is an asymmetric random matrix chosen in the beginning of the simulation.

Evolution and population dynamics will then be modeled using a fitness function,  $G$ , that depends on the traits of the species and their vector of population densities  $\mathbf{x}$ . The fitness landscape of a mutant with traits  $\mathbf{u}'$  in a resident population with traits  $\mathbf{u}_1, \mathbf{u}_2, \dots, \mathbf{u}_m$  will then be described by

$$G(\mathbf{u}', \mathbf{x}, \mathbf{u}_1, \mathbf{u}_2, \dots, \mathbf{u}_m) = \lambda \sum_j x_j \alpha(\mathbf{u}', \mathbf{u}_j) - \sum_j x_j \alpha(\mathbf{u}_j, \mathbf{u}').$$

The population growth will be proportional to the fitness function and the evolution will be governed by the canonical equation of adaptive dynamics derived for this fitness function.

The trajectory of the evolving community will be monitored and the resulting distribution of interaction strength will be measured. Community stability will be assessed using return time and statistics describing the variation in population dynamics. Other features characterizing the food web, such as connectance and proportion of basal species versus intermediate and top species will also be considered.

To start with, the interaction coefficients could be linear functions of the score,  $S_{ij}$ , as in Calderelli et al. (1998). A set of rules or restrictions taking into consideration energetic constraints will be applied to avoid unrealistic effects in the structure of the evolving food web. Further adjustments of the fitness function may be made in order to make the evolutionary process natural and smooth when species change the direction of their trophic links, for example when evolving from competitor to predator.

The model could then be extended to include more realistic functional responses, since these have been shown to be of crucial importance for the stability of communities (Drossel et al. 2004). Speciation events and possibly also extinctions could be included as parts of the evolutionary dynamics, in which the appearance of fitness minimas can give raise to evolutionary branching.

The analysis will be conducted both analytically (for simplified cases) and by employing computer simulations.

### **Relevance and link to ADN's research plan**

The project uses an integrative approach in which a complete food web is subject both to short-term ecological dynamics as well as to long-term evolutionary change. Moreover, evolution will take place in many traits simultaneously, inducing adaptations of species belonging to different levels of the trophic structure. The modeling techniques used in this study are inspired by adaptive dynamics theory, developed by researchers connected to ADN. The present study will apply this framework to a partly new setting, exploring evolutionary dynamics in the multi-dimensional trait space of a complex food web.

### **Expected output and publications**

The suggested project is expected to result in a jointly authored paper, which will be integrated in my PhD thesis.

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# From Individuals to Populations: Spatial Structure, Size Structure, and the Challenge of Moment Closure

Michael Raghieb Moreno

*Department of Mathematics,  
University of Glasgow, United Kingdom*

## Goal

To truncate the hierarchy of moment equations describing a population with spatial and size structure by (i) maximizing the entropy functional of the underlying point process or (ii) minimizing the  $L^2$ -norm of the hierarchy of moment equations. To construct numerical algorithms for computing the entropy of a realization of a (marked and unmarked) point process and for solving the truncated moment hierarchy.

## Background and motivation

Models of endogenously generated pattern, derived from individual-level interactions and capable of making predictions at the population level, are at the cornerstone of much current research on population dynamics (Bolker and Pacala, 1997; Bolker, 2003; Dieckmann and Law, 2000; Flierl et al., 1999; Law et al., 2003; Levin, 2002; Moorcroft et al., 2001), the main objective being the development of theoretical tools that can be of use in understanding the scaling mechanisms by which biological processes occurring at the level of the individual lead to patterns at the level of the population. In this setting, by pattern we mean deviations from complete spatial randomness (i.e. spatial aggregation or segregation of individuals) and deviations from uniformity in the distribution of sizes. The more mathematically inclined among these models have focused exclusively on either spatial pattern (Bolker and Pacala, 1999; Dieckmann and Law, 2000; Law et al., 2003), or size structure (Hara, 1994), a notable exception being Moorcroft et al. (2001), who nevertheless assumed uniformly distributed dispersal. This separation between size and space is somewhat artificial, given the ubiquity of size hierarchies *and* spatial structure in the field literature (Condit et al., 2000; Pfister and Stevens 2002; Weiner, 1985). The next generation of models should take into account that life-history traits are likely to be affected by placement in both size hierarchy and spatial configuration. The concept of a ‘plant’s eye-view’ of the community, on which previous models have been built, then requires to be extended to include dependences on the number and location of neighbors, as well as on their relative differences in size.

This project is based on preliminary attempts to construct a model extending current approaches in a manner that allows size hierarchies and spatial structure to arise naturally; the questions of interest being whether spatial effects vary in the presence of a size-driven competitive hierarchy and, from the opposite perspective, whether spatial pattern has a relevant role in shaping size variability. In order to address these questions, we developed a toolkit of theoretical and computational tools namely, (a) an individual-based model (IBM), defined by updating rules that depend on both differences in size and location. These rules were inspired by experimental work by Purves and Law (2002) on

*Arabidopsis Thaliana*; (b) a marked spatio-temporal point process (MSTPP), constructed from the rules of the IBM, mainly for the purpose of providing a theoretical basis for analytically approximating the dynamics of the IBM; and (c) a method for obtaining expected values and their rate of change from the MSTPP, in particular the conditional first- and second-order intensities of the process. We stopped at second order since most of the statistics of biological interest (i.e. total population numbers, subpopulations classified by size, total biomass, aggregation/segregation indices, coefficients of variation, size distributions, and mark correlation functions) are obtained from the first two moments.

## Research questions

The approach discussed in the previous section posits significant challenges. As a consequence of the nonlinear and non-local nature of the interaction terms in the rules of the IBM, the equation for the rate of change of the expected density of individuals (e.g. first-order conditional intensity), depends on the density of *pairs* of individuals. This in turn requires a second expression for the density of pairs of individuals which, once obtained, turns out to depend on the density of triplets of individuals, i.e. on the third-order moment. This trend continues up to the order that matches total population size. The occurrence of such moment hierarchies is unfortunate, and a major obstacle in deriving population-level models from individual behavior with realistic interaction terms. Clearly, some method for closing the hierarchy must be obtained. The main focus of this project will be to obtain such closure by means of entropy maximization methods. Given that we already have at our disposal the IBM, the MSTPP, and its deterministic approximation, what remains to be done in order to have a functioning model, is a method for truncating the hierarchy of moment equations.

## Methods and work plan

Given that a satisfactory analytical tool for dealing with the problem of closure is lacking to date, much work on the moment-closure problem has relied on a combination of heuristic reasoning and goodness of fit with numerical simulations. For example, Bolker and Pacala (1997) assumed that central third-order moments vanish, an assumption that seriously undermined the applicability of their model, particularly for clustered populations. Law et al. (2003) chose an asymmetric power-2 closure for the third moment, justified by additional arguments, such as positivity, (a)symmetry, and limiting behavior under complete spatial randomness. Their method, however, required the coefficients of the terms of the closure to be chosen on the basis of agreement with numerical simulations. This strategy has recently been taken a step forward by Murrell et al. (2004), who discussed the additional requirement of invariance under relabelling, which ensures that a closure predicts the same third moment independently of whether it is applied to a population as a whole or separately to arbitrary partitions of the population.

It is therefore desirable to strengthen the rationale for obtaining a closure, particularly by the application of some variational principle that can be justified by both the observed biology and the properties of the process. It seems plausible that such a principle can take the form of entropy maximization, justified by the assumption that the preferred state towards which the population settles is that of 'maximum ignorance'. We envision two

alternative ways of accomplishing this, either by maximizing the entropy functional of the process (Daley and Vere-Jones, 2003: 286), or by minimizing an  $L^2$ -norm in the hierarchy of PDEs, both under the constraint of fixed lower-order moments. The former has an important history on processes on the real line (McFadden, 1965), and an extension to spatial-temporal processes will be required. The  $L^2$ -norm approach has recently been proven to be successful in a similar setting (i.e. transport equations for velocity jump processes) by Hillen (2004).

The project will involve the following: (a) development of Matlab code for the computation of the entropy of a realization of a point process, in order to provide a 'test bed' for theoretical procedures, (b) extending the concept of entropy to realizations of marked spatio-temporal point processes, (c) construction of an  $L^2$ -norm satisfying an H-theorem for the hierarchy of PDEs, and (d) maximization of either measure of entropy to yield a closure.

## Relevance and link to ADN's research plan

This project falls within ADN's research focus on *Simplifying Spatial Complexity* and builds on previous ADN work by extending the results of Dieckmann and Law (2000) to size structure. Additionally we expect to obtain a justification of a moment closure via a variational principle (entropy maximization). Both have the potential of opening new lines of research and will make available for exploration a class of dynamical systems of direct relevance to population dynamics, derived consistently from individual-based models.

## Expected output and publications

The results of my project will form part of a chapter of my PhD thesis and will result in a co-authored journal article.

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# Joint Evolution of Predator Body Size and Prey-Size Preference

Tineke Troost

*Department of Theoretical Biology,  
Vrije Universiteit Amsterdam, The Netherlands*

## Goal

To study how patterns of predator size and prey-size preference depend on ecological and environmental parameters.

## Background and motivation

The range of body sizes encountered in nature is enormous. A bacterium with full physiological machinery has a volume of  $0.25 \times 10^{-18} \text{ m}^3$ , while a blue whale has a volume up to  $135 \text{ m}^3$ . These body sizes are associated with the different scales in time and space in which the organisms live, and they reflect the differences in physiological processes and life histories. A similarly wide range is found in the prey-size preference of these organisms. This becomes evident when considering, for example, whales feeding on plankton and hyena eating zebra.

Although body size and prey-size preference are essential properties determining the structure of a community, general rules that relate the two are not known. Several studies have been done to find prey-size preferences and to relate these to the size of the predator. In these studies various mechanisms have been proposed that attempt to explain such size-selective prey selection patterns. These include passive selection mechanisms such as ‘prey visibility’, in which the visibility and thus the vulnerability of the prey are assumed to increase with its size (Svensson, 1997; Rincon and Loboncervia, 1995). Another passive selection mechanism is ‘gape limitation’ of the predator, i.e. the restriction on prey-size choice that is imposed by the predator’s mouth size or morphology (Karpouzi and Stergiou, 2003; Mehner et al., 1998; Rincon and Loboncervia, 1995; Forsman, 1996). In some cases also the prey abundance or availability is found to affect the predator’s selectivity (Pryor and Epifanio, 1993; Rincon and Loboncervia, 1995; Forsman, 1996).

Active selection mechanisms, on the other hand, underlie ‘optimal foraging theory’, which assumes that predators select prey sizes that provide the best energy returns. This may for example be done by avoiding prey with high evasion capabilities (Manatunge and Aseada, 1998), by preying disproportionately on young, sick, or old individuals (Husseman et al., 2003), by selecting large prey because of their higher energy or nutrient content (Kristiansen et al., 2000; Ryttonen et al., 1998) or by selecting small prey when these are more profitable due to small handling times (Turesson et al., 2002; Ellison and Gibson, 1997). The energy return, however, does not only depend on the size of the prey, but also on the size of the predator. The size of the predator is thought to positively affect properties like prey handling ability and prey encounter rate. A large body size may also increase the range of possible prey sizes, and the probability of survival in times of starvation. On the other hand, a large body implies large maintenance requirements.

Although many studies have been carried out to find relations between predator size and prey-size preference, results vary both within and between predator-prey systems. Extracting from these studies general rules explaining these differences is very difficult. In this project we therefore use a modeling approach to study how predator size and prey-size preference interact and how patterns of predator size and prey-size preference depend on environmental parameters, such as food availability, and on ecological parameters, such as encounter rate and handling time. The modeling approach provides us with the possibility to test the effects of several (combinations of) parameters, which may correspond to various predator-prey systems. Results could provide insight in the factors that determine the evolutionary outcomes of predator sizes and corresponding prey-size preferences and may explain some of the patterns observed in nature. This may lead to a better understanding of the structure of natural communities.

## Research questions

We will study the evolutionary outcomes of the joint evolution of predator body size and prey-size preference. The study will focus on two questions.

First, how do patterns of predator size and prey-size preference depend on *environmental* parameters such as food availability and prey-size distribution? It is hypothesized that if food is abundant, predators will evolve to have a larger body size, as this will increase their prey handling ability, while their larger maintenance requirements will not pose a real problem under such conditions. At the same time predators will specialize on small prey, as this will decrease their handling time and thus increase their food intake rate. We denote the resulting pattern of large predator size and predator preference for small prey by L-S. If food becomes less abundant, the encounter rates rather than the handling rate will be limiting the food intake of predators, and preference will now evolve towards larger prey. For the same reason, the predators will still evolve towards larger body sizes, resulting in a pattern denoted as L-L. If food becomes really scarce, large predators will not be able to meet their maintenance requirements, which will then favor small predator body sizes; under these circumstances a preference for large prey will evolve, as this increases the encounter rate. We would thus expect a pattern denoted by S-L.

Secondly, how do patterns of predator size and prey-size preference depend on *ecological* parameters? We will focus on two ecological parameters, viz. encounter rate and handling rate, or, more precisely, the parameters that determine how these rates vary with prey and predator size and the relative importance of these two. For active predators, for example, encounter rates may depend primarily on predator size and less on prey size. This may again select for large predators and for a preference for smaller prey.

## Methods and work plan

*Tools.* A suitable framework to study the evolution of body sizes is provided by Dynamic Energy Budget (DEB) theory. This is a modeling framework for metabolic processes with physiological rules for uptake and use of material and energy. It respects the principles of energy and mass conservation, and stoichiometric constraints on the synthesis of biomass. Biomass is assumed to consist of structural biomass and reserves, which both have a fixed chemical composition. The overall body composition of the organism can still vary through the ratio of structure and reserves.

While DEB deals with mechanisms, rules are implied for the covariation of parameter values among species. Parameters that relate to the physical design of the organism are all proportional to ultimate body size, while the rest are size-independent. The latter parameters often relate to molecular processes, which are essentially concentration- or density-based. Because such body-size scaling relationships are implicit to DEB-theory, it provides a physiologically-based modeling framework that is very suitable for studying body size preference in an evolutionary context.

Predictions of the evolutionary outcomes of a system can be made by using Adaptive Dynamics (AD) theory. Expressions for fitness, invasion criteria, and trade-offs can be derived from the DEB formulation, which gives them a physiological basis.

*Model.* We will develop a model of a physiologically structured population of predators feeding on a range of prey populations in a chemostat environment. The predators are described by two state variables, structural biomass and reserves, and by two evolutionary traits, their maximum size and their preference for prey size. The two evolutionary traits are constant throughout an individual's life, but may change from parent to offspring by mutation. The predators are filter feeders and reproduce by division.

The various prey populations differ only in the size of their individuals, thus providing a range of prey sizes. As a start we will assume that the preys enter the system at a constant density and with a fixed size distribution.

The state variables and the evolutionary traits of the predator, as well as the size of the prey, will affect several physiological and ecological variables. For some of these variables (growth, maintenance, and reproduction) DEB has derived in a systematic way how they relate to (maximum) body size. Other variables such as starvation follow from the energy storage dynamics which are a basic part of DEB. Remaining variables (ingestion, mortality) may also depend on body size. In the functions describing these relationships, parameter values will determine the quantitative effect of both the prey and the predator size and of their relative importance. These parameter values will then be tested for their effects on the evolutionary outcomes.

*Analysis.* The invasion fitness of a predator can be measured by its specific growth rate averaged over its lifetime (from birth to division). Calculations will be done numerically, using the escalator boxcar train method. Evolutionary analysis may include evolutionary trajectories, pairwise invasibility plots, and simulation studies.

*Parameterization.* The model can be parameterized and tested with data on Didinium feeding on Paramecium. These ciliates become considerably larger when conditioned on large prey than when conditioned on small prey (Hewett, 1988). Although this size shift is not an evolutionary change, it may have a genetic and evolutionary origin. Data is available on how mortality, handling time, encounter rate, and attack success rate depend on Didinium size, Paramecium size, and density (Hewett, 1988; Hewett, 1987; Salt, 1974).

## Relevance and link to ADN's research plan

This study will apply Adaptive Dynamics methods to a Dynamic Energy Budget model. Results could provide insight into the relation between predators and their prey choice, which may lead to a better understanding of the structure of natural communities. Such information may be useful in areas such as conservation biology and fisheries management.

## Expected output and publications

The study is expected to be published in a jointly authored paper in an international scientific journal, and may be integrated in one chapter of my PhD thesis.

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