

Ecology and evolution of female mating preferences under size-selective fishing

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Goal

To develop a model for evaluating the ecological and evolutionary consequences of size-selective fishing in sexually reproducing populations exhibiting female mate preferences.

Background and motivation

Harvesting is increasingly recognized as a major selective force driving the evolution of life history traits (Stokes et al. 1993; Ashley et al. 2003). In particular, accumulating evidence suggests a role for commercial fishing in the evolution of fish populations towards maturation at younger ages and smaller sizes (Grift et al. 2003; Olsen et al. 2004; Olsen et al. 2005). By targeting the largest, oldest, and fastest-growing individuals, fisheries create intense directional selection favoring the survival of smaller, younger, and slower-growing phenotypes (Walsh et al. 2006). Consequently, size and age show truncated distributions towards smaller and younger individuals (Conover and Munch 2002), and proportions of individuals maturing at younger ages and smaller sizes are increasing (Olsen et al. 2004; Olsen et al. 2005). In fish populations, the magnitude and the size-selective nature of fishing mortality (Myers and Hoenig 1997), in conjunction with observations of rapid evolution of life history traits in natural populations (Reznick et al. 1990; Rijnsdorp 1993; Haugen and Vollestad 2001; Reznick and Ghalambor 2005) render this concern particularly important (Munch et al. 2005).

The rapid evolution under fishing-induced selection of traits such as adult size, growth rate, age and size at maturation has been discussed in a number of recent publications (Ratner and Lande 2001; Conover and Munch 2002; Grift et al. 2003; Ernande et al. 2004; Olsen et al. 2004; Olsen et al. 2005). Recent studies have found selective harvesting on large fish to result in indirect changes in additional traits such as fecundity (Walsh et al. 2006) and in traits expressed earlier in life such as larval growth and viability. All these characters are known to influence recruitment success (Berkeley et al. 2004a; Berkeley et al. 2004b; Munch et al. 2005).

Yet, little attention has been paid to the effect of harvesting on patterns of sexual selection, despite the potential impact of sexual selection on population growth rates (Côté 2003) and its importance for conservation biology (Legendre et al. 1999; Wedekind 2002; Côté 2003; Wedekind 2003). Among the variety of explanations for the evolution of female reproductive strategies or inter-sexual selection, the “good-genes” models of sexual selection have gained particular attention. These models are based on the prediction that inter-sexual selection improves the average genetic quality and hence the survival of the progeny (Neff and Pitcher 2005). Increased offspring survival might in particular result from a preference for mates with relatively high heritable viability over those with low heritable viability (Howard and Lively 2004): in such a case, mate preferences are expected to be uniform.

Harvesting inevitably restrains the pool of mates available for female choice. A sufficiently strong reduction in male density might result in an “Allee effect”, through the reduction in mating efficiency at low densities (Stephens and Sutherland 1999) caused by the inability of females to find a suitable mate (Bessa-Gomes et al. 2003). Additionally, selective harvesting might affect female reproductive success by acting on those traits on which inter-sexual selection relies. In particular, selective harvesting on size might directly interfere with female reproductive success because size is a commonly used criterion for mate choice. Female mating preferences for large males can be attributed to superior genes inherited by offspring (Williams 1966; Williams 1975; Beacham and Murray 1988b) and to a variety of direct benefits, such as increased sperm quality and/or quantity and better paternal care (Trivers 1972; Williams 1975; Cote and Hunte 1989). Additionally, differences in growth rates are often interpreted as variations in individual quality (Mangel and Stamps 2001). Examples of female preferences for large-sized males are found in several fish species (Beacham and Murray 1988a; Foote 1989; Blanchfield and Ridgway 1999), including numerous poeciliid species (Basolo 2004) and blenniidae (Cote and Hunte 1989; Neat and Locatello 2002). Other teleosts such as Atlantic cod, *Gadus morhua* (Hutchings et al. 1999; Rakitin et al. 2001) or salmonine fish such as brook trout, *Salvelinus fontinalis* (Blanchfield and Ridgway 1999), sockeye salmon, *Oncorhynchus nerka*, (Hanson and Smith 1967; Foote and Larkin 1988; Blanchfield and Ridgway 1999; Blanchfield et al. 2003), dolly varden, *Salvelinus malma*: (Maekawa et al. 1993) or Japanese char, *Salvelinus leucomaenis* (Maekawa et al. 1994) show a preference for males of similar size (size-assortative mating). Thus, by selectively removing individuals based on their size, fisheries might disrupt female preferences for particular individuals, leading to maladapted female preferences and favoring the evolution of alternative female preferences.

Research questions

The three questions at the core of my research project are as follows:

1. Can the maladaptation of female preferences reduce the yield, stability, or recovery potential of exploited stocks?
2. Should size-selective fishing be expected to cause evolutionary changes in the mating strategies adopted by females?
3. How do trajectories and outcomes of female preference evolution depend on harvesting regimes, natural ecological conditions, life history traits and the initial preference of females?

Methods and work plan

Eco-genetic model

To determine the ecological and evolutionary effects of size-selective fishing on stocks with female mating preferences, I intend to develop an individual-based eco-genetic simulation model. This model will describe an iteroparous species in which mate choice and harvesting are size-dependent.

Individuals will be characterized by their age, size, sex, intrinsic growth rate, and maturation status and females will additionally be characterized by their mate preference. The traits likely to evolve under harvesting will be growth, maturation reaction norms and the female preference, i.e. the decay constant of the exponential distribution describing female preference for males of increasing size (see below), and the mean and standard deviation of the normal distribution describing female preference

for size-assorted males (see below). A quantitative genetic approach will be used to express heritability in the evolving traits. Population dynamics will be based on annual time steps for maturation, reproduction, growth, and mortality.

Growth will be simulated with the bi-phasic somatic growth model (Roff 1983; Lester et al. 2004), which assumes growth to be linear prior to maturation and to follow the von Bertalanffy growth model after maturation. This allows taking into account the cost of reproductive investment at the adult stage. Intrinsic growth rates will be allowed to vary between years and individuals, to account for environmental stochasticity and micro-environmental variation.

Probabilistic maturation reaction norms will be used to describe changes in an individual's maturation status. These reaction norms will be linear and modeled with a constant width and evolving intercept and slope. Maturation reaction norms describe the maturation schedule of a genotype under different growth conditions (Stearns and Koella 1986). The probabilistic extension of this approach (Heino et al. 2002) describes the maturation process based on the probability that individuals of given age and size will mature in the next season. This overcomes the confounding effects of growth and mortality by estimating maturation probabilities conditional on individuals having reached a given age and size (Heino et al. 2002; Olsen et al. 2004; Olsen et al. 2005). While phenotypic plasticity in response to variations in growth only displaces expressed phenotypes along the reaction norm, selection acting on age and size-specific maturation probabilities will shift the reaction norm away from its original position (Haugen 2000; Heino et al. 2002; Olsen et al. 2004; Olsen et al. 2005). Thus, probabilistic maturation reaction norms are an efficient tool for detecting evidence suggestive of fishing-induced evolution.

Preference traits and mating

Size will be used as preference trait. Thus, it will be under sexual selection through female preferences and under natural selection through size-dependent vital rates. Initial female preferences will be of two kinds: (i) preference for overall large males and (ii) preference for size-assorted males. In the first scenario, size will be under directional selection, implying preference to increase with the size of males. The preference trait will therefore follow an exponential distribution. In the second scenario, females will prefer males of similar size. In this case the favored male will not be the same for all females. The strength of the preference will be at its maximum for a male to female size ratio close to one. The preference trait will follow a normal distribution. Considering these two types of female preference will help elucidating the importance of female preference for a stock's ecological and evolutionary responses to size-selective harvesting.

Harvesting regimes

Two different harvesting strategies will be adopted: one corresponding to a management policy prescribing a minimum size limit (i.e., all fish above a given size threshold may be caught) and the second corresponding to a size slot or permissive slot limit (i.e., only individuals within a given size window may be caught).

Work plan

First, I will investigate how structuring populations according to sex and considering different female mating preferences will affect their demographic response to the onset of fishing. Here I will focus on analyzing how this response is influenced by the type and strength of female mating preferences. This first step aims only at revealing

the ecological effects of sex structure and mating preference and will not yet involve an evolutionary perspective.

Second, I will allow female preferences to evolve and evaluate how the outcomes of evolution in mating preferences depend on the ecological conditions characterizing the stock. In particular, I will try to understand how varying the strength of harvesting will affect the evolutionary outcomes of preference evolution, without a focus on evolutionary transients.

Finally, armed with an understanding of the ecological consequences of mating preferences and of the evolutionary outcomes of preference evolution, I will characterize evolutionary transients and allow life-history traits and preference traits to evolve jointly. The predicted pace of evolution in female preference will be particularly important for characterizing these transients: slow preference evolution compared with faster life-history evolution and even faster changes in fishing pressure might result in time lags that cause preferences to be maladaptive under the current conditions.

Relevance and link to EEP's research plan

This project aims to evaluate the ecological and evolutionary effects of size-selective fishing on stocks with mating preferences and is therefore directly linked to EEP's focus on evolutionary fisheries management. Additionally, studying fisheries-induced evolution in sex-structured populations exhibiting female mating preferences is a novel contribution to existing applications of individual-based eco-genetic models.

Expected output and publications

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

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