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Fisheries-induced disruptive selection

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HIGHLIGHTS

- Commonly used fishing policies cause disruptive selection on fish stocks when harvest pressure is high.
- Necessary conditions are adaptive harvest of large individuals and strong life-history tradeoffs of early maturation on growth and fecundity.
- Fisheries-induced disruptive selection is more likely in stocks with a natural predisposition to early maturation.
- Sustainable yield after diversification is far below the MSY attained under lower fishing pressures, for which selection is not disruptive.

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ABSTRACT

Commercial harvesting is recognized to induce adaptive responses of life-history traits in fish populations, in particular by shifting the age and size at maturation through directional selection. In addition to such evolution of a target stock, the corresponding fishery itself may adapt, in terms of fishing policy, technological progress, fleet dynamics, and adaptive harvest. The aim of this study is to assess how the interplay between natural and artificial selection, in the simplest setting in which a fishery and a target stock coevolve, can lead to disruptive selection, which in turn may cause trait diversification. To this end, we build an eco-evolutionary model for a size-structured population, in which both the stock's maturation schedule and the fishery's harvest rate are adaptive, while fishing may be subject to a selective policy based on fish size and/or maturity stage. Using numerical bifurcation analysis, we study how the potential for disruptive selection changes with fishing policy, fishing mortality, harvest specialization, life-history tradeoffs associated with early maturation, and other demographic and environmental parameters. We report the following findings. First, fisheries-induced disruptive selection is readily caused by commonly used fishing policies, and occurs even for policies that are not specific for fish size or maturity, provided that the harvest is sufficiently adaptive and large individuals are targeted intensively. Second, disruptive selection is more likely in stocks in which the selective pressure for early maturation is naturally strong, provided life-history tradeoffs are sufficiently consequential. Third, when a fish stock is overexploited, fisheries targeting only large individuals might slightly increase sustainable yield by causing trait diversification (even though the resultant yield always remains lower than the maximum sustainable yield that could be obtained under low fishing mortality, without causing disruptive selection). We discuss the broader implications of our results and highlight how these can be taken into account for designing evolutionarily informed fisheries-management regimes.

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1. Introduction

The exploitation of renewable resources is a major source of mortality, which can trigger population collapse (Stokes et al., 1993; Hutchings and Reynolds, 2004) and adaptive changes in the life history of harvested species (Palumbi, 2001; Ashley et al., 2003). Indeed, in commercially exploited fish stocks harvest has been recognized a driver of evolutionary adaptations (Law, 2000; Heino and Godø, 2002; Jørgensen et al., 2007; Dieckmann et al., 2009). To date, most studies considering the genetic and phenotypic responses of fish stock to fishing have focused on fisheries-induced directional selection on life-history traits such as age and size at maturation (Barot et al., 2004; Ernande et al., 2004; de Roos et al., 2006; Gårdmark and Dieckmann, 2006; Dunlop et al., 2009; Poos et al., 2011).

In addition, a fishery itself can adapt, in terms of fishing policy, technological progress, fleet dynamics, and adaptive harvest

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(Salthaug, 2001; Hannesson, 2002; Walters and Martell, 2004). Fishing policies can be selective for both size and maturity stage of individuals in the stock: size selectivity results from mesh-size and gear regulation or from size-specific incentives (Hart and Reynolds, 2002; Fromentin and Powers, 2005), while maturity selectivity may arise when a stock's juveniles and adults are spatially segregated during spawning (Sinclair, 1992; Swain and Wade, 1993; Engelhard and Heino, 2004; Opdal, 2010). Harvest is readily adaptive, because fishers constantly tune their effort and selectivity for maximum profit, targeting stock components that are most profitable to harvest. Such adaptation is relatively fast, leading to a continuously changing selective pressure on the exploited stock. Accordingly, the effect of technological progress on a fishery's sustainability is often assessed while neglecting adaptive responses of the targeted stock (e.g., Dercole et al., 2010).

The coupled dynamics of adaptations in a stock and its fishery can be interpreted as a coevolutionary process, in which one component of the system is biological (the exploited stock) while the other component is economic (the exploiting fishery). In his pioneering work, Heino (1998) approached the stock-fishery system from this coevolutionary perspective: individuals in the considered stock could adapt their age at maturation in response to the selective pressure imposed by harvesting, while fishers adapted their strategy to maximize the sustainable yield on a slower timescale, causing directional selection on the age at maturation.

The interaction between adaptive harvest imposed by a fishery and biological evolution could possibly result in disruptive selection, as suggested by Carlson et al. (2007) and Edeline et al. (2007) and supported by statistical analysis of field data by Edeline et al. (2009). The objective of this study is to provide a first model-based investigation of this phenomenon. For this, we approach the stock-fishery system from the coevolutionary perspective, allowing harvest to adapt on the timescale of population dynamics, thus improving on Heino's (1998) timescale-separation assumption, and studying both directional and disruptive selective pressure. Disruptive selection can increase the genetic and/or phenotypic variance of adaptive traits (Gross, 1985; Edeline et al., 2009; Keller et al., 2013), and under some circumstances may even lead to evolutionary branching and dimorphic trait diversification (Maynard Smith, 1966; Geritz et al., 1998). Both impacts may increase a stock's capacity to respond to directional selective pressures (Roff, 1997), and may raise the stock's abundance and yield. Disruptive selection is notoriously difficult to predict and can also have negative effects on the ecosystem in which the fish stock is embedded (Jennings and Kaiser, 1998; Zhou et al., 2010). We conclude our investigation by discussing broad implications of our findings, which might be taken into account for the evolutionarily informed management of fisheries and the design of sustainable fishery policies.

2. Model and methods

We use a discretely size-structured life-history model, similar to that employed in Poos et al. (2011) and Bodin et al. (2012), to describe an adaptively harvested fish population divided into three size classes (Fig. 1). Individuals can mature either in the second or in the third size class, and accordingly differ in their sizes at maturation. We refer to the probability of maturing in the second size class as the probability of early maturation, and consider it an adaptive trait constrained by life-history tradeoffs (Roff, 1983; Stearns, 1992). From this stock-fishery model, we derive the stock's basic reproduction ratio in dependence of the adaptive trait, and from this, the evolutionary dynamics of maturation. Using bifurcation analysis (Kuznetsov, 2004) and numerical continuation techniques (Allgower and Georg, 2003), we study the selective pressures exerted on the stock by different levels of fishing mortality and by different levels of selectivity for size and/or maturity. In this way, we assess the potential for fish stocks to experience disruptive selection and thus potentially undergo maturation diversification (Fig. 2).

2.1. Population dynamics

We consider a stock in which individuals are classified into three size classes—juveniles, small, and large. An individual can become mature at small size (early maturation) with probability x or at large size with probability $1-x$ (Gross, 1985). The probability of early maturation is analyzed as an adaptive life-history trait under selection. Specifically, we denote by $\mathbf{N}(t)=(N_i(t))$ the vector of fish abundances at time t, with $i=1, 2, \tilde{2}, 3$, or $\tilde{3}$ ranging over all stock components (where tilde-subscripts refer to early-maturing individuals). Fig. 1 provides a schematic representation of the considered stock structure.

Newborn juvenile individuals grow into the second size class at rate r_1. With probability x, they are early-maturing, thus growing into stock component $\tilde{2}$, whereas with probability $1-x$ they are late-maturing, thus growing into stock component 2. Small individuals grow into the third size class at rates $r_{\tilde{2}}$ or r_2, depending on whether they are early-maturing or late-maturing, respectively. Early-maturing individuals give birth to juveniles in the second and third size classes,

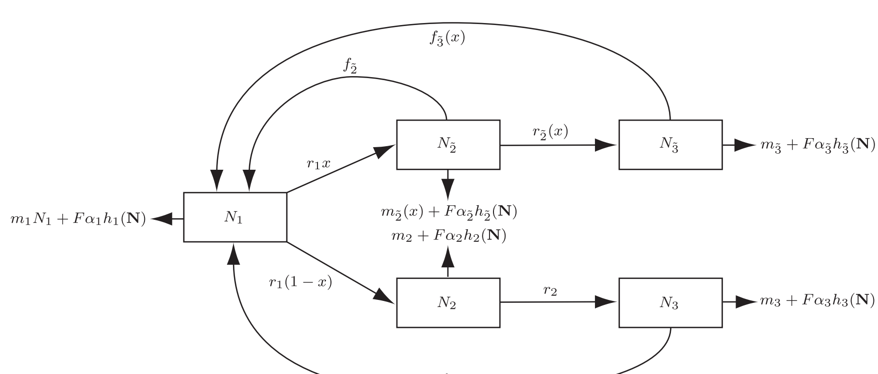

Fig. 1. Schematic representation of the life-history model. The harvested population is divided into juveniles (with density N_1), small individuals (with densities N_2 and $N_{\tilde{2}}$), and large individuals (with densities N_3 and $N_{\tilde{3}}$), where tilde-subscripts refer to early-maturing individuals. Individuals can either mature early (with probability x, growing into compartment $N_{\tilde{2}}$) or late (with probability $1-x$, growing into compartment N_2). The probability of early maturation is the adaptive trait considered in this study. Table 1 and Section 2 provide further details.

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