FISHERIES-INDUCED DISRUPTIVE SELECTION

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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.

Keywords: fisheries-induced evolution, coevolution, adaptive dynamics, disruptive selection, size at maturation.

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;

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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 (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

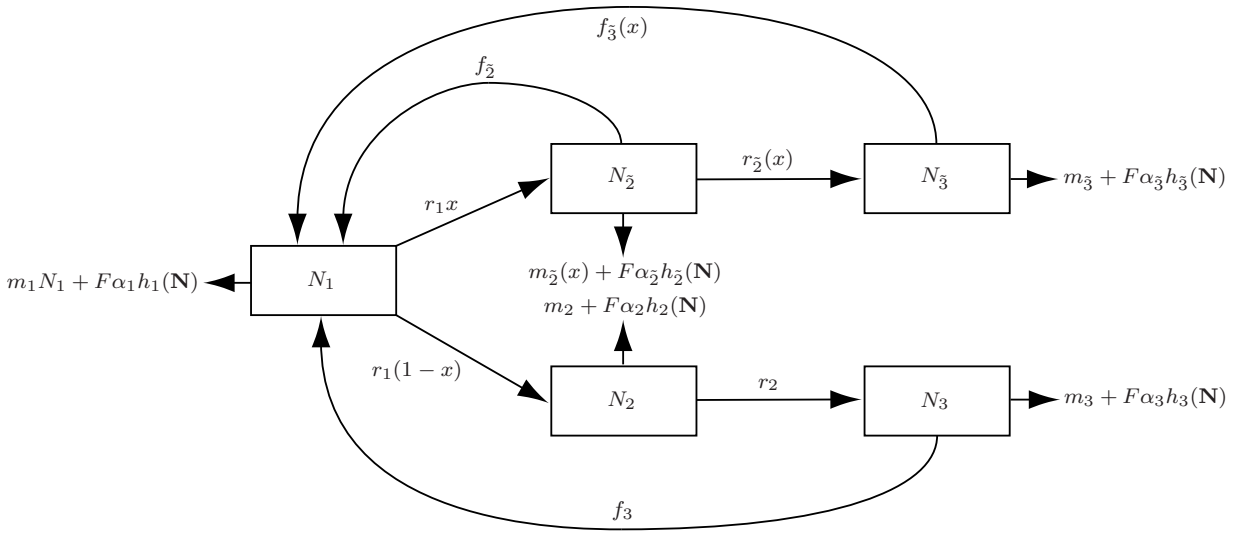

Figure 1: Schematic representation of the life-history model. The harvested population is divided into juveniles (with density N_1), small individuals (with densities $N_{\tilde{2}}$ and N_2), and large individuals (with densities $N_{\tilde{3}}$ and N_3), where tilde-subscripts refer to early-maturing 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.

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 (Figure 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 (Figure 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). Figure 1 provides a schematic representation of the considered stock structure.

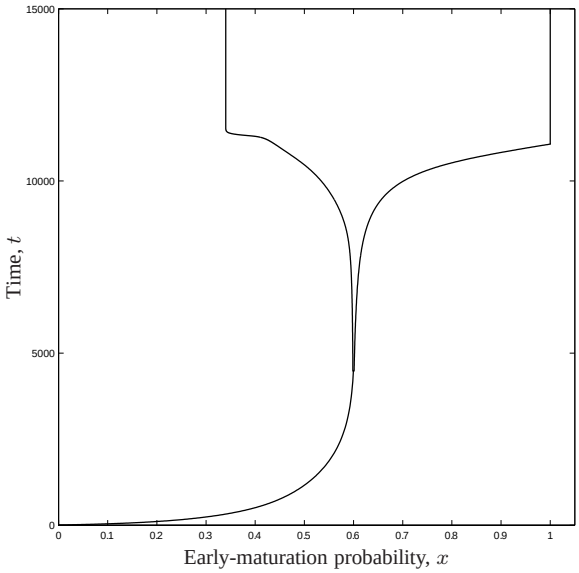

Figure 2: Model-based illustration of maturation diversification in response to fisheries-induced disruptive selection. The probability of early maturation, initially set at 0, gradually converges to a monomorphic evolutionary equilibrium at which selection turns disruptive and evolutionary branching takes place. The resultant two coexisting morphs, which initially are very similar, then diversify, eventually converging to a dimorphic evolutionary equilibrium. Parameters at their reference value (see Table 1) and $F = 1.1$ yr^{-1}.

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, at rates $f_{\tilde{2}}$ and $f_{\tilde{3}}$, respectively, while late-maturing individuals produce offspring only once they reach the third size class, at rate f_3. The natural mortality of juveniles is considered to be density-dependent, at rate $m_1 N_1$, indicating resource competition at the juvenile stage, since we assume juveniles critically depend on scarce resources in the environment. In contrast, we assume that small and large individuals experience density-independent mortality, as the spectrum of their feeding resources is often wide. Specifically, the natural mortality rates are assigned $m_{\tilde{2}}$ and m_2 in the small size class and $m_{\tilde{3}}$ and m_3 in the large size class, depending on whether they are early-maturing or late-maturing, respectively.

We assume that early-maturing individuals face several life-history tradeoffs, since energy allocation to maturation reduces the energy available for other life-history processes, including growth, survival, and reproduction (Poos et al., 2011; Bodin et al., 2012). We make the simplest possible assumptions for these three tradeoffs, by considering the mortality of small early-maturing individuals to be increased relative to small late-maturing individuals according to $m_{\tilde{2}}(x) = m_2(1+\beta_{\mathrm{m}}x)$, the growth rate of small early-maturing individuals to be decreased relative to small late-maturing individuals according to $r_{\tilde{2}}(x) = r_2(1-\beta_{\mathrm{r}}x)_+$, and the fecundity of large early-maturing individuals to be decreased relative to large late-maturing individuals according to $f_{\tilde{3}}(x) = f_3(1-\beta_{\mathrm{f}}x)_+$. In each case, the considered costs of early maturation are thus proportional to the probability x of early maturation, with proportionality constants β_{m}, β_{r}, and β_{f} measuring the strengths of the respective tradeoffs. The subscript $(\dots)_+$ means that negative values in the

	Notation	Description	Reference value	Unit
		Variables		
(a)	x	Early-maturation probability	n.a.	n.a.
	N_1	Density of juvenile individuals	n.a.	km^{-2}
	$N_{\tilde{2}}$	Density of early-maturing small individuals	n.a.	km^{-2}
	N_2	Density of late-maturing small individuals	n.a.	km^{-2}
	$N_{\tilde{3}}$	Density of early-maturing large individuals	n.a.	km^{-2}
	N_3	Density of late-maturing large individuals	n.a.	km^{-2}
(b)	$r_{\tilde{2}}(x)$	Growth rate of early-maturing small individuals	n.a.	yr^{-1}
	$f_{\tilde{3}}(x)$	Fecundity rate of early-maturing large individuals	n.a.	yr^{-1}
	$m_{\tilde{2}}(x)$	Mortality rate of early-maturing small individuals	n.a.	yr^{-1}
	$h_i(\mathbf{N})$	Relative adaptive harvest of component i	n.a.	n.a.
		Parameters		
(c)	r_1	Growth rate of juvenile individuals	1	yr^{-1}
	r_2	Growth rate of late-maturing small individuals	0.8	yr^{-1}
	$f_{\tilde{2}}$	Fecundity rate of early-maturing small individuals	0.8	yr^{-1}
	f_3	Fecundity rate of late-maturing large individuals	1	yr^{-1}
	m_1	Mortality rate of juvenile individuals	0.4	yr^{-1}
	m_2	Mortality rate of late-maturing small individuals	0.3	yr^{-1}
	$m_{\tilde{3}}$	Mortality rate of early-maturing large individuals	0.2	yr^{-1}
	m_3	Mortality rate of late-maturing large individuals	0.2	yr^{-1}
	β_r	Strength of growth tradeoff	1	n.a.
	β_f	Strength of fecundity tradeoff	1	n.a.
	β_m	Strength of mortality tradeoff	1	n.a.
	s_i	Size of individuals in component i	$0.3i$	m
	k	Allometric coefficient relating size to weight	0.01	tonnes $\text{m}^{-\theta}$
	θ	Allometric exponent relating size to weight	3	n.a.
	w_i	Weight of individuals in component i	ks_i^θ	tonnes
(d)	$\boldsymbol{\alpha} = (\alpha_i)$	Fishing policy	n.a.	n.a.
	F	Fishing-mortality rate	n.a.	yr^{-1}
	γ	Degree of harvest specialization	5	n.a.

Table 1: Variables and parameters of the stock-fishery model in Equations (1a). The index i refers to the five stock components, $i = 1$, 2, $\tilde{2}$, 3, or $\tilde{3}$. (a) Trait and densities. (b) Trait-dependent and density-dependent functions. (c) Stock parameters. (d) Fishery parameters.

parenthesis are mapped to 0, while positive values remain unchanged. This means that for values of $\beta_\text{r} > 1$ and $\beta_\text{f} > 1$ the growth rate $r_{\tilde{2}}(x)$ and the fecundity rate $f_{\tilde{3}}(x)$, respectively, may become zero as x increases, but can never become negative.

Based on these considerations, we obtain the following stock-fishery model

$$\begin{aligned}
\dot{N}_1 &= f_{\tilde{2}}N_{\tilde{2}} + f_{\tilde{3}}(x)N_{\tilde{3}} + f_3N_3 - m_1N_1^2 - r_1N_1 - F\alpha_1h_1(\mathbf{N})N_1,\\
\dot{N}_{\tilde{2}} &= xr_1N_1 - m_{\tilde{2}}(x)N_{\tilde{2}} - r_{\tilde{2}}(x)N_{\tilde{2}} - F\alpha_{\tilde{2}}h_{\tilde{2}}(\mathbf{N})N_{\tilde{2}},\\
\dot{N}_2 &= (1-x)r_1N_1 - m_2N_2 - r_2N_2 - F\alpha_2h_2(\mathbf{N})N_2,\\
\dot{N}_{\tilde{3}} &= r_{\tilde{2}}(x)N_{\tilde{2}} - m_{\tilde{3}}N_{\tilde{3}} - F\alpha_{\tilde{3}}h_{\tilde{3}}(\mathbf{N})N_{\tilde{3}},\\
\dot{N}_3 &= r_2N_2 - m_3N_3 - F\alpha_3h_3(\mathbf{N})N_3,
\end{aligned} \tag{1a}$$

where $\dot{N}_i$ is the time derivative of the abundance N_i of each component of the fish stock, while the last terms in each

		Juvenile	Late-maturing small	Early-maturing small	Late-maturing large	Early-maturing large	Results
(a)	No regulation	**Yes**	**Yes**	**Yes**	**Yes**	**Yes**	**Disruptive selection**
(b)	Only juvenile	**Yes**	No	No	No	No	No disruptive selection
	Only small	No	**Yes**	**Yes**	No	No	No disruptive selection
	Only large	No	No	No	**Yes**	**Yes**	**Disruptive selection** ($\beta_r < 1$)
	Juvenile or small	**Yes**	**Yes**	**Yes**	No	No	No disruptive selection
	Small or large	No	**Yes**	**Yes**	**Yes**	**Yes**	**Disruptive selection**
(c)	Only immature	**Yes**	**Yes**	No	No	No	No disruptive selection
	Only mature	No	No	**Yes**	**Yes**	**Yes**	**Disruptive selection**
(d)	Only immature and small	No	**Yes**	No	No	No	No disruptive selection
	Only mature and small	No	No	**Yes**	No	No	No disruptive selection

Table 2: Overview of the ten fishing policies examined in this study. Entries in the five central columns indicate whether harvesting the corresponding stock component is allowed by the considered fishing policy. The last column gives a summary of the results. (a) Non-selective fishing policy. (b) Size-selective fishing policies. (c) Maturity-selective fishing policies. (d) Size- and maturity-selective fishing policies.

equation describes harvest, as explained in the next subsection. All variables and parameters of our stock-fishery model are summarized in Table 1.

2.2. Fishery dynamics

Fishing activities imply an extra mortality in each stock component of the form $F\alpha_i h_i(\mathbf{N})N_i$, where i ranges over all five stock components, $i = 1$, 2, $\tilde{2}$, 3, or $\tilde{3}$, F denotes the fishing-mortality rate, the binary vector $\boldsymbol{\alpha} = (\alpha_i)$ characterizes the selective fishing policy according to fish size and maturity, and $h_i(\mathbf{N})$ is the relative adaptive harvest of stock component i.

We consider ten different fishing policies, with different selectivity according to size and maturity (Ajiad et al., 1999; Law, 2000; Poos et al., 2011; Bodin et al., 2012). These are detailed in Table 2. For example, fishing with no restrictions on size and maturity translates into the vector $\boldsymbol{\alpha} = (1, 1, 1, 1, 1)$, while a policy that allows fishing only of mature individuals is represented by the vector $\boldsymbol{\alpha} = (0, 0, 1, 1, 1)$. We assume the absolute implementation of the policies: there is perfect selectivity, no by-catch or other non-intended mortality.

The relative adaptive harvest $h_i(\mathbf{N})$ of stock component i is described by a power law (Egas et al., 2005),

$$h_i(\mathbf{N}) = \frac{(\alpha_i w_i N_i)^\gamma}{\sum_j (\alpha_j w_j N_j)^\gamma}, \tag{1b}$$

with the sum extending over all five stock components $j = 1$, 2, $\tilde{2}$, 3, or $\tilde{3}$. In this equation, w_i is the weight of a fish in stock component i, which is given by the allometric scaling relation $w_i = k s_i^\theta$, where k and θ are the allometric coefficient and allometric exponent, respectively, and s_i is the size of a fish in stock component i. Notice that the allometric coefficient cancels in Equation (1b); its only effect is that of scaling the yield, see Equations (1c) and (A2). The multiplication with fish weights translates the density of individuals into their biomass density. Therefore, the product $w_i N_i$ is the catch obtainable from harvesting stock component i. The parameter γ measures the degree of harvest specialization and ranges from 0 to ∞. When $\gamma = 0$, the harvest is not adaptive and is randomly distributed over all five stock components (in

analogy to random foraging). When $\gamma = 1$, the relative harvest for each stock component equals the relative catch from that compartment (in analogy to foraging according to the ideal free distribution). When γ tends to ∞, the harvest is completely focused on the stock component yielding maximum catch (in analogy to optimal foraging). We suggest the value of $\gamma = 5$ for a weakly specialized fishery and $\gamma = 25$ for a highly specialized fishery (see Table 1 and Figure 3).

The total sustainable yield of the fishery for a monomorphic stock with trait value x^* is given by

$$Y_{\mathrm{M}} = \sum_i F\alpha_i h_i(\mathbf{N}^*) N_i^* w_i \Big|_{x=x^*}, \tag{1c}$$

that is, the sum of the yields obtained by harvesting the five stock components $i = 1, 2, \tilde{2}, 3$, and $\tilde{3}$ at the eco-evolutionary equilibrium $(\mathbf{N}^*, x^*)$, following the fishing policy $\boldsymbol{\alpha} = (\alpha_i)$. A very similar expression gives the total sustainable yield for a dimorphic stock, see Equation (A2) in the Appendix.

2.3. Evolutionary dynamics

Following Poos et al. (2011) and Bodin et al. (2012), we derive the basic reproduction ratio R_0, measuring an individual's expected reproductive success in terms of offspring produced during its lifetime. This reproductive success depends both on the trait value of the focal individual and on the other trait values represented in the population. When an individual with trait value x' experiences a resident population with trait value x at its demographic equilibrium $\mathbf{N}^*(x)$, the focal individual's basic reproduction ratio is given by

$$R_0(x, x') = r_1 D_1 \{(1 - x') r_2 D_2 D_3 f_3 + x' [D_{\tilde{2}} f_{\tilde{2}} + r_{\tilde{2}}(x') D_{\tilde{2}} D_{\tilde{3}} f_{\tilde{3}}(x')]\}, \tag{2a}$$

where $D_1 = [m_1 N_1^* + r_1 + F\alpha_1 h_1(\mathbf{N}^*)]^{-1}$, $D_2 = [m_2 + r_2 + F\alpha_2 h_2(\mathbf{N}^*)]^{-1}$, $D_{\tilde{2}} = [m_{\tilde{2}}(x') + r_{\tilde{2}}(x') + F\alpha_{\tilde{2}} h_{\tilde{2}}(\mathbf{N}^*)]^{-1}$, $D_3 = [m_3 + F\alpha_3 h_3(\mathbf{N}^*)]^{-1}$, and $D_{\tilde{3}} = [m_{\tilde{3}} + F\alpha_{\tilde{3}} h_{\tilde{3}}(\mathbf{N}^*)]^{-1}$ are the average durations spent by individuals in each of the five stock components. These are inversely related to the exit rate from those stock components, see Figure 1 and Equations (1a). Thus, the product $r_i D_i$ is the probability that an individual in component i reaches the next size class, while the product $D_i f_i$ is the expected number of offspring produced by the individual while being in component i. The focal individual's basic reproduction ratio $R_0(x, x')$ is a fitness proxy and can be used for evolutionary invasion analysis. Specifically, if $R_0(x, x') > 1$, individuals with trait values x' can invade and, generically, substitute individuals of a population with resident trait value x; otherwise, such invasion is not possible.

The selection gradient

$$G(x) = \frac{\partial R_0(x, x')}{\partial x'} \Big|_{x' = x} \tag{2b}$$

is the slope of the fitness landscape $R_0(x, x')$ around x, and measures the strength of the directional selection on x. The rate of evolutionary change is proportional to this selection gradient, independent of whether one considers the gradual reshaping of a polymorphic resident trait distribution through selection (as in quantitative genetics theory) or changes in a monomorphic trait distribution through mutation and selection (as in adaptive dynamics theory) (Dieckmann et al., 2006).

Using the selection gradient, we can apply the canonical equation of adaptive dynamics theory (Dieckmann and

Law, 1996; Champagnat et al., 2006; Dercole and Rinaldi, 2008), an ordinary differential equation that deterministically approximates the evolutionary dynamics of the adaptive trait x. Specifically, the rate of change $\dot{x}$ in the trait value x is proportional to $G(x)$,

$$\dot{x} \propto \epsilon G(x), \tag{2c}$$

multiplied with half the product of population density, mutation probability, and mutation variance; since the latter three factors are positive, they only regulate the speed of the monomorphic dynamics on the evolutionary timescale, but do not affect the asymptotic evolutionary regime. While the time-scaling parameter ϵ is used to separate the slow evolutionary timescales from the fast demographic timescale (see also next section). Trait values $0 < x^* < 1$ for which $G(x^*) = 0$ are equilibria of the adaptive dynamics, and hence are called evolutionarily singular points. The boundaries $x^* = 0$ and $x^* = 1$ are also evolutionary equilibria, even if, generically, the selection gradient $G(x)$ does not vanish at such points (Bodin et al., 2012). Internal equilibria $(0 < x^* < 1)$ and boundary equilibria ($x^* = 0$ or $x^* = 1$) represent mixed strategies and pure strategies, respectively (see Gross 1996 for a review).

If the dynamics of the adaptive trait x described by the canonical equation (2c) converges to an evolutionary equilibrium x^*, that trait value is said to be convergence stable. For internal equilibria, the slope of the fitness landscape then vanishes, and the curvature of the fitness landscape $R_0(x^*, x')$ in x' determines whether x^* is evolutionarily stable or not. If the fitness landscape has a maximum at x^* (negative curvature), no mutants can invade and x^* is evolutionarily stable: since it is also convergence stable, it is a so-called continuously stable strategy (CSS) (Eshel, 1983; Geritz et al., 1998), characterizing an endpoint of the evolutionary dynamics. Otherwise, if the adaptive dynamics converge to a fitness minimum, it is evolutionarily unstable. Thus, the condition for evolutionary instability is given by

$$\left.\frac{\partial^2 R_0(x^*, x')}{\partial x'^2}\right|_{x' = x^*} > 0. \tag{2d}$$

If Condition (2d) is satisfied, x^* is a fitness minimum, so mutants on both sides of x^* can invade. Such mutants and the former residents then coexist on the ecological timescale, forming a new dimorphic resident population. Their traits will experience further disruptive selection and, in the case of asexual populations, are expected to diversify on the evolutionary timescale (Figure 2). Such diversification can occur also in sexual populations, provided reproductive isolation between the incipient species arises concomitantly (e.g., Keller et al. 2013): here we do not dwell on such complications, which would deserve and require a dedicated separate study, but we assume the concomitant evolution of reproductive isolation. Monomorphic convergence stable singular points satisfying condition (2d) are called evolutionary branching points (Geritz et al., 1997, 1998; Dercole and Rinaldi, 2008). In our analysis below, we will thus test Condition (2d) at monomorphic evolutionary equilibria x^* under different fishing policies, as well as for different levels of fishing mortality and different degrees of harvest specialization.

2.4. Outline of analysis

In our further analysis, we use numerical bifurcation analysis and continuation techniques, in an approach similar to that in Landi et al. (2013), to which interested readers are invited to refer for more detailed explanations and discussions.

As the fishing-mortality rate F is the driver of fisheries-induced selection on the stock, we use it as our primary bifurcation parameter. We then extend the analysis by adding a secondary bifurcation parameter, for which we choose γ, measuring the degree of harvest specialization. In this way, we can assess the effects of fishing, in terms of fishing mortality and fishing specialization, on the occurrence of disruptive selection. To evaluate the generality of results, we also consider as alternative secondary bifurcation parameters the tradeoff strengths β_{r}, β_{f}, and β_{m}. Eventually, we consider all other demographic and environmental parameters as secondary bifurcation parameters. This procedure will pinpoint the characteristics of stocks that are more likely to experience fisheries-induced disruptive selection, as well as the characteristics of fishing regimes that are more likely to cause such selection. To conclude, we evaluate the effect of fisheries-induced diversification on sustainable yield.

As the analytic form of the demographic equilibrium $\mathbf{N}^*(x)$ is unknown for calculating $R_0(x, x')$ in Equation (2a), we numerically integrate a fast-slow eco-evolutionary dynamics according to Equations (1a) and (2c), where the time-scaling parameter $\epsilon = 10^{-3}$ regulates the relative speed of the (slow) evolutionary dynamics relative to the speed of the (fast) demographic dynamics (Abrams et al., 1993; Landi et al., 2013). Extensive and systematic numerical analyses of Equations (1a) reveal that there can only be one nontrivial stable equilibrium $\mathbf{N}^*(x)$ for all $0 \leq x \leq 1$. This simplifies the analysis of the adaptive dynamics by ruling out possible bifurcations of the demographic dynamics that could complicate the evolutionary dynamics (Dercole et al., 2002).

We first consider the case without fishing mortality ($F = 0$), with all other parameters set as in Table 1; those parameter values are suitable to model, e.g., the Northern Atlantic Cod stock and are chosen for convenient illustration. Other values have been found to produce qualitatively similar results. We start the fast-slow eco-evolutionary dynamics from the demographic initial condition $\mathbf{N}(0)$ and the evolutionary initial condition $x(0)$ and integrate these dynamics until they converge to the unique eco-evolutionary equilibrium $(\mathbf{N}^*, x^*)$. This equilibrium turns out to be a CSS, suggesting that the unharvested stock never experiences disruptive selection and at evolutionary equilibrium has a low probability of early maturation. We then successively consider each of the ten fishing policies listed in Table 2 and examine how the eco-evolutionary equilibrium responds to increasing fishing-mortality rate F (Figure 3). While doing so, we continuously monitor Condition (2d), which is not satisfied at $F = 0$. Depending on the fishing policy, the fishing mortality may reach a threshold $F = F_{\mathrm{B}}$ at which a branching bifurcation occurs, i.e., selection turns disruptive. This means that the initial CSS turns into an evolutionary branching point. We continue to follow this branching bifurcation point while changing both the fishing-mortality rate F and the degree of specialization γ, obtaining the bifurcation curve in the bivariate (F, γ) space that separates regions of disruptive and stabilizing selection (Figure 4).

3. Results

We first examine which fishing policies can cause disruptive selection, then investigate which kinds of fish stocks are susceptible to fisheries-induced disruptive selection, and finally, analyze the effects of fisheries-induced diversification on sustainable yield.

3.1. Which fishing policies can cause fisheries-induced disruptive selection?

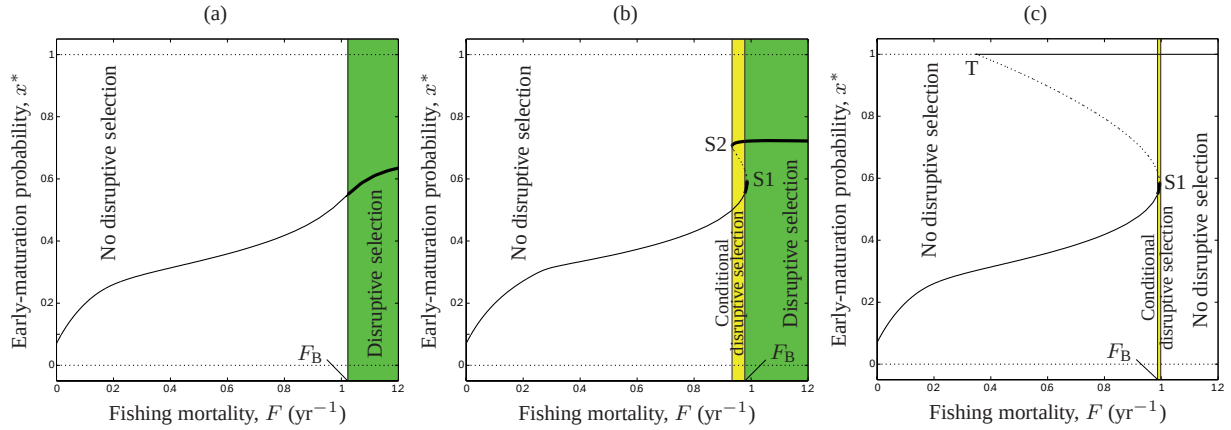

Figure 3: Three qualitatively different routes to fisheries-induced disruptive selection on the probability of early maturation as fishing mortality is increased. In panel (a) there is only a single internal equilibrium for any value of the fishing mortality. In panel (b) there is bistability between two internal equilibria for a range of fishing mortalities. In panel (c), there is bistability between an internal equilibrium and a boundary equilibrium. Panels (a) and (b) show results for the no-regulation fishing policy; results are qualitatively equivalent for the small-or-large and the only-mature fishing policies, as well as for the only-large fishing policy when $\beta_r < 1$. Panel (c) shows results for the only-large fishing policy when $\beta_r \geq 1$. Throughout the panels, convergence stable and evolutionarily stable equilibria (continuously stable strategies or CSSs) are represented by a thin line, convergence stable but evolutionarily unstable equilibria (evolutionary branching points) are represented by a thick line, and convergence unstable equilibria (evolutionary repellors) are represented by a dotted line. The fishing mortality at the bifurcation point at which selection turns disruptive, and thus can cause evolutionary branching, is indicated by F_B. Saddle-node bifurcations, at which a convergence stable internal equilibrium collides with a convergence unstable internal equilibrium, are indicated by S1 and S2. A transcritical bifurcation, at which a convergence stable boundary equilibrium collides with a convergence unstable internal equilibrium, is indicated by T. Yellow and green regions represent intervals of fishing mortality causing conditional disruptive selection and disruptive selection, respectively. In the former case, two convergence stable equilibria coexist, but only one of them is evolutionarily unstable: it thus depends on the ancestral condition whether or not disruptive selection will occur. Initial conditions: $\mathbf{N}(0) = (1, 1, 1, 1, 1)$ km^{-2}, $x(0) = 0.5$. Parameters at their reference value (see Table 1), except for $\gamma = 25$ in (b).

Figure 3 shows three qualitatively different routes to fisheries-induced disruptive selection revealed by our model. As fishing mortality is increased in each scenario, the globally convergence stable evolutionarily stable equilibrium at low early-maturation probability shifts to higher early-maturation probabilities before losing its stability: in scenario (a), it loses its evolutionary stability, while in scenarios (b) and (c), it first loses its global convergence stability and then its evolutionary stability.

Scenario (a). At all levels of fishing mortality, only a single internal equilibrium $(0 < x^* < 1)$ is present, which is always globally convergence stable. Both boundary equilibria ($x^* = 0$ and $x^* = 1$) are convergence unstable. The early-maturation probability increases with fishing mortality. At high levels of fishing mortality ($F > F_B$; green region), the internal equilibrium loses its evolutionary stability, so selection becomes disruptive. This scenario occurs for four of

the ten studied fishing policies: it applies to the no-regulation, small-or-large, and only-mature fishing policies, as well as to the only-large fishing policy when $\beta_r < 1$ (see below).

Scenario (b). At intermediate levels of fishing mortality ($F_{S1} < F < F_{S2}$), two alternative convergence stable internal equilibria are present. At either end of the interval, two different saddle-node bifurcations occur ($F = F_{S1}$ and $F = F_{S2}$, with $F_{S2} < F_{S1}$), annihilating one of the convergence stable internal equilibria. The upper internal convergence stable equilibrium is always an evolutionary branching point, whereas the lower internal convergence stable equilibrium is an evolutionary branching point only for $F > F_B$. In this scenario, selection is conditionally disruptive, depending on the ancestral condition $x(0)$, when $F_{S2} < F < F_B$ (yellow region), as the early-maturation probability can either converge to the upper internal convergence stable equilibrium (which is an evolutionary branching point; thick line) or to the lower internal convergence stable equilibrium (which is a CSS; thin line). Selection is always disruptive for $F > F_B$ (green region), no matter which one of the two internal convergence stable equilibria is reached from the ancestral condition. This scenario occurs for four of the ten studied fishing policies: it applies to the no-regulation, small-or-large, and only-mature fishing policies, as well as to the only-large fishing policy when $\beta_r < 1$ (see below). Notice that this set of fishing policies is the same as for scenario (a), highlighting that it depends on model parameters other than fishing mortality which of the two scenarios applies.

Scenario (c). At intermediate levels of fishing mortality ($F_T < F < F_{S1}$), a convergence stable internal equilibrium coexists with a convergence stable boundary equilibrium. At either end of the interval, two different bifurcations occur, annihilating one of the convergence stable equilibria. First, a transcritical bifurcation happens at $F = F_T$, when the convergence unstable internal equilibrium (dotted line) collides with the convergence stable boundary equilibrium $x^* = 1$ (thin line), exchanging their convergence stability. Second, a saddle-node bifurcation happens at $F = F_{S1}$ when the same convergence unstable internal equilibrium (dotted line) collides with the internal evolutionary branching point (thick line). In this scenario, selection is conditionally disruptive, depending on the ancestral condition, when $F_B < F < F_{S1}$ (yellow region): if the ancestral condition $x(0)$ lies below the convergence unstable internal equilibrium (dotted line), the early-maturation probability converges to the convergence stable internal equilibrium (which is an evolutionary branching point; thick line), so selection becomes disruptive. In contrast, if the ancestral condition lies above the convergence unstable internal equilibrium, the early-maturation probability converges to the boundary equilibrium $x^* = 1$, where selection cannot be disruptive, as trait values $x > 1$ are unfeasible. This scenario occurs for only one fishing policy: it applies to the only-large fishing policy when $\beta_r \geq 1$ (see below).

These results imply that fisheries-induced disruptive selection is readily caused by commonly used fishing policies, namely those targeting large adult and mature individuals while protecting juveniles and immature individuals (Fenberg and Roy, 2008; Darimont et al., 2009). By contrast, scenarios (a) to (c) cannot occur for six of the ten studied fishing policies: this applies to the only-juvenile, only-small, juvenile-or-small, only-immature, only-immature-and-small, and only-mature-and-small fishing policies. Consequently, these six types of fisheries can never cause fisheries-induced disruptive selection (see Table 2).

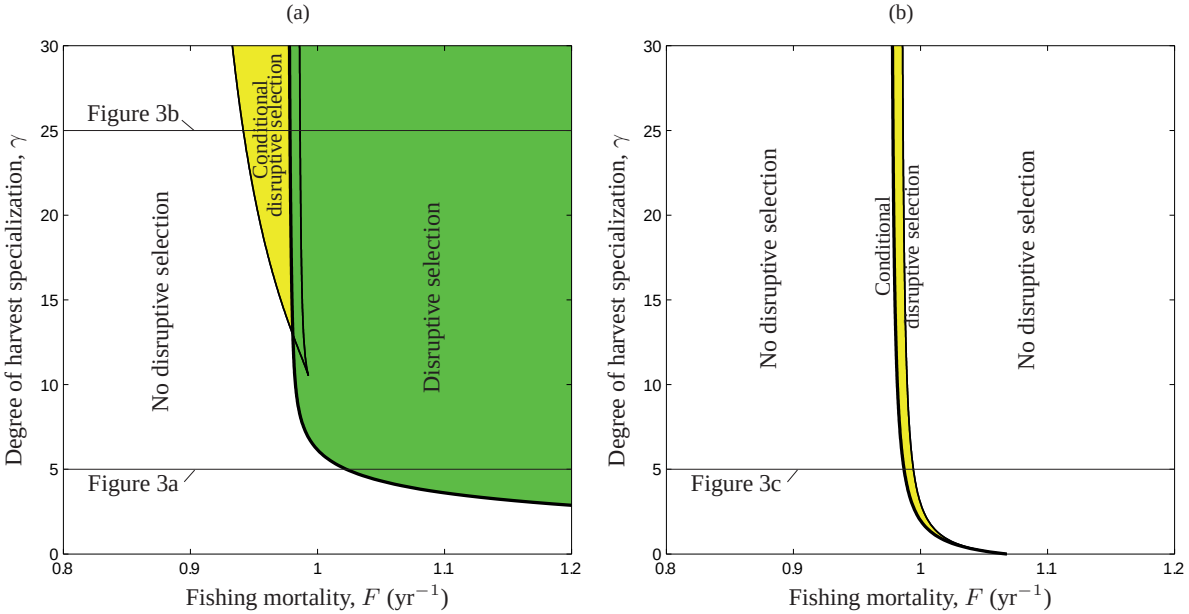

Figure 4: Two qualitatively different routes to fisheries-induced disruptive selection on the probability of early maturation as fishing mortality and harvest specialization are varied together. White, yellow, and green regions indicate parameter combinations for which selection is not disruptive, conditionally disruptive (depending on the ancestral evolutionary condition), and disruptive, respectively. The bifurcation curves along which evolutionary branching starts to be possible are represented as thick lines, while saddle-node bifurcation curves are represented as thin lines. The univariate scenarios shown in Figure 3 are slices of the bivariate scenarios shown here, as indicated by labeled horizontal lines in both panels. Panel (a) shows results for the no-regulation fishing policy; results are qualitatively equivalent for the small-or-large and only-mature fishing policies, as well as for the only-large fishing policy when $\beta_\mathrm{r} < 1$. Panel (b) shows results for the only-large fishing policy when $\beta_\mathrm{r} \geq 1$. Parameters at their reference value (see Table 1).

We can now expand our analysis by considering the effect of harvest specialization on disruptive selection. For this, we need to continue the aforementioned bifurcations in the bivariate (F, γ) space, obtaining the bivariate disruptive-selection scenarios shown in Figure 4. These plots provide a full qualitative characterization of the effects of fishing—in terms of policy, fishing mortality, and the degree of harvest specialization—on disruptive selection. Notice that the univariate scenarios shown in Figure 3 can be understood as slices, for fixed degrees of harvest specialization γ, of the bivariate scenarios shown in Figure 4. In particular, Figures 3a and 3b are slices of Figure 4a for two different degrees of harvest specialization, while Figure 3c is a slice of Figure 4b. For this reason, we only have two bivariate scenarios, one applying to the no-regulation, small-or-large, and only-mature fishing policies, as well as to the only-large fishing policy when $\beta_\mathrm{r} < 1$ (Figure 4a) and the other one applying to the only-large fishing policy when $\beta_\mathrm{r} \geq 1$ (Figure 4b).

From these bivariate scenarios we obtain the following results. First, disruptive selection occurs only for high levels of fishing mortality. Second, harvest specialization promotes disruptive selection: at high values of γ, selection turns disruptive already for lower fishing mortalities (this effect becomes saturated as harvest specialization is increased). Third, random, and thus non-adaptive, harvest ($\gamma = 0$) prohibits disruptive selection, demonstrating that adaptive harvest is a necessary condition for the occurrence of fisheries-induced disruptive selection. Fourth, all four fishing policies causing disruptive selection target large individuals, which therefore is a second necessary condition for the occurrence of fisheries-induced disruptive selection.

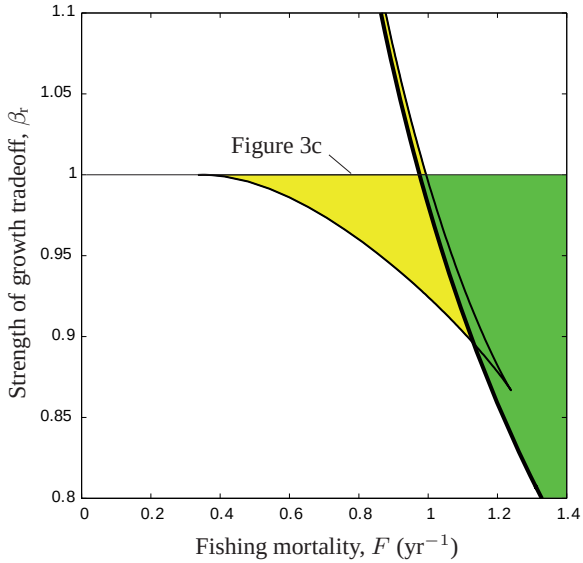

Figure 5: Limited realism and generality of the fisheries-induced disruptive selection scenario for the only-large fishing policy with $\beta_r \geq 1$. As explained in the text, this scenario unrealistically allows the stock to escape all fishing by maturing early. Also, it can never cause unconditional fisheries-induced disruptive selection, and can cause conditional fisheries-induced disruptive selection only for the restrictive conditions in the narrow yellow band in the upper part of the figure. Hence, the more realistic and general scenario is that in Figure 4a. Colors and lines as in Figure 4. Parameters at their reference value (see Table 1).

3.2. Which kinds of fish stocks are susceptible to fisheries-induced disruptive selection?

To find out which kinds of stocks are susceptible to fisheries-induced disruptive selection, we carry out a sensitivity analysis for the two fisheries-induced disruptive selection scenarios in Figure 4 with respect to the tradeoff strengths β_m, β_r, and β_f (Figures 5 and 6), continuing all detected bifurcations in the (F, β_j) spaces, with j spanning all three tradeoffs, $j =$ m, r, or f.

We find that the univariate and bivariate scenarios for disruptive selection under the only-large fishing policy (Figures 3c and 4b, respectively) occur only when $\beta_r \geq 1$ (Figure 5), that is, when the growth tradeoff is very strong. Figure 3c shows that for $\beta_r = 1$ and large fishing mortality F only the boundary equilibrium $x^* = 1$ exists: at that evolutionary equilibrium, $r_{\tilde{2}} = 0$, i.e., early-maturing individuals stop growing. The stock will then be composed of only juveniles and early-maturing small individuals, so that, under the considered only-large fishing policy, it escapes all fishing. Such a complete escape from fishing seems clearly unrealistic: at the very least, it would trigger a switch to a different fishing policy. Figure 5 shows that, when $\beta_r \geq 1$, this unrealistic situation occurs for even smaller fishing mortalities F. We therefore discard the scenarios in Figures 3c and 4b as unrealistic for larger fishing mortalities F. In addition, these scenarios can never cause unconditional fisheries-induced disruptive selection, while the conditions under which they cause conditional fisheries-induced disruptive selection are very restrictive, as the narrowness of the yellow regions in Figures 3c, 4b, and 5 documents. For these reasons, we focus our further analyses on the scenarios in Figures 3a, 3b, and 4a, which also cover the only-large fishing policy for $\beta_r < 1$. For the purpose of illustration, we consider the no-regulation fishing policy, as all effects shown in Figure 6 are qualitatively equivalent for all four fishing policies that can

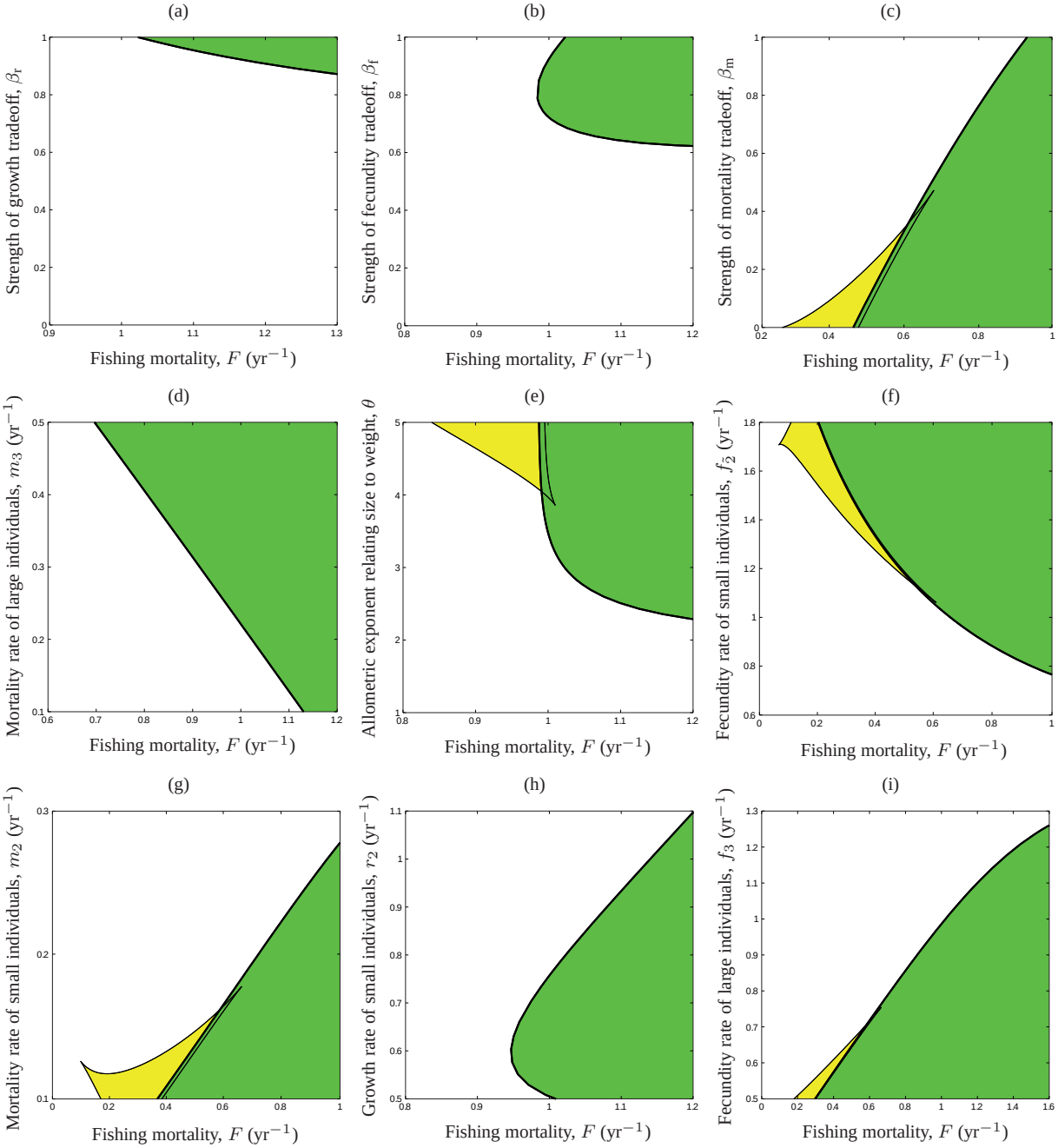

Figure 6: Effects of tradeoff strengths, demographic parameters, and environmental parameters on fisheries-induced disruptive selection. (a, b) Tradeoffs in growth and fecundity promote disruptive selection: the presence of both tradeoffs is a necessary condition for disruptive selection. (c) Tradeoffs in mortality restrain disruptive selection. (d, e, f) parameters that promote disruptive selection. (g, h, i) other parameters that restrain disruptive selection. All shown effects are discussed in Section 3.2. Parameter ranges along the axes are chosen so as to exclude parameter combinations for which the stock would go extinct on the evolutionary timescale. Colors and lines as in Figure 4. Parameters at their reference value (see Table 1).

cause disruptive selection in the scenarios in Figures 3a, 3b, and 4a (no-regulation, small-or-large, only-mature fishing policies, as well as only-large fishing policy when $\beta_r < 1$).

Relaxing the tradeoffs in growth and fecundity restrains disruptive selection (Figures 6a and 6b). Disruptive selection is impossible when either one of these tradeoffs is absent (i.e., when $\beta_r = 0$ or $\beta_f = 0$; Figures 6a and 6b): this means

that the joint presence of growth and fecundity tradeoffs of early maturation is a necessary condition for the occurrence of disruptive selection. In contrast, relaxing the tradeoff in mortality promotes disruptive selection (Figure 6c), and disruptive selection is still possible even when this tradeoff is absent (i.e., when $\beta_{\mathrm{m}} = 0$; Figure 6c).

To identify other characteristics of fish stocks that are susceptible to fisheries-induced disruptive selection, we now analyze the effects of all demographic and environmental parameters. In this way, we obtain the following findings. First, the juvenile growth rate r_1 and the juvenile mortality rate m_1 do not have any effect on disruptive selection (not illustrated). This is because all individuals have to pass through the juvenile stage in a way that cannot be affected by their adaptive trait. Second, disruptive selection is promoted by increasing the mortality rate m_3 of large individuals (Figure 6d), the allometric exponent θ relating size to weight (Figure 6e), and the fecundity rate $f_{\tilde{2}}$ of early-maturing small individuals (Figure 6f). Increasing the first two parameters can reduce the time individuals spend in the large size class, lowering that class' contribution to fitness according to Equation (2a). Equivalently, increasing the last parameter increases the contribution of small individuals to fitness. Hence, all three cases select for earlier maturation: this, in turn, strengthens the impacts of the considered tradeoffs and thereby promotes disruptive selection. Third, by contrast, disruptive selection is restrained by increasing the mortality rate m_2 of late-maturing individuals (Figure 6g), the growth rate r_2 of late-maturing small individuals (Figure 6h), and the fecundity rate f_3 of late-maturing large individuals (Figure 6i). Hence, all three cases select for later maturation; this, in turn, weakens the impacts of the considered tradeoffs and thereby restrains disruptive selection.

In general, therefore, selection is more likely to be disruptive if large individuals make a smaller contribution to fitness according to Equation (2a), that is, when selection for early maturation is naturally strong. Then the resultant high early-maturation probability will strengthen the impact of life-history tradeoffs in growth and fecundity so as to promote fisheries-induced disruptive selection.

3.3. What are the effects of diversification on sustainable yield?

We now analyze the situation in which, after diversification, two coexisting resident populations exhibit alternative trait values x and y close to the evolutionary equilibrium x^* of the monomorphic stock. These two coexisting resident traits then diverge on the evolutionary timescale, under the continuous influence of disruptive selection, and eventually settle onto a dimorphic evolutionary equilibrium $(x^*_{\mathrm{D}}, y^*_{\mathrm{D}})$ (Figure 2). The corresponding dimorphic evolutionary dynamics are specified in the Appendix. In principle, a dimorphic evolutionary equilibrium might be an evolutionary branching point for one or both of the diverged populations. However, in our case, y^*_{D} always equals 1, i.e., individuals of one resident population are always maturing as early as possible; as highlighted above, such a boundary equilibrium cannot be an evolutionary branching point. By contrast, x^*_{D} is evolutionarily stable. Therefore, no further diversification is possible at the dimorphic evolutionary equilibrium.

Once the dimorphic evolutionary equilibrium is attained, the stock's density, and thus its sustainable yield, change relative to the monomorphic evolutionary equilibrium. Using Equations (1c) and (A2), we can evaluate the sustainable yield for different fishing-mortality rates F (Figure 7), again using numerical continuation. We thereby find that, for

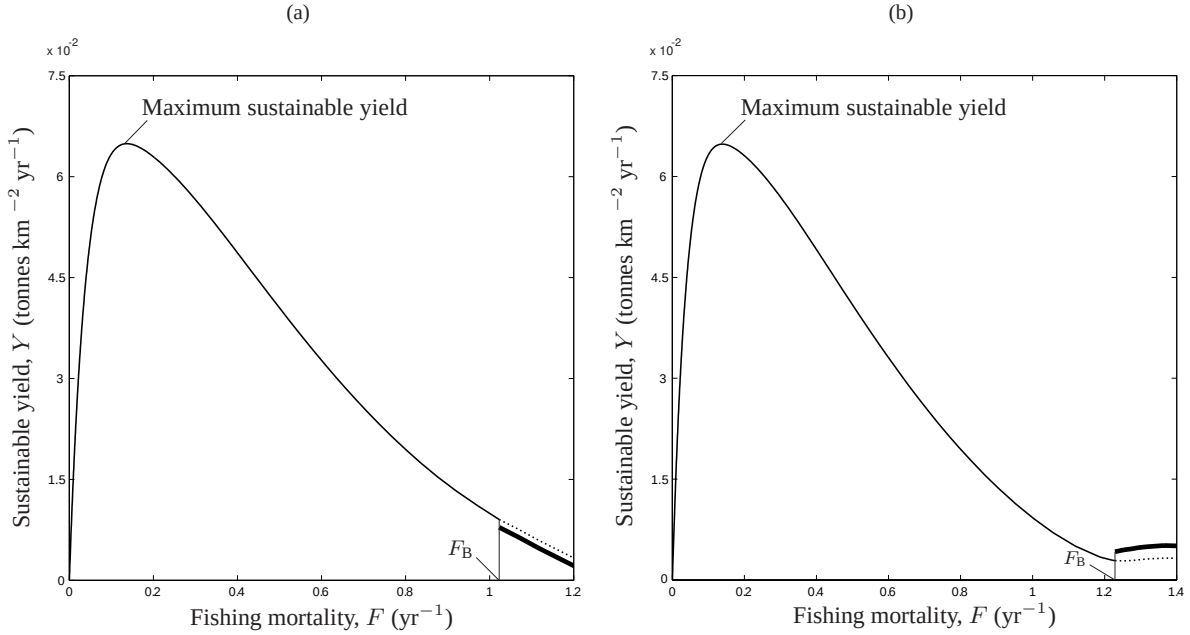

Figure 7: Effects of fisheries-induced diversification on sustainable yield. Panel (a) shows results for the no-regulation fishing policy; results are qualitatively equivalent for the small-or-large and the only-mature fishing policies. Panel (b) shows results for the only-large fishing policy when $\beta_{\mathrm{r}} < 1$. Selection is not disruptive for low fishing mortality rates ($F < F_{\mathrm{B}}$), including those resulting in maximum sustainable yield. By contrast, when the stock is heavily exploited ($F > F_{\mathrm{B}}$), diversification may occur. The sustainable yield is represented by thin lines for the monomorphic stock when selection is not disruptive, by dashed lines for the monomorphic stock when selection is disruptive, and by thick lines for the dimorphic stock. As shown in (a) and (b), diversification can cause either a decrease or an increase in yield, respectively, depending on the fishing policy. Parameters at their reference value (see Table 1), except for $\beta_{\mathrm{r}} = 0.85$ in (b).

$0 < F < F_{\mathrm{B}}$ (where F_{B} again denotes the fishing mortality rate at the branching bifurcation) the stock stays at its monomorphic evolutionary equilibrium x^*, while for $F > F_{\mathrm{B}}$ the monomorphic evolutionary equilibrium becomes evolutionarily unstable, and the stock, following a two-dimensional canonical equation, Equation (A1), converges to $(x^*_{\mathrm{D}}, y^*_{\mathrm{D}})$. Note that discontinuities in yield at $F = F_{\mathrm{B}}$ shown in Figures 7a and 7b are not surprising, as the outcome of the evolutionary dynamics does not vary continuously with the fishing mortality F across the branching bifurcation.

After diversification, the sustainable yield can slightly increase, but only for the only-large fishing policy when $\beta_{\mathrm{r}} < 1$. Even then, it remains far below the maximum sustainable yield, defined by the peaks in Figures 7a and 7b. When the fishing-mortality rate F is increased beyond F_{B}, the sustainable yield continuously declines toward zero for the no-regulation, small-or-large and only-mature fishing policies, but remains practically constant (after slightly increasing) for the only-large fishing policy when $\beta_{\mathrm{r}} < 1$. This is because the only-large fishing policy, in contrast to the other three fishing policies, does not allow fishing on the early-maturing small individuals in stock component $\tilde{2}$, which are vital for sustaining the stock under very high exploitation rates.

4. Discussion

Human exploitation of fish stocks as renewable resources often causes massive mortality. This alters the fitness landscapes of the exploited fish stocks, which in turn may cause adaptive responses of the stocks' phenotypic and genotypic variability (Hutchings and Fraser, 2008). In general, coexisting life-history strategies and corresponding polymorphism can be induced and maintained by negatively frequency-dependent selection (as, for example, in the size at maturation of male coho salmon; Gross 1985). In this study, we have considered a life-history trait given by a discrete probabilistic reaction norm for the size at maturation (Dieckmann and Heino, 2007), representing the amount of energy allocated to early maturation. In particular, we assume limited energy availability only in the juvenile stage (which translates into density-dependent mortality due to resource competition), while no such limitations are present for the small and large life stages. However, early maturation imposes limitations for other physiological activities, such as growth, reproduction, and survival. For this reason, we introduced trait-dependent tradeoffs: the more energy is allocated to early maturation, the higher the resultant costs in terms of reduced growth, survival, and reproduction. Here we have demonstrated that fisheries-induced selection on such a trait can be disruptive: this means not only that dimorphism in fish populations can be maintained, but also that such dimorphism may evolve *de novo* (Keller et al., 2013), thereby giving rise to a coexistence of maturation strategies (Gross, 1996). Several empirical studies have argued the possibility of disruptive selection in fish populations through the interplay of natural selection and adaptive harvesting (Carlson et al., 2007; Edeline et al., 2007, 2009): here we have systematically analyzed, for the first time, under which specific conditions such disruptive selection may arise.

Fishing imposes a strong selective pressure for early maturation, even though this is accompanied by increased physiological costs via life-history tradeoffs. In our model, such selection forces first give rise to a convergence stable mixed strategy, consistent with the argument by Carlson et al. (2007) that natural selection and fisheries-induced selection often act in opposite directions and hence produce strongly stabilizing selection. We have found that, however, with sufficiently strong tradeoffs in growth and fecundity, this convergence stable mixed strategy can become evolutionarily unstable, implying disruptive selection and enabling the coexistence of two maturation strategies, consistent with the argument by Edeline et al. (2009) that fisheries-induced disruptive selection tends to increase trait variance. Specifically, a harvested stock may split into two life-history types: one exploits the advantages of early maturation, while the other reduces the losses imposed by growth and fecundity tradeoffs. By contrast, an analogous life-history tradeoff in mortality has the opposite effect: disruptive selection is enhanced when this tradeoff is relaxed. Moreover, we have shown that strong growth and fecundity tradeoffs both act as indispensable prerequisites for disruptive selection (Figures 6a and 6b), while a weak mortality tradeoff merely serves as a dispensable promotor of disruptive selection (Figure 6c).

In addition to strong life-history tradeoffs in both growth and fecundity, we have identified two other necessary conditions for a stock-fishery system to experience disruptive selection: (i) fishing policies that target large individuals, and (ii) adaptive harvesting that adjusts the harvest distribution for optimal benefit (Figure 4). Ultimately, these two condi-

tions emerge from the same mechanism described in the previous paragraph. For selection to turn disruptive, the impact of growth and fecundity tradeoffs must become large, and this happens more readily when the probability of early maturation becomes high. Harvesting a stock's large individuals, as happens through many widely adopted fishing policies (Table 2), increases the directional selection pressure toward early maturation, as recurrently highlighted by earlier studies (e.g., Law 1979; Law and Grey 1989; Abrams and Rowe 1996). Moreover, when harvesting is adaptive, a fishery behaves similar to an optimally foraging predator that maximizes its intake rate (e.g., Egas et al. 2005): this tends to increase the mortality of large individuals, as these are more profitable to harvest (Fenberg and Roy, 2008; Darimont et al., 2009). Due to economic, technological, or regulation reasons, large and mature individuals are often the target of fishing. For example, the trawl fisheries of North Sea sole and plaice mainly target only large individuals; a scientific gill net fishery in Windermere, UK, has targeted large individuals of Northern pike for four decades (Carlson et al., 2007; Edeline et al., 2009). Size-selective gill nets were also used for catching striped bass in Maryland during 1950s (Mansueti, 1961); size-selective harvesting of British Columbia pink salmon has been recorded since 1950 (McAllister and Peterman, 1992). Mature individuals of Norwegian spring-spawning herring have been harvested at their spawning grounds throughout the 20th century, while mature individuals of Northeast Arctic cod have been harvested during their spawning migration until the mid-20th century (Poos et al., 2011). Therefore, adaptive harvesting under policies that allow the targeting of large individuals alters natural adaptive landscapes in a way that selects for increased reproductive investment early in life. This, in turn, reduces somatic growth and fecundity later in life through life-history tradeoffs (Edeline et al., 2007), and thereby strengthens the mechanism that leads to disruptive selection. Poos et al. (2011) and Bodin et al. (2012) have considered a rather similar model, yet without considering adaptive harvesting and trait-dependent tradeoffs: this explains why disruptive selection was not found in their analyses. For the same reason, they did not detect evolutionary bistability. In contrast, other studies on fisheries-induced evolution did report the presence of bistability in some traits (Gårdmark and Dieckmann, 2006; de Roos et al., 2006; Boukal et al., 2008). Our study appears to be the first in which evolutionary bistability co-occurs with disruptive selection, and consequently such bistability can be interpreted as an early warning signal for potential disruptive selection (see Figure 3).

In line with these findings and explanations, our results have also shown that populations with demographic conditions that penalize large individuals and/or favor small individuals are more sensitive to disruptive selection. This is because such populations are naturally prone to early maturation, strengthening the impacts of the tradeoffs in growth and fecundity that turn selection disruptive. Therefore, there are three different ways to promote the mechanism that turns selection disruptive via growth and fecundity tradeoffs: first, the tradeoffs themselves may be strong due to physiological reasons; second, fishing mortality may select for early maturation, making the impacts of those tradeoffs strong; and third, a stock's other demographic and environmental conditions may predispose it to early maturation. Overall, this pattern of chasing the benefits of early maturation while avoiding the costs in growth and fecundity can be considered as an important general mechanism for the origin of dimorphism in exploited fish populations and other coevolving systems (e.g., Zhang et al. 2013).

Our study can be expanded in several directions. First, the target fish stock is only one component in its embedding ecosystem, where feedbacks to and from its resources and/or predator species intertwine in a complicated web. However, considering these feedbacks could significantly complicate the model and its results. Second, energy-budget approaches can be used for formulating the tradeoffs due to early maturation. Finally, as fishing fleets in many regions of the world are composed of high-technology large commercial boats and low-technology small private boats, the fishery component in this coevolving stock-fishery system could have experienced selective pressures promoting the coexistence and divergence of different fleet segments. In other words, the fleet can experience an analogous disruptive selection and adaptive diversification, as suggested by Dercole et al. (2010) and illustrated by standard eco-evolutionary predator-prey models (Doebeli and Dieckmann, 2000; Landi et al., 2013); this warrants future research and model extensions. Specifically, fishery dynamics could happen at many levels: at the level of the fleet (adaptive harvesting on a short timescale, fleet size and structure on an intermediate timescale, and technological adaptation on a longer timescale; Egas et al. 2005), at the level of fishing strategy (constant effort, fixed quota, or fixed stock size; Hilborn and Walters 1992), and/or at the level of fishing regulations (limitations on the size and maturity of target individuals; Cole and Ward 1994; Matsumura et al. 2011). Here we have examined only the simplest setting, that is, adaptive harvesting with a constant-effort strategy. To detect disruptive selection on the fishery, adjustments in fleet size, fleet structure, and fleet technology must be explicitly modeled. As a starting point, the degree of harvest specialization in our model, Equation (1b), could be interpreted as characterizing the technological level of the fleet (affecting, e.g., the probability of locating aggregations of fish, catchability, and/or the efficiency of handling and transporting the catch). On this basis, this parameter could be used as an adaptive trait of the fishery using the framework of adaptive dynamics theory (Dercole et al., 2008, 2010).

An ultimate target of fishery management is to increase sustainable yield (e.g., Heino 1998). This raises the question of whether fisheries-induced disruptive selection could, and should, be managed: as such selection pressures result from the interplay between natural selection and fishing mortality (Carlson et al., 2007; Edeline et al., 2007, 2009), they are human-induced and may arguably be controlled by fishing policies and fleet and harvest regulations. In practice, this can be achieved through legal limitations and incentives. Our results show that sustainable yield can slightly increase after diversification when only large individuals are targeted (Figure 7b), even though it still remains far below the maximum sustainable yield obtained at low fishing mortality when the stock is monomorphic. As many fish stocks are still overexploited, being managed considerably below their maximum sustainable yield, our findings imply that diversification triggered by fisheries-induced disruptive selection under high fishing mortality might slightly increase the yield from its level before diversification, if only large individuals are targeted. However, our results also suggest that such a population dimorphism can be taken as a sign of extreme harvesting pressure, as trait diversification is a way for species to escape from severe selection pressures resulting from human exploitation. Hence, when such a pattern is observed, our analysis suggests that sustainable yield can usually be improved by reducing fishing mortality.

Fisheries-induced disruptive selection could also increase phenotypic variability (Edeline et al., 2009), without promoting life-history dimorphism: favoring extreme phenotypes may just widen an existing population polymorphism. This

could have positive consequences beyond those analyzed in our study, since higher variability makes a population more reactive to future adaptation needs. This means that the population can react more promptly to any rapid changes in its environmental conditions, both for natural and anthropogenic causes. In other words, fisheries-induced disruptive selection could lead to a better capacity of an exploited stock to cope with environmental disturbances and changes (Roff, 1997).

In summary, fisheries-induced disruptive selection can indicate overexploitation, can slightly increase or decrease the yield depending on the adopted fishing policy, and can enhance a stock's resilience to abrupt changes in its environmental conditions. Weighting these three aspects, decision makers can manage a fishery in pursuit of their economic, social, and conservation objectives.

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Appendix

In this appendix, we specify the population dynamics and the evolutionary dynamics of a dimorphic stock, with population densities $\mathbf{N}_x = (N_{ix})$ for individuals with an early-maturation probability x and of $\mathbf{N}_y = (N_{iy})$ for individuals with an early-maturation probability y. The dimorphic population dynamics are given by

$$
\begin{aligned}
\dot{N}_{1x} &= f_{\tilde{2}} N_{\tilde{2}x} + f_{\tilde{3}}(x) N_{\tilde{3}x} + f_3 N_{3x} - m_1 N_{1x}(N_{1x} + N_{1y}) - r_1 N_{1x} - F\alpha_1 h_1(\mathbf{N}_x, \mathbf{N}_y) N_{1x},\\
\dot{N}_{\tilde{2}x} &= x r_1 N_{1x} - m_{\tilde{2}}(x) N_{\tilde{2}x} - r_{\tilde{2}}(x) N_{\tilde{2}x} - F\alpha_{\tilde{2}} h_{\tilde{2}}(\mathbf{N}_x, \mathbf{N}_y) N_{\tilde{2}x},\\
\dot{N}_{2x} &= (1-x) r_1 N_{1x} - m_2 N_{2x} - r_2 N_{2x} - F\alpha_2 h_2(\mathbf{N}_x, \mathbf{N}_y) N_{2x},\\
\dot{N}_{\tilde{3}x} &= r_{\tilde{2}}(x) N_{\tilde{2}x} - m_{\tilde{3}} N_{\tilde{3}x} - F\alpha_{\tilde{3}} h_{\tilde{3}}(\mathbf{N}_x, \mathbf{N}_y) N_{\tilde{3}x},\\
\dot{N}_{3x} &= r_2 N_{2x} - m_3 N_{3x} - F\alpha_3 h_3(\mathbf{N}_x, \mathbf{N}_y) N_{3x},\\
\dot{N}_{1y} &= f_{\tilde{2}} N_{\tilde{2}y} + f_{\tilde{3}}(y) N_{\tilde{3}y} + f_3 N_{3y} - m_1 N_{1y}(N_{1x} + N_{1y}) - r_1 N_{1y} - F\alpha_1 h_1(\mathbf{N}_x, \mathbf{N}_y) N_{1y},\\
\dot{N}_{\tilde{2}y} &= y r_1 N_{1y} - m_{\tilde{2}}(y) N_{\tilde{2}y} - r_{\tilde{2}}(y) N_{\tilde{2}y} - F\alpha_{\tilde{2}} h_{\tilde{2}}(\mathbf{N}_x, \mathbf{N}_y) N_{\tilde{2}y},\\
\dot{N}_{2y} &= (1-y) r_1 N_{1y} - m_2 N_{2y} - r_2 N_{2y} - F\alpha_2 h_2(\mathbf{N}_x, \mathbf{N}_y) N_{2y},\\
\dot{N}_{\tilde{3}y} &= r_{\tilde{2}}(y) N_{\tilde{2}y} - m_{\tilde{3}} N_{\tilde{3}y} - F\alpha_{\tilde{3}} h_{\tilde{3}}(\mathbf{N}_x, \mathbf{N}_y) N_{\tilde{3}y},\\
\dot{N}_{3y} &= r_2 N_{2y} - m_3 N_{3y} - F\alpha_3 h_3(\mathbf{N}_x, \mathbf{N}_y) N_{3y},
\end{aligned}
$$

where

$$h_i(\mathbf{N}_x, \mathbf{N}_y) = \frac{(\alpha_i w_i (N_{ix} + N_{iy}))^\gamma}{\sum_j (\alpha_j w_j (N_{jx} + N_{jy}))^\gamma},$$

with the sum extending over all five stock components $j = 1$, 2, $\tilde{2}$, 3, or $\tilde{3}$.

Indicating by x' and y' the trait values of mutants appearing in a population with resident trait values x and y we obtain the basic reproduction ratios of such mutants as

$$R_0(x, y, x') = r_1 D_1 \{(1 - x') r_2 D_2 D_3 f_3 + x' [D_{\tilde{2}x} f_{\tilde{2}} + r_{\tilde{2}}(x') D_{\tilde{2}x} D_{\tilde{3}} f_{\tilde{3}}(x')]\},$$
$$R_0(x, y, y') = r_1 D_1 \{(1 - y') r_2 D_2 D_3 f_3 + y' [D_{\tilde{2}y} f_{\tilde{2}} + r_{\tilde{2}}(y') D_{\tilde{2}y} D_{\tilde{3}} f_{\tilde{3}}(y')]\},$$

where $D_1 = [m_1(N^*_{1x} + N^*_{1y}) + r_1 + F\alpha_1 h_1(\mathbf{N}^*_x, \mathbf{N}^*_y)]^{-1}$, $D_2 = [m_2 + r_2 + F\alpha_2 h_2(\mathbf{N}^*_x, \mathbf{N}^*_y)]^{-1}$, $D_{\tilde{2}x} = [m_{\tilde{2}}(x') + r_{\tilde{2}}(x') + F\alpha_{\tilde{2}} h_{\tilde{2}}(\mathbf{N}^*_x, \mathbf{N}^*_y)]^{-1}$, $D_{\tilde{2}y} = [m_{\tilde{2}}(y') + r_{\tilde{2}}(y') + F\alpha_{\tilde{2}} h_{\tilde{2}}(\mathbf{N}^*_x, \mathbf{N}^*_y)]^{-1}$, $D_3 = [m_3 + F\alpha_3 h_3(\mathbf{N}^*_x, \mathbf{N}^*_y)]^{-1}$, and $D_{\tilde{3}} = [m_{\tilde{3}} + F\alpha_{\tilde{3}} h_{\tilde{3}}(\mathbf{N}^*_x, \mathbf{N}^*_y)]^{-1}$ are the average durations spent by individuals in the stock components, and $(\mathbf{N}^*_x, \mathbf{N}^*_y)$ are the population densities at the dimorphic demographic equilibrium.

On the evolutionary timescale, the traits x and y evolve following a two-dimensional canonical equation

$$\dot{x} = \epsilon k_x \sum_i N^*_{ix} \frac{\partial R_0(x, y, x')}{\partial x'}\bigg|_{x' = x}, \quad \dot{y} = \epsilon k_y \sum_i N^*_{iy} \frac{\partial R_0(x, y, y')}{\partial y'}\bigg|_{y' = y}, \tag{A1}$$

where ϵ is the time-scaling parameter, separating the (slow) evolutionary dynamics from the (fast) demographic dynamics, k_x and k_y are half the product of probability and variance of mutations, scaling the speed of evolutionary dynamics in x and y, respectively, and the sum extends over all five stock components $i = 1$, 2, $\tilde{2}$, 3, and $\tilde{3}$. These dimorphic dynamics converges to the dimorphic evolutionary equilibrium $(x^*_{\mathrm{D}}, y^*_{\mathrm{D}})$.

Finally, the sustainable yield of the dimorphic stock with trait values $(x^*_{\mathrm{D}}, y^*_{\mathrm{D}})$ is given by

$$Y_{\mathrm{D}} = \sum_i F\alpha_i h_i(\mathbf{N^*}_x, \mathbf{N^*}_y)(N^*_{ix} + N^*_{iy}) w_i\Big|_{x = x^*_{\mathrm{D}}, y = y^*_{\mathrm{D}}}, \tag{A2}$$

with the sum extending over all five stock components $i = 1$, 2, $\tilde{2}$, 3, and $\tilde{3}$.

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