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Evolution of boldness and life-history in response to selective harvesting

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Abstract

Whether intensive harvesting alters the behavioural repertoire of exploited fishes is currently unknown, but plausible. We extend a fish life-history model to account for boldness as a personality trait that affects foraging intensity, which affects energy intake and risk from predation and fishing gear. We systematically investigate life-history and behavioral trait evolution along the boldness-timidity axis in response to the full range of common selectivity and exploitation patterns in fisheries. In agreement with previous studies we find that any type of harvesting selects for fast life histories and that merely elevated, yet unselective, fishing mortality favors boldness. We also find that timid-selective fishing (which can be expected in selected species targeted by active gear types) selects for increased boldness. By contrast, increased timidity is predicted when fishing targets bolder individuals common to passive gears, whether in combination with selection on size or not. Altered behavior caused by intensive harvesting should be commonplace in nature, which can have far-reaching ecological, evolutionary and managerial impacts. Evolution of timidity is expected to strongly erode catchability, which will negatively affect human well-being and influence the reliability of stock assessments that rely on fishery-dependent data.

Key words: fisheries-induced evolution, timidity syndrome, personality traits, selection gradients, life-history evolution
Résumé

Il est actuellement encore incertain, mais plausible, que la pêche intensive puisse alterer le répertoire de comportements des poissons exploités. Nous étendons un modèle décrivant l’histoire de vie des poissons pour y incorporer un trait de personnalité, l’audace, et examiner de façon systématique l’évolution des traits d’histoire de vie et comportementaux le long de l’axe audace-timidité, en réponse à différents types de sélectivité et d’exploitation couramment rencontrés dans les pêcheries. En accord avec les études précédents, nous montrons que tous les types d’exploitation favorisent une histoire de vie plus rapide et qu’une faible augmentation de mortalité, même non sélective, favorisent une plus grande audace. À l’inverse, une timidité accrue est prédite quand la pêche cible les individus les plus audacieux, cas typique des engins de pêche passifs, que ce soit en combinaison avec la taille ou non. Les modifications du comportement causés par la pêche intensive sont probablement courants dans la nature, ce qui peut avoir d’importantes conséquences écologiques, évolutives et en termes de gestion. En particulier, l’évolution vers une plus grande timidité peut éroder l’attrapabilité, affectant le bien-être des pêcheurs et la fiabilité des évaluations de stock reposant sur des données dépendantes de la pêche.
Introduction

Assuming that phenotypes expressed by animals in the wild have a heritable basis (Mousseau & Roff 1987; Dochtermann et al. 2015), harvesting can cause phenotypic and genetic, i.e., evolutionary, changes in exploited populations (Jørgensen et al. 2007; Allendorf & Hard 2009). For harvesting-induced evolution of life-history traits, such as maturation size or reproductive investment, to occur, it is sufficient that the mortality induced by humans is elevated beyond natural mortality levels because the now altered fitness landscape will select for different phenotypes than natural selection alone would favor (Dieckmann & Heino 2007; Heino et al. 2015). Evolutionary responses caused by fisheries will be magnified if fishing mortality is not only elevated but selective for fitness-related traits, such as body size (e.g., Edeline et al. 2007; Matsumura et al. 2011; Heino et al. 2015).

Most fishing gear is size-selective, preferentially capturing a certain range of sizes (e.g., in gill nets) or predominantly harvesting individuals that are larger than a minimum retention size (e.g., in trawls). A key finding of a range of models and experiments studying the consequences of fisheries-induced selection is that the typical positive-size selection by a trawl that catches both large juvenile and adult individuals induces evolution of fast life histories (Andersen & Brander 2009; Laugen et al. 2014; Heino et al. 2015). Fast life-histories can be characterized by fast juvenile growth, young age and small size at maturation and high reproductive investment, which reduce post-maturation growth rate and increase natural mortality. From a management
perspective, it is important to understand the population dynamical and social and
economic consequences of fisheries-induced evolution, to, if possible, design
management tools that minimize undesired evolutionary effects on outcomes valued by
humans, such as yield, recovery or the catch prospects of exceptionally large fishes

Most empirical and theoretical research on phenotypic and evolutionary
changes caused by fisheries has focused on life-history traits (Devine et al. 2012; Heino
et al. 2015). Our understanding of fisheries-induced selection and potential for
evolutionary changes in traits other than life-history traits, such as behavioral or
physiological traits, is far less developed (Uusi-Heikkilä et al. 2008; Heino et al. 2015;
Arlinghaus et al. 2017). In particular, there is a gap in the knowledge related to the
potential for adaptive effects of fishing on behavioral traits in wild-living fish
populations. Arlinghaus et al. (2016, in press) recently proposed that wildlife hunting
and fishing may foster the evolution of a “timidity syndrome” where adapted
populations become shyer, less explorative, less aggressive, less active and/or less bold
due to a combination of learning within the realm of plasticity and evolution. Very few
on fisheries-induced evolution are available to support these predictions given the lack
of behavioural mechanisms present in most theoretical investigations on fisheries-
induced evolution. One exception is a study that included behavioral mechanisms in the
analysis of life-history evolution caused by fisheries found that elevated, yet
unselective, fishing mortality selected for bolder and/or more aggressive foraging
among juveniles (Jørgensen & Holt 2013). This finding is the opposite effect of the one proposed by the “timidity syndrome”. However, the generality of the results by Jørgensen and Holt (2013) is limited because no size or behavior-selective situations were addressed. In another recent model, Mee et al. (2017) focused on studying the evolution of movement rates in a spatially explicit framework in a sexual fish, but they authors omitted corresponding selection acting on life-history traits. Given the limited scope of previous models, it remains unclear what to expect when fishing not only acts on size, but also on behavioral traits alone or in combination with size, as in most fisheries (Arlinghaus et al. 2017; Diaz Pauli & Sih 2017).

A rich literature has shown that the behavior expressed by individual fish plays a key role in exposing individuals to fishing gear (Pitcher 1995; Conrad et al. 2011; Løkkeborg et al. 2014). However, the specific behaviors that may be under selection depend on the species and the type of gear. Of relevance is whether the gear is passive, such as gill-nets, traps, commercial long-lines and recreational angling with rod and line, or active, such as trawling or seining. Most passive gear types have been found to select for bold fishes, leaving behind shy individuals (reviewed in Arlinghaus et al. in press, see also Monk and Arlinghaus 2017). For example, an experimental study by Diaz-Pauli et al. (2015) in guppies (Poecilia reticulata) showed that traps selected for shy fishes (by preferentially capturing bold fishes), while experimental trawls selected for bold fishes (by preferentially capturing timid and social fishes). In another experimental study in minnows (Phoxinus phoxinus), Killen et al. (2015) found that experimental trawls
captured fishes with small swimming ability, low basal metabolic rates and low
anaerobic scope. Fish with low basal metabolism and often also shy following ideas of
the pace-of-life hypothesis (Réale et al. 2010). Based on these findings, one can
reasonably assume that passive and active gear types systematically select for opposing
behavioural traits. Note, however, that the empirical research based on the relationship
of behavioural traits and vulnerability to active gears is much less well developed
compared to passive gear types (Diaz-Pauli and Sih in press). Consequently, it is not
clear that active gears will always preferentially select shy fishes, but it is safe to
assume that fisheries will be generally selective for both size and behavioral traits
(Allendorf & Hard 2009; Heino et al. 2015; Arlinghaus et al. 2017). We therefore
explored the whole “sphere of opportunities” in terms of selection acting on the
boldness-shyness axis with and without additional selection on size to understand the
direction and strength of selection on behaviour and life-history traits in a range of
contexts.

For fisheries-induced selection to operate on behavior, it is paramount that
behavioral traits are stable phenotypes that characterize individuals within populations.
A plethora of recent studies has revealed that fishes indeed reveal less plasticity in their
behaviors than previously believed, forming stable among-individual differences in
behavioral types (Conrad et al. 2011; Mittelbach et al. 2014). One of the key personality
traits in animals in general is boldness (Réale et al. 2007), which is often correlated with
other personality traits such as aggression, exploration, sociability or activity, thereby
creating behavioral syndromes (Sih et al. 2004). Behavioral traits are in turn often
correlated with physiological and life-history traits, resulting in an integrated phenotype
(pace-of-life hypothesis, Réale et al. 2010). For example, boldness (i.e., risk-taking
during foraging) has been shown to be correlated with traits associated with a fast-life
history (Wolf et al. 2007; Biro & Stamps 2008; Réale et al. 2010). Hence, life-history
traits such as growth rate may change due to direct selection operating on size or due
to indirect selection responses caused by direct selection on correlated behavioral traits
(Biro & Post 2008; Biro & Sampson 2015).

The question addressed here is what selection differentials and life-history
responses to expect when a fishery is either unselective, size-selective of various degree
or size- and boldness-selective. The baseline prediction is that an entirely unselective
fishery with respect to traits and states should lead to the evolution of a fast-life
history, which is associated with intensified foraging behavior (i.e., elevated boldness;
Jørgensen & Holt 2013). The reason is simply that intensified foraging allows the
individual to gain sufficient resources to achieve fast growth rate as juvenile to invest
eyearly into reproduction and devote a large fraction of surplus energy into gonads
(Jørgensen and Holt 2013). Such effects should be magnified in a trawl-like fishery that
targets large, but possibly shy fishes (Diaz Pauli et al. 2015), if the behavioural selection
directly operates on shyness and not on other behavioural traits (e.g., schooling or
swimming ability). By contrast, in most passively operated fishing gears (e.g., traps or
angling) where the capture probability is usually both size (Kuparinen et al. 2009) and
boldness-related (Klefoth et al. 2012), evolution of a fast-life history with a timid behavioral phenotype should be expected (Arlinghaus et al. 2016, in press). To examine these predictions, we use a quantitative genetics calculation based on a size-based model of fish life history (Andersen and Brander 2009). We included a similar behavioral mechanism to the one used by Jørgensen and Holt (2013) and present the first complete analysis of what selection responses to expect on fish behavioral traits across a range of selectivities, representing a variety of gear types and possible management tools directed at modifying which sizes of fishes can be retained (e.g., variants of size-based harvest limits).

**Material & methods**

The model estimates the evolutionary responses of three fundamental adaptive and heritable traits: boldness $\tau$, size at maturation $w_m$, and size-specific reproductive investment $k_r$. The (fixed) population average of trait $x$ is denoted by a bar: $\bar{x}$. The selection differential $S(\bar{x})$ and the rate of evolutionary change in the average trait, $d\bar{x}/dt$, are calculated using quantitative genetics as in Andersen and Brander (2009). Changes in the three fundamental traits affect growth rate and asymptotic (maximum) body size. The description of the model is divided into three parts: the life-history model, the quantitative genetics calculations, and the determination of the fixed trait values of the unexploited population.
Life-history model

The life-history model presented here is based on earlier work by some of us (Andersen & Brander 2009). It constitutes a complete description of individual growth, reproduction and survival. The model resolves the vital processes in an average individual as a function of its body size (represented by weight) $w$, and accounts for the trade-off between growth and reproduction (Roff 1983; Lester et al. 2004). Rates of maximum consumption, standard metabolism and natural mortality are assumed to scale with body weight following standard metabolic scaling rules (Brown et al. 2004).

Consequently, maximum consumption and standard metabolism is proportional to $w^n$, where $n$ is the metabolic exponent, and mortality is proportional to $w^{n-1}$. This way of linking the size-scaling of metabolism and mortality has support from size-spectrum theory, where the exponent $1 - n$ on mortality is a result of predation by predators whose need for food scale with exponent $n$ (Sheldon et al. 1977; Andersen & Beyer 2006). We use the canonical value of the metabolic exponent $n = 3/4$ but examine the sensitivity of the results to this assumption. The values of the scaling exponents also have empirical support: metabolism and maximum consumption scales with $\frac{3}{4}$ for fish (Kiørboe & Hirst 2014), and mortality with exponent $-1/4$ (Peterson & Wroblewski 1984; Lorenzen 2000). We introduce the fundamental trade-off between consumption (leading to growth) and natural mortality (Stamps 2007) into our established model framework to explicitly consider behavioral dynamics and the fishing mortality due to increased risk of predation or exposure to gear while foraging.
Our description of the trade-off related to behaviour is inspired by the classic literature on optimal foraging (Lima & Bednekoff 1999; Werner & Anholt 2014). Behaviour is represented by a parameter \( \tau \in [0:1] \), which conceptually is the fraction of time the individual spends foraging. While foraging in risky foraging arenas outside refuges (Ahrens et al. 2012), the individual encounters food, but exposes itself to predation as it typically observed (Lima & Dill 1990; Biro et al. 2005) and described by optimal foraging theory (McNamara et al. 2001). Given this trade-off, the behavioral process in our model is best described by boldness as personality trait, which is defined in modern behavioural ecology as risk-taking during foraging (Réale et al. 2007). The trade-off implies that bold individuals (those with high \( \tau \)) will have higher consumption and faster growth at the expense of higher predation mortality than timid individuals (low \( \tau \)), for which there is abundant empirical support (Biro et al. 2005; Biro & Post 2008; Nakayama et al. 2017).

The trade-off between growth and mortality is assumed linear: an increasing foraging activity implies a similar increase in predation risk. In reality the trade-off might be non-linear, i.e. with relatively higher or lower mortality risk associated with increased foraging activity. Here, we are only interested in selection responses and therefore only the fitness gradient matters. The trade-off can therefore equally well be viewed as a linearization of the trade-off around the current fixed trait value. It will therefore matter little whether the trade-off is linear or non-linear.
In the following we show how the three fundamental traits, boldness $\tau$, size at maturation $w_m$, and size-specific reproductive investment $k_r$, affect available energy, growth, reproduction, and ultimately mortality.

### Available energy

A foraging individual encounters food with a rate $\tau R_f$ where $R_f$ is the encountered food (unit biomass per time). The assimilated energy can be described with a Holling functional response type II as

$$E_a = \epsilon_a C_m \frac{\tau R_f}{\tau R_f + C_m}, \quad (1)$$

where $C_m$ is the maximum consumption rate and $\epsilon_a$ the assimilation efficiency. The maximum consumption rates scales with body weight $w$ as $C_m = A_m w^n$, where $A_m$ is a constant, $n$ the metabolic exponent, and $w$ the body weight. By defining $A = \epsilon_a A_m$ and $R = R_f/C_m$, the assimilated energy can be rewritten in a simpler form as:

$$E_a = A w^n \frac{\tau R}{\tau R + 1}. \quad (2)$$

Here $R$ is the ratio between encountered food and what can be maximally be consumed. If $R > 1$ there is more food available than can be consumed and vice versa. A value of $R \approx 1$ for a fully foraging individual ($\tau = 1$) corresponds to a predator.
assimilating at half its assimilative capacity. Assimilation at less than half capacity is usually observed under field conditions (Armstrong & Schindler 2011), and we therefore assume $R = 1$, which with $\tau < 1$ leads to assimilation at less than half capacity.

258 **Growth and reproduction**

The consumed energy is used for standard metabolism $k_0 w^n$ and activity $k_a \tau w$, where the $k$’s are constants and the cost of activity is proportional to the boldness trait $\tau$. Standard metabolism is assumed to scale with the same exponent as the maximum consumption ($n = 3/4$) while activity is proportional to weight, in accordance with calculations of optimal foraging (Ware 1978). The available energy (assimilated energy minus costs) then becomes

$$E = A w^n \frac{\tau R}{\tau R + 1} - k_0 w^n - \tau k_a w. \quad (3)$$

To simplify notation, we define the critical feeding level $f_c = k_0 w^n/(A_m w^n)$ as the ratio between standard metabolism and maximum consumption. This makes it possible to write available energy as

$$E = A \left( \frac{\tau R}{\tau R + 1} - f_c \right) w^n - \tau k_a w. \quad (4)$$
Reproductive investment is proportional to body mass as is typical for fish (Roff 1983), with a proportionality factor \( k_r \). Maturation is described with a function that switches between 0 and 1 around the size at maturation, \( w_m \):

\[
\psi(w, w_m) = \left( 1 + \left( \frac{w}{w_m} \right)^{-10} \right)^{-1}. \quad (5)
\]

Growth can then be determined as the remaining available energy after reproduction in adults:

\[
g(w) = A \left( \frac{\tau R}{\tau R + 1} - f_c \right) w^n - (\tau k_a - \psi(w, w_m) k_r) w. \quad (6)
\]

As in Andersen and Beyer (2015), we assume that energy is divided between reproduction \( k_r \) and activity \( k_a \) with a constant fraction \( \varepsilon_a \). This means that \( k_a = k_r \varepsilon_a / (1 - \varepsilon_a) \). The asymptotic (maximum) size \( W \) is reached when somatic growth is zero, i.e., \( g(W) = 0 \):

\[
W = \left[ A \left( \frac{\tau R}{\tau R + 1} - f_c \right) \frac{1}{\tau k_a + k_r} \right]^\frac{1}{1-n}. \quad (7)
\]

which shows that asymptotic size will decrease if investments in reproduction \( k_r \) are increased and typically increase if boldness increases (Figure 1).
Mortality

Survival from one size $w_a$ to another size $w_b$ is found as the solution to $dP/dt = -\mu(w)$ which is:

$$P_{w_a \rightarrow w_b} = \exp\left[ -\int_{w_a}^{w_b} \frac{\mu(w)}{g(w)} \, dw \right] \quad (8),$$

where $\mu(w)$ is the mortality with contributions from predation and fishing.

Predation mortality $\mu_p$ declines with size $\propto w^{n-1}$ as is typical for fish (Peterson & Wroblewski 1984; Lorenzen 2000) and is assumed proportional to boldness $\tau$:

$$\mu_p = \alpha_p \tau w^{n-1} \quad (9).$$

Therefore, increased foraging activity by individuals with higher boldness $\tau$ leads to increased predation mortality (as in Jørgensen and Holt 2013). The parameter $\alpha_p$ describes the overall level of predation mortality.

Fishing is assumed to be unselective or selecting solely on size, solely on boldness or jointly on size and boldness/shyness. The size-selective term is described by a sigmoidal curve (typical for trawling and long-lining, Myers & Hoenig 1997), switching from zero to one around a size $w_F$. Variation in mesh sizes or changes in allowable landing size...
(e.g., minimum or maximum-length limit or the combination, a harvest slot) alters size-selectivity (Jørgensen et al. 2009; Matsumura et al. 2011; Mollet et al. 2016) and is simulated by changing $w_F$ (Figure 2a). To simulate a harvest slot fishery (not to be confused with a protected slot-fishery) where only a certain intermediate size-range is targeted (as is common in gill-nets) the selectivity may again go down to zero at a size $w_{FF}$ (here taken to be 10 times larger than the size where fishing starts) (Figure 2b). The selection on behavior is assumed proportional to boldness, switching around the fixed trait value $\bar{\tau}$ with a steepness $b_F$ (Figure 2c). Taken together the fishing mortality $\mu_F$ then becomes:

$$
\mu_F(w, \tau) = F_0 \psi(w, w_F) \left(1 - \psi(w, w_{FF})\right) \left(1 + b_F(\tau - \bar{\tau})\right), \quad (10)
$$

where $F_0$ is the overall fishing mortality, and the dimensionless parameter $b_F$ describes the selection on boldness. Since we only need to evaluate derivatives of $\mu_F$ with respect to $\tau$ around $\bar{\tau}$ we will not obtain negative values of $\mu_F$. The function $\psi$ is the same that is used to describe maturation around the size at maturation $w_m$. Here it describes how selection changes from zero to full selection at the size $w_F$ and back again to zero at the size $w_{FF}$. Assuming that selection on boldness by fishing is the same as the boldness-induced predation mortality corresponds to a value of $b_F = 1$. However, we also explore other scenarios of boldness selection, including negative selection where bolder individuals are better at escaping fishing gear as per the research by Diaz-Pauli et al. (2015). The four cases examined further are: 1) random harvest; only elevated
fishing mortality; 2) only size-selective harvest \((w_F \text{ and } w_{FF} \text{ varied; } b_F = 0)\); 3) only boldness-selective harvest \((w_F = 0, w_{FF} = \infty, b_F \text{ varied around } 1)\); and 4) both size- and boldness-selective harvest (all parameters are non-zero). A base-case for the size-selectivity is trawl-like fishing in commercial fisheries, which is conceptually similar to exploitation with a minimum-length limit typical in recreational fisheries (positive size-selection) with \(F_0 = 0.3 \text{ yr}^{-1}, w_F = 0.05W\) and \(w_{FF} = \infty\) (Figure 2a).

Quantitative genetics

Responses to selection depend on the selection differential \(S\), which is the mean change in the trait before and after selection (Matsumura et al. 2012). The selection differential is also proportional to the gradient of the life-time reproductive output evaluated around the mean of the fixed trait \(\bar{x}\) (Andersen et al. 2007):

\[
S(\bar{x}) = \sigma_x^2 \frac{1}{R_0(\bar{x})} \frac{\partial R_0(x)}{\partial x} \bigg|_{x=\bar{x}}, \quad (11)
\]

where \(\sigma_x\) is the standard deviation of the variation of the trait in the population and the life-time reproductive output is found by integrating individual output multiplied by the survival from egg weight \(w_{egg} \approx 1 \text{ mg to asymptotic size}:

\[
R_0 \propto k_r \int_{w_{egg}}^{W} P_{w_{egg} \rightarrow w} \psi(w, W) w \, dw. \quad (12)
\]
The constant of proportionality is immaterial because it vanishes when the ratio between the derivative and the value of $R_0$ is formed during the calculation of the selection differential.

In a natural population unaffected by fishing the selection differential is expected to be zero. However, with given the chosen parameters that was not the case for the traits size at maturation and reproductive investment, meaning that these traits were not in an evolutionarily stable state prior to the commencement of fishing. To address this, we calculate the relative selection differential $S_{\text{fish}}$ due to the selective force from fishing as the difference between the selection responses with and without fishing:

$$S_{\text{fish}}(\bar{x}) = S(\bar{x}, F_0 \neq 0) - S(\bar{x}, F_0 = 0).$$  \hspace{1cm} (13)

We choose two variants of normalized selection strength to compare selection on the three adaptive traits. We first calculated the mean-standardized selection gradient (which is perhaps the most suited measure of strength of selection to compare across traits different in mean and variance) and second the proportional selection response.

The mean-standardized selection gradient is given as (Matsumura et al. 2012):

$$\beta_{\mu}(\bar{x}) = \frac{1}{\bar{x} \sigma_x} \left( \frac{\bar{x}}{\sigma_x} \right)^2 S_{\text{fish}},$$  \hspace{1cm} (14)
which has dimensions of $1/generation$ and represents a fitness elasticity. $\sigma_x / \bar{x}$ is the coefficient of variation (CV) of the trait. For simplicity, we choose identical CVs for the three traits examined.

The proportional selection response is the rate of change normalized by the trait value itself, while accounting for the heritability of the trait. It follows from the selection differential as:

$$r(\bar{x}) = \frac{h^2}{\bar{x}} s_{fish} \quad (15)$$

where $h^2 = 0.2$ is the (realistically moderate, compare Mousseau & Roff 1987; Dickerson et al. 2005; Thériault et al. 2007) heritability of each of the three traits. Note that the heritability of behavioural traits is often much higher than 0.2 (Dickerson et al. 2005; Dochtermann et al. 2015), such that our model predictions underestimate the evolvability of behavioural traits compared to life-history traits. In the final results, we only report the proportional selection response because the two measures are proportional when the heritability is identical on all traits (Matsumura et al. 2012; eq. 7):

$$r(\bar{x}) = h^2 \left( \frac{\sigma_x}{\bar{x}} \right)^2 \beta_\mu \quad (16)$$
and with the parameters used (Table 1) the constant of proportionality is 0.008. To obtain the values in units of per year, the mean-standardized selection gradient and the selection response are divided by the generation time, approximated as the age of maturation.

Parameter values

The mean values of the three fundamental traits, boldness $\tau$, reproductive investment $k_r$ and size at maturation $w_m$, must be defined at the onset. The value of boldness in the absence of fishery $\bar{\tau}$ is assumed to be the one that optimizes $R_0$. We calculate this numerically by finding the value of $\tau$ that gives the highest value of $R_0$. The value of the mean reproductive investment $k_r$ effectively determines the asymptotic size via eq. (7). We use $k_r$ to conceptually represent different species of fishes, but report results as a function of asymptotic size. Finally, the size at maturation $w_m$ is assumed proportional to asymptotic size; $w_m = \eta_m W$. This does not imply that $w_m$ and $k_r$ are directly correlated through the calculation of $W$ with eq. (7); this relation is only used to calculate the starting value in the absence of fishing and not in the process of calculating selection responses. The values of the other parameters of the model are given in Table 1.

The model is solved numerically by discretizing the weight-axis in 1000 logarithmically spaced size bins, as described in Andersen & Beyer (2015, app. C).
Results

The predicted evolution in the four cases of selectivity patterns (1: random harvest; 2: only size-selective harvest; 3: only boldness-selective harvest; 4: both size- and boldness-selective harvest) on the three fundamental traits examined here (Figure 3).

The first two cases – random harvest and size-selectivity with a trawl-like selectivity pattern – confirms that harvesting leads to the evolution of a fast-life history characterized by reduced size at maturation and increased investment in reproduction. Clearly, the effects of added mortality late in life, where the mortality is large compared to natural mortality, dominates over the effect of added mortality early in life where the mortality is much smaller than the natural mortality (Figure 2). Regarding boldness, both cases leads to evolution of bolder individuals, and the rate of evolution on the boldness trait is much faster than the selection on the life-history traits. Evolution of increased boldness therefore occurs even if fishing gear selects neutrally with respect to boldness. The optimum for the boldness trait before selection is the result of a balance between the benefit of the faster growth that results from higher boldness and the costs of increased predation risk. When mortality is elevated regardless of the boldness, this balance shifts in the direction where the cost of predation mortality becomes less compared to the total mortality. This generates a selection response towards increased boldness. The effect is further compounded by the increased investment in reproduction that comes at the cost of reduced adult growth, which can be compensated by the higher consumption of bolder individuals. Finally, increased
mortality increases the pressure to ensure survival to maturation to ensure at least one spawning event. This is facilitated by faster juvenile growth.

Fishing gear selecting on boldness traits, either solely (case 3) or in conjunction with size-selectivity (case 4), has the same selection responses on size at maturation and reproductive investment as without selection for boldness, i.e., fast life-histories are favored. The main outcome of selection on boldness is an additional selection response towards more timid individuals, leading to a weakening of the selection on boldness. If the selection on boldness is increased ($b_F > 1$) then the selection response on the personality trait is completely reversed, and instead of selecting for bolder individuals, there is now selection for more timid individuals (Figure 4b). The reason is simply that now there is an increasing cost to be bold by elevating the chances of being captured, which reverses and sharply reduces the evolution of fish boldness in our model. While this outcome is fairly intuitive, it is less obvious, yet in line with expectations, why the absence of selection on boldness leads to increased boldness (case 1 and 2).

The selection responses are roughly proportional to the fishing mortality and, for boldness, to the selection strength acting on boldness (Figure 4). The order of magnitude of the selection responses of the three traits are roughly 0.1 % per year. The selection responses of timidity only exceed the selection responses of the two other traits when selection on boldness is exceedingly large (parameter $b_F$) (Figure 4b).
contrast, when timid fish are more likely to be captured (negative values of $b_F$ in Figure
4b), evolution of boldness occurs also under size- and timidity-selective fisheries.

Changes in growth and asymptotic size

The combined effects of the selection responses of the three adaptive traits (maturation size, investment in reproduction and boldness) are summarized in the impact of fishing on size-at-age and asymptotic size (Figure 5). In the cases without selection on boldness, the effects of evolution of boldness (leading to faster growth) and increased investment in reproduction (leading to slower growth) cancel one another, and growth is largely unchanged. This result was anticipated by Eq. (7). Clearly, boldness-selectivity in addition to mere size-selectivity has the potential for a magnified change in growth rate leading to a reduction in asymptotic size, in particular for small-bodied fish species.

While the result that selecting bolder individuals leads to evolution of more timid individuals (cases 3 and 4) can be understood intuitively, there are two aspects of the results which are less intuitive: $i)$ why does selection on boldness not affect the direction of the selection responses of life history traits? $ii)$ why does random and trawl selectivity (cases 1 and 2) lead to the same selection responses on the life history traits (reproductive investment and size at maturation)? Regarding the first question, the reason lies in the life-time reproductive output being only influenced by the level of mortality imposed, not whether it is selective on boldness or not. The level of mortality,
and thus the level of selection, is only affected when differences in boldness are considered. We can understand the answer to ii) by examining the effects of size selection, as we do next.

Sensitivities in response to altered size-selectivity patterns

The selection responses depend on the size-selectivity imposed by the fishery as described by size of 50% selection relative to asymptotic size $\eta_F$ (Figure 6). Most importantly, a shift is seen in when selection changes from targeting both juveniles and adults to when only adult are targeted ($\eta_F W > \text{size at maturation}$) (Figure 6a). When only adults are targeted the strength of selection declines and the sign of the selection response on boldness changes as the minimum-size limit in the trawl-like selectivity moves up. Selecting only large mature individuals thus is expected to induce timidity, while selecting smaller fishes (including juveniles) selects for boldness when the fishery is entirely size-selective. The reason for this change is that as mortality is decreased on adults it becomes less important to grow fast, and the push towards increased boldness diminishes. When juveniles are also selected ($\eta_F \ll \text{size at maturation}$), the selection responses on the life history traits become independent on the size at selection. This is likely because for these small sizes natural mortality, which declines with body size, is higher than the fishing mortality, and the effect of the elevated fishing has less selective power. This is the reason why random selection and size-specific selection have similar effects. As before, selection for boldness when the size-selectivity targets also juveniles or small adults is entirely reversed (i.e., timid fish are favoured) when there is also
boldness-selectivity common to many passive fishing gears (Figure 6b). The selection on life-history traits with elevation of minimum-length limits works as before, i.e., direct selection on boldness does not alter the life-history responses of a fast life-history, but the evolutionary response is reduced if only very large adults are targeted.

Gill-net selectivity (which resembles management in recreational fisheries using a harvest slot) leads to more complex selection responses, but does not avoid selection on the three traits (Figure 6c+d). The results are similar to the trawl selectivity pattern when the gill-net only harvests mature individuals. In that case, there is no selection on boldness, and only reproductive investment is predicted to rise (Figure 6c). However, compared to the trawl-like fishery (Figure 6a) the life-history responses and the evolution of boldness are overall reduced (particularly in relation to boldness evolution) when fishing using a harvest slot only selects juvenile individuals (Figure 6c). The lowered selection responses on all three traits is particularly visible when selection operates on both size and boldness (Figure 6d). Then, although under a gill net selectivity, evolution of timidity is predicted when the slot targets mature fishes.

Selection responses with gill net selectivity are overall lower compared to a trawl-like selectivity because the cumulative mortality, i.e. the mortality summed over the whole size range, is smaller at a given fishing mortality rate when only a limited size range is selected compared to the range selected by a trawl.

Sensitivity to changes in fundamental parameters
The model relies on the nine parameters in Table 1 ($k_p$ is a free parameter that determines the asymptotic size). Selection responses are directly proportional to the heritability $h^2$ and to the C.V. of the traits $\sigma_x/\bar{x}$. This follows directly from Eqs. (11) and (15). These parameters therefore only affect the absolute magnitude of the selection responses prediction and do not affect the qualitative results of the different selection scenarios. The sensitivity of the selection responses to the other 7 parameters are explored in Figure 7. The selection responses on the three traits are remarkable insensitive to changes in most parameters. Even changing the metabolic exponent $n$ has a small effect. While the traits themselves are relatively insensitive to changes in the parameter values, the asymptotic size is more sensitive. We therefore conclude that the predictions on changes in the traits, including boldness, are relatively robust to parameter choices, while the predictions on changes in asymptotic size are less robust and might vary more between species than predicted by the model.

**Discussion**

The model replicates earlier model studies showing that increased mortality by fishing selects for individuals with a fast life history with earlier maturation and higher reproductive investment. This result emerges regardless of whether selection was size selective or boldness selective. Increased mortality by fishing favours early-maturing individuals at small size, which have a chance to reproduce before being caught.

Similarly, individuals that invest more in reproductive output early in life are better off because the likelihood of a future spawning event is greatly diminished when mortality
rate increases due to fishing. These results are well-known from life-history theory (Stearns 1992), evolutionary fisheries models of various structure (Arlinghaus et al. 2009; Poos et al. 2011; Dunlop et al. 2015a), laboratory experiments with model fish species (Uusi-Heikkilä et al. 2015) and from time-series analysis of phenotypic field data of harvested natural populations (Jørgensen et al. 2007; Devine et al. 2012; Heino et al. 2015). We demonstrate that selection on boldness can have strong additional impacts on growth rate and asymptotic size. Selection on boldness has the potential to either enhance or mitigate the selection on growth rate depending on whether fisheries selection is mainly directed at boldness (enhanced response) or whether it acts on top of size-selection (mitigated response). Our work thus underscores Biro and Post’s (2008) and Biro and Sampson's (2015) reasoning that any observed changes in growth rate may be caused by direct selection on boldness rather than being caused by size-selection or by life-history adaptation to elevated mortality alone.

As a further new finding we show that we can expect boldness to either increase or decrease depending on the degree of selection acting on behavioral traits. Based on our findings, elevated, but random mortality favors boldness (as in the model of Jørgensen and Holt 2013), whereas direct selection on boldness alone or in addition to size-selection favors timidity, qualitative corresponding to the hypothesis by Arlinghaus et al. (2016, in press). In passively operated fishing gear, vulnerability to capture is likely strongly and often mainly boldness-driven (Klefoth et al. 2012; Biro & Sampson 2015), which is why one can expect changes in growth rate and evolution of timidity.
particularly in reaction to exploitation by gill nets, traps or hook-and-line. It will be important to test this clear-cut prediction in the future in empirical settings, because increased timidity will have substantial effects on catchability and hence on stock assessment, fisher well-being and effectiveness of management tools such as protected areas (Januchowski-Hartley et al. 2011; Alós et al. 2016; Arlinghaus et al. 2017).

Evolution of behavior

Selection on boldness has the potential to somewhat mitigate the selection response towards a faster life history by inducing timidity and thus slower juvenile growth rates. It does, however, not change the selection on size at maturation and investment in reproduction. However, if timid fish are selectively captured (as might be the case in some active gear types; Diaz-Pauli et al. 2015; Killen et al. 2015), evolution of boldness is also predicted under size- and boldness selective fisheries. How a given fishery selects on boldness depends on the nature of the fishing operation in relation to species-specific behavioral patterns and life-styles, which constitutes a much needed research area for the future (Heino et al. 2015; Arlinghaus et al. in press; Diaz-Pauli and Sih in press). Before that research becomes available, we can tentatively propose that because passive gears, such as a gill nets, traps, or hooks, require individuals to actively enter the gear, these gears should preferentially target bold individuals and hence select for elevated timidity (the “timidity syndrome”, Arlinghaus et al. 2016, in press).

How active gear, such as trawl or purse seines, targets different behavioral types is less known, but if they preferentially target timid individuals (Diaz-Pauli and Sih in press),
according to our model they will select for bold individuals, amplifying the selection
generations induced by elevated mortality and leading to even faster life histories and
strongly elevated natural mortality (Jørgensen and Holt 2013). However, trawls might
also select on other personality traits such as swimming activity or sociability or
physiological traits such as metabolic scope and ability for sustained swimming (Diaz-
Pauli et al. 2015; Killen et al. 2015) – traits not considered in our model. Similarly, there
is evidence that other active gear types such as spear guns favor less explorative and
timid individuals rather than bold ones (Januchowsky-Hartley et al. 2011), suggesting
that not all active gear types preferentially exploit shy fishes. Without a dedicated
model that considers a range of behavioural traits and their correlations, it is very hard
to come up with precise predictions about which behaviours will exactly change in trawl
and other active gear-type fisheries. Future theoretical and empirical research is
needed in this underexplored area.

Model limitations

The changes in three fundamental life-history and behavioural traits (size at
maturation, investment in reproduction and boldness) were found to lead to changes in
adult growth rate and a reduction in asymptotic size, which is a classical prediction
about the consequences of fisheries-induced evolution (Jørgensen et al. 2007, Laugen
et al. 2014). However, we find that the prediction on changes in asymptotic size is at
the same time fairly uncertain, as it relies on the value of the parameter $\epsilon_A$ that
describes the partitioning of energy between activity and reproduction, which is not
well known empirically (Andersen & Beyer 2015). Changes in asymptotic size may also be driven by changes in allocation to reproduction during ontogeny, which is unresolved by the model. Instead, we have assumed that allocation to reproduction is directly proportional to individual size, as is customary in many life-history models, however, if allocation increases faster than proportional with size (Edeline et al. 2007; Quince et al. 2008) more energy will be allocated to reproduction in larger individuals, and the reductions in asymptotic size will be even stronger than we predict.

Importantly, however, the downsizing of adults is reduced if behavior is considered under selection in addition to size, which will be the default case in many fisheries (Biro and Post 2008; Uusi-Heikkilä et al. 2008; Arlinghaus et al. in press). Therefore, evolutionary costs while considering behavior with respect to size are smaller from an adult size (and likely yield) perspective than assumed before in life-history models that omit behavioral dynamics. Importantly, a recent experimental harvesting experiment in zebrafish (*Danio rerio*) that strongly selected on size found evolution of timidity and at the same time only subtle changes in terminal size and no evolution of juvenile growth rate (Uusi-Heikkilä et al. 2015), agreeing with our findings.

Another limitation of our modelling approach is the absence of population regulation through density-dependent processes, which is a key ingredient of alternative individual-based eco-genetic models of fisheries-induced evolution (Dunlop et al. 2015b; Eikeset et al. 2016). A previous modelling study that examined the impact of a range of density-dependent processes acting on fecundity and mortality on selection
differentials on reproductive investment in pike (*Esox lucius*) (Arlinghaus et al. 2009)

indeed found that the predictions were rather sensitive to density-dependent somatic growth but insensitive to density-dependent mortality. However, the sign of the selection differentials on reproductive investment remained identical whether density-dependence was acting on growth or not. Moreover, the key predictions emerging from our stylized model were roughly similar to the predictions of more complex eco-genetic models in terms of the expected evolution of fast life histories under most situations in fisheries (Eikeset et al. 2013; Dunlop et al. 2015b). Nevertheless, it is clear that our work shall be extended and replicated with other model frameworks to analysis its stability. Further, our model assumes that the entire stock is only exposed to one gear type selectivity. Our findings do not hold for mixed gear situations, which demand careful calibration to actually selection pressures caused by varying gear and the modelling of spatial gene flow. The scope of our work is beyond this, but some recent work has started to look at spatial explicit models (Mee et al. 2017). Finally, it is important to consider multi-species contexts in future evolutionary models and a range of behavioural traits that are either correlated with each other forming behavioural syndromes (Sih et al. 2004) or independently affecting vulnerability to capture and resource intake (e.g., boldness and activity or space use). Empirical research is needed to provide the data about correlations among traits to inform such models. Until that research becomes available our predictions on the relative impact of size-selectivity and boldness-selectivity represents the best possible estimates, and they were found to be independent of specific assumptions and size-selectivity of fishing. Our results on the
magnitudes of evolutionary rates, however, are more uncertain as they depend on
exact values of parameters. Least robust are our predictions on changes in asymptotic
size. Moreover, our findings on the relative impacts of gill net selectivity confounded
effects stemming from altered size-selection with altered effective exploitation rates
(not the case in Mollet et al. 2016), warranting further study in the future.

Consequences

Based on our current knowledge, we propose that predicting the evolutionary
consequences of fisheries for populations will benefit from explicit consideration of
behavioral dynamics. In the absence of more detailed knowledge, it is possible that
active gear that targets timid individuals (Diaz-Pauli and Sih in press) will select for
bolder fishes. This result is valid even in the absence of direct selection on boldness, but
will be even stronger if timid fishes are preferentially captured (as might be the case in
active gear types Diaz-Pauli et al. 2015). Conversely, passive gear is more robustly
known to target bold individuals (which often have faster life histories, Réale et al.
2010), thereby evolutionarily favoring increased timidity. Many commercial and
recreational fisheries operate with passive gear – long lining for pelagic top predators in
the ocean, gill netting in coastal areas or recreational fishing of freshwater lakes. It is
conceivable that a century of such fishing has created shyer individuals with lower
consumption rates and more risk averse life-styles, which may in turn translate to
reduced parental care in species providing this care (Sutter et al. 2012). This likely has
consequences for social groups, populations and food webs (Arlinghaus et al. in press;
Diaz-Pauli and Sih in press), and we also predict systematic erosion of catchability through evolution of timidity (Alós et al. 2015; Philipp et al. 2015; Tsuboi et al. 2016) largely independent of which harvest regulations (minimum-size limits, maximum-size limit or harvest slot) are put in place. This is a major difference to previous studies who found that life-history responses to fishing mortality can well be addressed by cutting fishing mortality and changing selectivity patterns to a dome-shaped selectivity typical of harvest slots and gill nets (e.g., Jørgensen et al. 2009; Matsumura et al. 2011; Zimmermann & Jørgensen 2017). Our work instead suggests that evolution of timidity by passive gear cannot be avoided unless the harvest slot leads to an exclusive removal of juveniles, which is uncommon in most fisheries but indeed reported from selected recreational fisheries (e.g., in shore recreational fisheries in Florida).

Importantly, because evolution in boldness, in either direction, will erode the index value of fishery-dependent data by changing catchability over time, and have potentially have large community and food web as well as managerial and fisheries consequences (Arlinghaus et al. in press), we (and others, Diaz-Pauli and Sih in press) suggest increasing attention to the possibility of fisheries shaping the mean and variance of behavioral expressed by exploited fishes in nature.

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Table 1. Value of parameters

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value and units</th>
<th>Eq.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Reproductive investment</td>
<td>$k_r \ (yr^{-1})$</td>
<td></td>
</tr>
<tr>
<td>Size at maturation</td>
<td>$w_m \ (g)$</td>
<td></td>
</tr>
<tr>
<td>Boldness</td>
<td>$\tau$</td>
<td></td>
</tr>
<tr>
<td>Critical feeding level (1)</td>
<td>$f_c = 0.2$</td>
<td>4</td>
</tr>
<tr>
<td>Available food (2)</td>
<td>$R = 1$</td>
<td>2</td>
</tr>
<tr>
<td>Mortality constant (3)</td>
<td>$\alpha_p = 1.9$</td>
<td>9</td>
</tr>
<tr>
<td>Metabolic exponent (5)</td>
<td>$n = 3/4$</td>
<td>2</td>
</tr>
<tr>
<td>Max. consumption parameter (4)</td>
<td>$A = 19 \ g^{1-n}/yr$</td>
<td>2</td>
</tr>
<tr>
<td>Activity coefficient (6)</td>
<td>$\epsilon_a = 0.8$</td>
<td></td>
</tr>
<tr>
<td>Maturation rel. to $W$ (7)</td>
<td>$\eta_m = 0.25$</td>
<td></td>
</tr>
<tr>
<td>Heritability</td>
<td>$h^2 = 0.2$</td>
<td>15, 16</td>
</tr>
<tr>
<td>Coef. of variation of traits</td>
<td>$\sigma_x/\bar{x} = 0.2$</td>
<td>14</td>
</tr>
</tbody>
</table>

(1) Hartvig et al. (2011).

(2) Leads to a functional response where the individual neither starves nor is satiated. Corresponds to a resource concentration equal to the half-saturation coefficient.

(3) Gives a factor for the mortality $\alpha_p \tau \approx 1.6 \ yr^{-1}g^{n-1}$, which
corresponds to the level of mortality used in Andersen and Beyer (2015).

(4) Set to correspond to the growth coefficient in Andersen and Beyer (2015):
\[ A \left( \frac{FR}{FR+1} - f_c \right) \approx 5 \text{ g}^{1/2} / \text{yr at } 10^\circ \text{C}. \]


(6) Found by fitting observations of annual reproductive output (Andersen and Beyer 2015)

Figure 1. Size at age of a long-lived species with asymptotic weight of 14,000 g (thick lines). (a) Size at age with various boldness $\tau$ shown with thin lines for bolder individuals (above) and timid individuals (below). (b) Size at age with various investment in reproduction $k_r$; higher investment (below) and less investment (above). The growth curves are drawn until 5 times the age at maturation.
Figure 2. Mortality and fisheries selectivity. (a+b) Predation mortality (black) and fishing mortality (grey) for a species with asymptotic size 14,000 g with boldness $\tau = 0.9$ (thick) and $\tau = 0.8$ (thin) and fishing mortality $F_0 = 0.3$ $\text{yr}^{-1}$. (a) Fisheries trawl selectivity defined by the inflection point at $w_F$; (b) harvest slot (aka gill-net) selectivity where the width is fixed and the entire slot is moved with $w_F$; (c) Boldness-selective harvest for three values of the selection strength $b_F$: 0 (horizontal dashed) and 0.5, 1 (thick line) and 2.
Figure 3. Proportional selection response for four selectivity scenarios: 1: random harvest; 2: size-selective harvest with a trawl-like selectivity; 3: boldness-selective harvest, and 4: both size- and boldness-selective harvest. The colour codes show proportional selection response for: reproductive investment (orange), boldness $\tau$ (black) and maturation size (magenta). Asymptotic size $14,000$ g and fishing mortality $F_0 = 0.3$ yr$^{-1}$. 
Figure 4. Proportional selection responses as a function of fishing mortality without selection on behavior ($b_F = 0$) (a) and as a function of the strength of selection on boldness for $F_0 = 0.3 \text{ yr}^{-1}$ for the case with a trawl-type size selection. Line width represents asymptotic size; thin: 140 g, thick: 14,000 g. The vertical dashed line in panel b corresponds to the selection on behavior used in Figure 3 for case 3. Reproductive investment (orange), boldness $\tau$ (black) and maturation size (magenta).
Figure 5. Size-at-age curves after 200 years of selection on species with asymptotic size 140 g (a) and 14,000 g (b). Curves represent the three cases of selection: without selection (thick), after only size-dependent selection (case 2; thin), after selection on boldness only (irrespective of size) (case 3; grey dashed), and combined selection on size and boldness (case 4; grey). The curves are drawn until 5 times the age at maturation to illustrate the effect of selection on age at maturation. $F_0 = 0.3 \, \text{yr}^{-1}; b_F = 1$; the dotted line is at size at maturation.
Figure 6. Proportional selection responses as functions of the mid-point of selectivity relative to asymptotic size ($n_F$) for a trawl selectivity pattern (Figure 2a) (a and b) and for a slotted size-selectivity (Figure 2b) (c and d). Panels and c: without selection on boldness $b_F = 0$; panels b and d: with selection on boldness $b_F = 1$. Reproductive investment (orange), boldness $\tau$ (black) and maturation size (magenta). Vertical dotted line shows size at maturation. The case with entirely unselective mortality as baseline case corresponds to the left edge of panel a, while selection only on boldness corresponds to the left edge of panel b. Line width represents asymptotic size; thin: 140 g, thick: 14,000 g.
Figure 7. Sensitivity of selection responses to changes in the fundamental parameters. Reproductive investment (orange), boldness $\tau$ (black) and maturation size (magenta), asymptotic size (grey). Solid lines are without selection on boldness $b_F = 0$; dashed lines with selection on boldness $b_F = 1$. 