Fitness consequences of fish circadian behavioural variation in exploited marine environments

Running title: Marine fish chronotypes

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Abstract

The selective properties of fishing that influence behavioural traits have recently gained interest. Recent acoustic tracking experiments have revealed between-individual differences in the circadian behavioural traits of marine fish; these differences are consistent across time and ecological contexts and generate different chronotypes. Here, we hypothesised that the directional selection resulting from fishing influences the wild circadian behavioural variation. We predicted this would differentially affect individuals in the same population that varied in certain traits like such as awakening time or rest onset time. We developed a spatially explicit social-ecological individual-based model (IBM) to test this hypothesis. The parametrisation of our IBM was fully based on empirical data that represent a fishery formed by patchily distributed diurnal resident fish that are exploited by a fleet of mobile boats (mostly bottom fisheries). We ran our IBM with and without the observed circadian behavioural variation and estimated selection gradients as a quantitative measure of trait change. Our simulations revealed significant and strong selection gradients against early-riser chronotypes when compared with other behavioural and life-history traits. Significant selection gradients were consistent across a wide range of fishing effort scenarios. Our theoretical findings enhance our understanding of the selective properties of fishing by bridging the gaps among three traditionally separated fields: fisheries science, behavioural ecology and chronobiology. We derive some general predictions from our theoretical findings and outline a list of empirical research needs that are required to further understand the causes and consequences of circadian behavioural variation in marine fish.

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Introduction

Humans have exploited fish populations through trait-selective harvesting since the origin of our species (Allendorf & Hard 2009). In fact, fishing is widely recognised today as a major driver of contemporaneous evolution and trait change in wild fish populations (Sullivan et al. 2017). There is substantial evidence that size-selective harvesting (e.g., gear selectivity) usually selects for fast life-histories and favours early maturation and high reproductive investment 404-409(Alós et al. 2014; Heino et al. 2015; Laugen et al. 2014; Matsumura et al. 2011). The behavioural dimension of fisheries selection has recently gained interest among fisheries scientists and managers due to the growing evidence of consistent between-individual differences in the behaviour of exploited fish and the study of selection in real fisheries (Arlinghaus et al. 2017; Diaz-Pauli & Sih 2017, Uusi-Heikkilä et al. 2008). Currently, there is a large quantity of literature demonstrating the existence of consistent between-individual differences of fish behavioural traits in temporal and ecological contexts, such as boldness or aggressiveness, that define behavioural types within fish populations (Conrad et al. 2011; Mittelbach et al. 2014). In addition, with the recent development of aquatic telemetry, fisheries scientists have a powerful tool available to study behavioural types of free-living fishes (Hussey et al. 2015; Lennox et al. 2017a) and how fisheries may promote the selection of behavioural types in real-world fisheries (e.g., Alós et al. 2016b; Monk & Arlinghaus 2017; Olsen et al. 2012). Together, these two developments have generated substantial empirical evidence demonstrating that bold and high-exploratory individuals (e.g., Alós et al. 2012b; Biro & Sampson 2015; Härkönen et al. 2014; Klefoth et al. 2011; Olsen et al. 21012) are more prone to harvest; thus, this evidence supports the idea that timidity syndrome can give rise to exploited fish populations that are composed of shy, less active and less exploratory individuals (Arlinghaus et al. 2017; Arlinghaus et al. 2016).

Surprisingly, behavioural traits that determine timing have been poorly considered in the context of the selective properties of fishing. Recently, Tillotson & Quinn (2017) proposed the timing of migration or breeding as candidate traits that are targeted by fisheries selection. Both the timing of migration and the timing of the breeding season have strong impacts on population dynamics (Lowerre-Barbieri et al. 2017), and selection imposed by these traits would strongly impact the long-term trajectory of the fish stocks. Similarly, an ubiquitous behaviour related to timing in fish that has been overlooked by the scientific fisheries community is the manifestation of underlying circadian rhythms. Life on earth is governed by a 24-h rotation cycle that has led to the evolution of endogenous circadian clocks across taxa, including fish species (Kreitzman & Foster 2005). Similar to behavioural types, humans and some terrestrial animals show temporally consistent between-individual variation in different

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circadian-related behaviours, such as awakening time or sleep onset, that are the result of the interactions between those endogenous individual circadian clocks and the environment; furthermore, these interactions define chronotypes (Roenneberg et al. 2007; Bloch et al. 2013; Rattenborg et al. 2017). Although chronotypes should be ubiquitous across animal taxa, only few studies have demonstrated the existence of chronotypes by exploring the amount of behavioural variation explained by between-individual differences (Randler 2014), and these studies have mainly focused on bird species (Dominoni et al. 2013; Steinmeyer et al. 2010; Stuber et al. 2015; Stuber et al. 2014).

Regardless of whether fish sleep or not (Reebs 1992), most fish species show a circadian-related behaviour in which they change from an active state to a resting state, leading to a “sleep-like” behaviour that is consistent with the sleep architecture observed in mammals (Schmidt 2014; Siegel 2008). This diel active/resting cycle is widely observed in free-living fish across species (e.g., Krumme 2009; Alós et al. 2012a; Alós et al. 2016b; Koeck et al. 2013). Recently, Alós et al. (2017) found the first evidence supporting the existence of chronotypes in fish focused on the pearly razorfish, *Xyrichtys novacula*. Similar to humans and birds, fish chronotypes arise from between-individual differences in circadian behavioural traits that are consistent over time and ecological contexts (Fig. 1). Far from being anecdotal, chronotypes have been frequently linked to many fitness processes in terrestrial animals, such as predation mortality or finding a reproductive mate (Roenneberg et al. 2003, and see review by Adan et al. 2012), and any directional selection pressure (i.e., either natural or human-induced) acting on chronotypes could lead to trait changes in terms of circadian behavioural rhythms (Helm et al. 2017). In fact, one recent study demonstrated how a potential environmental-induced change in a behavioural traits can influence circadian behavioural variation and impact fitness (Dominoni et al. 2013), i.e., city birds that started their activity earlier than their forest conspecifics highlighted that urban environments (i.e., those with artificial lighting) can significantly modify biologically important rhythms in wild organisms and explained the potential reproductive advantages conferred to the early-rising birds in such an artificial environments. Similarly, we assumed here that early-riser fish chronotypes would be more vulnerable to fishing simply because the number of encounters between the fish and fishers was expected to be higher.

Based on this assumption, the objective of this work was to explore the plausibility of selection acting on fish chronotypes using a spatially explicit individual-based model (IBM). Our IBM assumed relatively simple movement rules that dictated the encounters between fish and fishers, and it was based on the real properties of a general bottom coastal fishery; additionally, the IBM explicitly incorporated social-ecological factors to add realism to our

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model (and simulations). The selection gradient (*S*), as a central measure of selection in traditional quantitative genetics with heritability (Price 1970), has been widely used to describe trait changes in commercial and recreational fisheries (e.g., Alós et al. 2016b; Monk and Arlinghaus 2018). We aimed here to estimate mean-standardised selection gradients on circadian behavioural traits to determine whether they were different from zero, and we compared them with previously reported gradients of other traits. Although the economic consequences of fisheries selection can be addressed by proper fisheries management (Eikeset et al. 2013), it can generate undesirable consequences in terms of ecosystem functioning (Audzijonyte et al. 2013; Jørgensen et al. 2007); specifically, this selection can notably reduce the recovery of overexploited stocks (Uusi-Heikkilä et al. 2015; Walsh et al. 2006) and decrease the recreational utility of fisheries (Sutter et al. 2012). Therefore, our final objectives were to make broader predictions about our findings and to stimulate research on the topic by providing a list of empirical research needs to fully disentangle the causes and consequences of fish chronotypes in exploited environments.

Material and methods

To explore whether fishing selection influences circadian behavioural traits, we developed a computational IBM where a fish population spatially behaves in a 2-D landscape and is exploited by a fleet of fishing boats during a fishing session (see Fig. 2 and video in SM1). Our IBM is spatially explicit because fish and fishers move (i.e., change position every minute) across the landscape according to different types of movement models. Encounters between the fish and fishers determined the mortality of the fish. Although encounters between fish and fishers do not always predict harvest (e.g., Monk and Arlinghaus, 2018), these encounters are among the most important components related to the vulnerability of most fishes (Lennox et al., 2017), especially in bottom coastal fisheries (e.g., Alós et al. 2012b; Alós et al 2016b). Our model was built under a prototypical bottom fishery where *i*) target fish performed a sedentary behaviour that lead to the establishment of a home range (HR) area, *ii*) the centres of activity were patchily distributed and formed a patchy landscape (which could be the consequence of a fragmented habitat), and *iii*) fish were exploited by a fleet of mobile fishing boats. Our model was parametrised using empirical data from a popular recreational baited hook-and-line fishery located in Mallorca Island (Spain) that targeted pearly razorfish (see full details in Alós et al. 2016b); however, the model is generalizable to any other system that displays these three main properties. Our computational IBM simulation was implemented and run in R (R Core Team 2017). The R code is provided in the Supplementary Material (SM2).

(a) The ecological landscape: fish moving with individual heterogeneity in circadian and spatial behaviour

We created a 2-D landscape of 12.1 km^2 with open boundaries, of which 6.4 km^2 formed the preferred habitat of the pearly razorfish (hereinafter, the targeted species) to create a realistic ecological landscape (see map in Fig. 2). We randomly distributed 2,000 centres of activity (centre of the HR, see below) in the preferred habitat to create a patchy distribution of fish across the ecological landscape, and each centre of activity was designated to one identified fish (initial population = 2,000 individuals, density = 312 individuals per km^2, see Fig. 2). Then, fish survival was monitored every minute during the entire prototypical fishing season; here, survival was monitored for 15 full fishing days after the opening of the fishery on September 1st at 00:00, according to Alós et al. (2016b). Thus, the IBM was discretised on time (every 1 min), had 21,600 time-steps (*n*), and the position (latitude and longitude) of each fish was mechanistically generated based on its movement and circadian behavioural variation, as described below.

Fish movement is usually mechanistically explained by different types of random walks (Smouse et al. 2010). Different from the purely random walks that generate standard diffusion across space, many fish species use a confined area and form stable HR areas (Alós et al. 2016a). The idea behind HR movement is that an individual moves within a harmonic potential field following random stimuli (i.e., a random walk); however, the individual has a general tendency to remain around a central place of residence (Börger et al. 2006). In such cases, there is a need for an additional behavioural rule that keeps the individual within its designated core site (Benhamou 2014; Smouse et al. 2010), and this can be described by the Ornstein-Uhlenbeck process that defines a biased random walk (BRW) (Alós et al. 2016a).

For the purpose of this study, we focused on two descriptors of this BRW movement model described in Alós et al. (2016a): *i*) the size of the circular HR *radius* (in metres) that can be interpreted as a surrogate for the total foraging area and activity space, and *ii*) the harmonic force (*k*, in min^{-1}) that can be interpreted as the strength of the drift or attraction force towards the centre of the HR, which ultimately determines the slope of the curve describing the cumulative space used in a period of time (we refer this as *exploration*). We randomly assigned values for both parameters to our virtual population of fish based on the real data estimated in Alós et al. (2016a); range for *radius*: 67-470 m and *exploration*: 0.0005-0.025 min^{-1}, using the function *sample* of the base package of R. See Fig. 2 for a visualisation of the realised daily trajectories of a given fish.

Each of the 2,000 fish was assigned an individual mean and s.d. value for its awakening time and a daily value for its rest onset time based on the real data published in Alós et al.

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(2017); this generated the daily transition between the resting and active states at the individual level (see simulation scenarios below).

Once a set of movement parameters and circadian behaviours was assigned to each identified fish, we generated a daily sequence of states (active vs. resting) based on the individual mean and s.d. values for each fish for the entire simulated fishing. Accordingly, we re-sampled the mean and s.d. of both circadian traits (i.e., awakening and rest onset times) daily for each individual, and we generated one value from this distribution for each day and individual (see Fig. 1). We then constructed the sequence of active and resting states based on the local sunset and sunrise times and the daily individual values that were generated. Finally, a position for all time-steps in an active state was generated for the entire fishing season based on our HR mechanistic model and the individual movement parameters of each fish (Fig. 2 and see SM1). During the resting state, the individual remained in the same position, and the fish was invulnerable to fishing as long as it remained in shelter (e.g., the pearly razorfish remains buried in the sand at night, according to Alós et al. 2012a). The complete sequence of time-steps and positions for each fish was used to create a realistic dynamic ecological landscape (see movie SM1).

b) The social landscape: a fleet of mobile boats targeting the ecological landscape

A fleet of mobile fishing boats exploited the ecological landscape. The entire fleet exploited the fishery every day during the entire fishing season (i.e., 15 days). On a daily basis, the IBM carefully considered different arrival and departure times for boats in the fishery (and the local sunrise data were used to synchronize the times with the ecological landscape), as this aspect is highly relevant for the objectives of our study. Specifically, we put effort into reproducing the real daily dynamics of fishing pressure by assigning a time of arrival and a time of departure for each boat (see Fig. 2), and these times were derived from a visual census of the actual fleet (Alós et al. 2016b); specifically, fishers exploited the fishery for a duration that ranged from 160 to 460 min after sunrise, with an effective fishing effort of 4.6 ± 1.2 h. For simplicity, no within-individual variability in the time of arrival and departure was considered (i.e., each fisher arrived at the fishery at the same time every day); however, some individuals arrived earlier than others, which is similar to the idea of fish chronotypes.

As fishers arrived at the fishery (depending on their individual arrival time), their spatial behaviour was based on a movement model that included two states. Individual boat fisher trajectories are usually composed of different states, and typically there are three main states: cruising, searching and fishing (Vermard et al. 2010; Walker & Bez 2010). In our scenario, once fishers arrived at the fishery, they performed a classical search pattern that

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included two states, i.e., fishing and searching (see Fig. 2). Here, we considered relatively simple hidden Markov model (HMM) movement with two types of random walks describing each state (Auger-Méthé et al. 2015). HMMs are widely used for modelling any type of animal or fisher movement data (Patterson et al. 2017), and the R package *moveHMM* was recently developed to perform simulations of movement trajectories (Michelot et al. 2016).

Accordingly, for each fisher, a bi-variate time-series composed of step-lengths (in m) and turning angles (in rad) was generated to describe the trajectory of each fisher every day. These temporal series were drawn by a state-dependent process at moment *n* (unobserved in a real situation; the hidden Markov chain) using two distributions of the step-lengths and turning angles (one per state; fishing vs. searching). The transition among the two states was generated by a 2 × 2 transition probability matrix, $\Gamma = (\gamma_{ij})$, where γ_{ij} was the probability of the fisher switching from the current state (at time-step *n*) to the future state (at time-step *n+1*). Here, we considered $\Gamma = \begin{pmatrix}0.95 & 0.05\\ 0.5 & 0.5\end{pmatrix}$, meaning that each fisher spent most of his/her time fishing to obtain realistic fisher trajectories (see a realised trajectory of the fisher in Fig. 2).

Each state of the sequence was associated with a distinct random walk movement model that included a BRW for fishing and a correlated biased random walk (CBRW) for searching to adequately reproduce the spatial dynamics of the fleet (Fig. 2). When the fisher was in the fishing state, the boat drifted with the current. Though this process is not a random walk, for simplicity, we used the mathematical description of a conventional BRW by biasing the angle of the trajectory according to the surface current in the area and adding some noise (see Fig. 2 and SM1). Accordingly, the step-lengths of this state were described by a gamma distribution (because velocity cannot obtain negative values), with the mean = 1 m and the s.d. = 0.5 m; additionally, the angle was described by a von Mises distribution, with the mean equal to the angle of the surface current and the concentration = 1.2 rad (noise) to reproduce similar real-life patterns observed in the fishery. To add realism, we used the real observed angle of the surface current for each time-step *n* since September 1st, 2016 at 00:00; these data were obtained from an oceanographic buoy located in the study area by the SOCIB (www-socib.es) (Tintoré et al. 2013).

The searching state of the fisher was modelled using the CBRW model described by Langrock et al. (2014), which was developed to model the group dynamics of animal movement. Accordingly, the searching state was mathematically described by a mixture of a BRW, where the bias was imposed by the social information that generated a tendency to move to the centroid of the positions of the other boats while searching (i.e., watching other

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boats, social information); and a conventional correlated random walk (CRW), where searching was described by a turning angle drawn from a von Mises distribution with a mean = 0 and a concentration = 5 rad. In both cases, the step-lengths were described by a gamma distribution of step-lengths with mean = 150 m and s.d. = 130 m (i.e., searching velocity). The BCRW developed by Langrock et al. (2014) is unique due to the existence of a parameter (η) that specifies the weight of the BRW with respect to the CRW portion of the BCRW. Here, we considered η = 0.7, which generated a behaviour of the fleet characterised by the tendency to remain close to the other fishing boats; this was based on the observations of real-life data. The full-day fisher trajectory was generated according to the Markov chain of the two states (see Fig. 2) and the movement model, and one independent trajectory was generated every day. The initial location of each fisher in the fishery was randomly generated in the 2-D landscape, and the first state of the day was searching. For simplicity, no among-fisher movement variability was considered.

c) Simulation scenarios: with and without circadian behavioural variation

Here, we were interested in the individual differences in the daily timing of switching the circadian state in fish, and we were particularly interested in the repeatability score (*R*) of two behavioural manifestations of fish circadian rhythms (Fig. 1): *i)* awakening time and *ii)* rest onset time (referred to as minutes from sunrise or sunset, respectively). *R* assesses the degree of consistency of the behaviours displayed by individuals over time (Nakagawa & Schielzeth 2010) and represents the phenotypic variation that is attributable to individual heterogeneity; additionally *R* is often used to characterise animal personalities and, in our context, to detect chronotypes (Alós et al. 2017; Dingemanse & Dochtermann 2013; Stuber et al. 2015). To test our hypothesis on how fishing selection acts on this circadian behavioural variation, we simulated two scenarios. In the first scenario (i.e., the real scenario), the fish population showed significant repeatability in the awakening and rest onset times, which generated chronotypes (Fig. 1). Each of the 2,000 fish was randomly assigned an individual mean and standard deviation (s.d.) in the awaking and rest onset times according to the real data published in Alós et al. (2017) to generate chronotypes using the function *sample* of the R package (range of individual means of awakening time: 18.2-271 minutes; range of individual means of rest onset time: -9.3-13.4 minutes, see Fig. 1). In the second scenario, all individuals in the population had an awakening time and a rest onset time with the same normal distribution (mean = 0 min, s.d. = 15 min) to obtain an ecological landscape where chronotypes did not exist (i.e., no real circadian behavioural variation nor between-individual differences

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were simulated), and all individuals were vulnerable to the fishing fleet. This second simulation scenario was used to confirm that the potential selection gradients obtained in the first scenario were not caused by the indirect selection of other behavioural traits or by other unknown dynamics of the IBM. We initially considered a total number of 133 fishing boats (spatial fishing effort: 11 boats per km^2) based on the empirical data found for our target fishery, and the main results are discussed using this relatively realistic scenario (Alós et al. 2016b). However, both simulation scenarios were finally run using 6 fishing pressure scenarios that differed in the number of mobile fishing boats exploiting the ecological landscape. We used a wide range of different fishing effort scenarios to evaluate the strength of the potential selection under different fishing pressures (i.e., 2, 4, 6, 8, 10 and 12 boats per km^2). These different fishing pressure values generated increasing exploitation rates that ranged from 24% to 70% of the population, which indicates our conclusions can be interpreted for a wide range of scenarios.

d) Model outcomes: exploitation model and estimation of selection gradients

The coupled social-ecological landscapes were simulated, and the encounters between fish and fishers were quantified in the two simulation scenarios under the different fishing pressures described above (Fig. 2 and see movie in SM1). We defined an encounter as successful when *i*) the distance between the fish and the fisher was less than 5 m (a reasonable distance to assume visual contact of the bait by the fish) in a given time-step, *n*; *ii*) the fish was in a vulnerable state (i.e., active); *iii*) the fish had not previously encountered another fisher (emulating harvest with depletion); and *iv*) the fisher was in the fishing state. When the four conditions were met, the fish ID was considered as harvested and was removed from the simulation to emulate fishing with depletion. Once the simulated fishing season ended, we characterised the surviving individuals (i.e., the exploited population) in terms of their circadian and spatial behavioural variation. We then estimated the selection gradient (*S*) of the two circadian (awakening time and rest onset) and spatial (radius of the HR and exploration) behaviours. *S* was computed as the difference between the phenotypic mean trait of the initial population and the mean of the surviving population, and values were mean-standardised (S_μ) to generate a normalised measure of selection strength following Matsumura et al. (2012), and to ensure they were comparable with previously reported data on other traits. S_μ is a measure of selection strength and allows the strength of selection acting on each of the various behavioural traits to be ranked independent of the trait's mean and variance. S_μ can

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be interpreted as the elasticity of fitness to trait change. For example, a value of S_{μ} = 0.5 means that doubling the trait value increases fitness by 50%. We computed the 95% confidence intervals of S_{μ} for each behavioural trait by bootstrapping (1,000 iterations) the results of the simulation scenarios developed here using the *boot* function of the R package (Canty and Ripley 2017).

Results

The first simulation scenario that considered real wild circadian behavioural variation (i.e., observed fish chronotypes) adequately reproduced the existence of chronotypes (Fig. 1). The *R* scores in this scenario were 0.43 [0.37-0.6] for awakening time and 0.45 [0.39-0.6] for rest onset, which were similar to the scores obtained from the real data by Alós et al. (2017). Fish started their activity as late as 400 min after sunrise, and among-individual differences in awakening time were clearly recognisable, enabling the identification of an early-riser chronotype (Fig. 1). In contrast, fish finished their activity within a shorter period (up to 20 min after sunset), but some individuals extended their activity by an average of a few minutes according to the real data (Fig. 1).

The mean and s.d. of the four behavioural traits in the initial and exploited populations are shown in Table 1. In total, 650 individuals survived (exploitation rate = 67.5%) in the simulation scenario, and in general, the exploited population was composed of individuals with later awakening times, similar rest onset times, smaller HRs and slower exploration (Table 1). These results generated significant S_{μ} that differed from zero in terms of awakening time (mean S_{μ} = 0.85), HR size (mean S_{μ} = -0.52), and exploration rate (mean S_{μ} = -0.22) (Table 1). These results were consistent along the simulated gradient of fishing effort, and the strength of significant S_{μ} values increased as fishing effort increased (Fig. 3).

In the second simulation scenario, i.e., where no fish chronotypes were simulated, the number of surviving individuals was 315 (exploitation rate = 84.2%). In this case, the exploited population was composed of individuals with similar awakening times and rest onset times and smaller HRs and exploration rates (Table 1). These results generated significant S_{μ} different form zero values for only the HR size (mean S_{μ} = -0.49) and exploration (mean S_{μ} = -0.36, Table 1), and we discarded significant S_{μ} that differed from zero for the circadian behavioural traits (Table 1). These results were also consistent across the simulated gradient of fishing effort (Fig. 3). Therefore, we assumed that the results from the observed fish chronotypes simulation scenario were caused by factors other than circadian behavioural variation.

Discussion

Circadian behavioural variation has important implications for individual fitness, and many eco-evolutionary trends are dependent on the realised expression of circadian rhythms (Roenneberg et al. 2003; Wicht et al. 2014); however, very little information is known about the consequences of fish chronotypes. Here, we found that fishing selection may influence the variation in circadian behaviours by differentially harvesting early-riser chronotypes, and the strength of this selective process is linked to fishing pressure. We demonstrated these potential consequences of fish chronotypes in exploited environments using a novel social-ecological IBM. IBMs are especially appropriate for formulating and testing emergent population properties from individual processes in predator-prey systems (Barbier & Watson 2016; Watkins & Rose 2017), including fisheries (Alós et al. 2012b). The *R* score or the within-population behavioural variation are classic examples of an emergent population property from individuals, and this value makes IBMs particularly suited to test our hypotheses (Bell et al. 2009). In addition, our IBM allowed us to test our working hypotheses using two different ecological simulation scenarios using real data and a wide range of fishing pressure scenarios. Therefore, we feel our approach, although theoretical, properly reproduces some of the potential fitness consequences of circadian behavioural variation in exploited marine environments and provides novel insights in the selective properties of fishing.

The results of the first simulation scenario, i.e., that which used real wild circadian variability, revealed a significant selection gradient in terms of the awakening time. Fish that survived the simulated fishing season were clearly not a random sample of the initial population, and early-riser chronotypes were more prone to capture by the fleet of boats. This finding adds a new variable to the complex concept of the vulnerability of fish to fishing (Lennox et al. 2017b). This result was consistent across all fishing pressure levels, suggesting that even in low fishing pressure scenarios (i.e., 2 boats per km^2), fishing selection may influence circadian behavioural traits. In fact, the strength of selection was expected to increase as fishing pressure (i.e., mortality) increased. In contrast, no evidence was found for any selective properties regarding the time of rest onset, which was likely related to the fact that simulated fishing activity mainly occurred during the daytime. In the second scenario, where no wild circadian behavioural variation was simulated, the selection gradient of the awakening time was not significantly different from zero, confirming that chronotypes were

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major drivers of selection force; this result is consistent with the results of the first simulation scenario that was based on real-world data.

The potential for eco-evolutionary changes in chronotypes under human pressure has been recently proposed (Helm et al. 2017). In fact, Dominoni et al. (2013) demonstrated that city European blackbirds, *Turdus merula* began their activity earlier and had faster circadian oscillation than did their forest con-specifics. The results by Dominoni et al. (2013) suggested that humans (through artificial lighting) may have selected for individuals by favouring those with large circadian period lengths. In this example, the selective force imposed by artificial lighting acts in the opposite direction than that of our working hypothesis. In our work, the selective force is imposed by the timing of the fishing pressure (Fig. 2); thus, the selective force should favour small foraging periods. What is relevant in this context is that both artificial lighting in the city and fishing pressure in the sea may impose selection gradients in circadian behavioural traits and may act as eco-evolutionary drivers in wild populations, and this information should be further studied (Helm et al. 2017). In addition, our work provides the first evidence that suggests fishing may play a role in the circadian rhythms found in oceans.

Our theoretical selection gradients were mean-standardised, which allowed them to be compared with other traits. First, we found significant selection gradients in the two spatial behavioural traits considered here, indicating selection against large HRs and fast exploration rates. Although both were smaller than the values obtained by the circadian behavioural traits, significant selection gradients were consistent between the two simulation scenarios and across all fishing pressures. Interestingly, the direction of selection was consistent with the empirical selection gradients of hook-and-line recreational fisheries on these spatial behavioural traits, indicating that our IBM was robust (Alós et al. 2016b). Moreover, the strength of the obtained selection gradient on awakening time was also stronger when compared with other life history (S_μ = 0.66) and morphological (S_μ = 0.29) traits that have previously been reported (Hereford et al. 2004), although in function of the fishing scenario simulated. In fact, the strength of selection may vary according to the morality pressure, as revealed by the different fishing effort scenarios in our simulations. This fact highlights the relevance of estimating selection gradients in real populations that are exposed to mortality pressure and the importance of using realistic scenarios (i.e., those based on data from the wild). However, our results demonstrated that the potential of selection on circadian behavioural traits certainly exists, and the selection strength could be similar or even stronger than that of previously considered traits.

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Although our work is mainly theoretical, we can derive some ecological implications about the selective properties of fishing acting against early-riser chronotypes. Chronotypes are important determinants of reproductive success in birds; for instance, females choose males with early awakening times (Helm & Visser 2010). Assuming this also occurs in fish, one could predict a reduction in the overall reproductive output of a population due to the absence of highly reproductive early-rising males. In addition, fish such as the pearly razorfish play a key role in the food-web by preying on other taxa (Castriota et al. 2005) and serving as prey for larger animals, such as dolphins. Thus, a change in the daily timing in a population of pearly razorfish could induce foraging behavioural changes with impact in the lower and upper levels of the food-web. We can also speculate that fishing-induced selection against early risers is currently occurring, and the results observed by Alós et al. (2017) are the result of such selective processes. Therefore, we suggest that the ecological consequences of the selective properties acting on circadian behavioural traits are plausible but may already be occurring. In all cases, there is a need to delve into the causes and consequences of fish chronotypes selection, and more empirical work is needed in clarifying the ecological consequences (Bloch et al. 2013; Helm & Visser 2010).

The selection gradient is, however, only one component that addresses trait change and derives eco-evolutionary trajectories (Price 1970). The heritability, or the degree of variation in a phenotypic trait in a population caused by genetic variation between individuals, is a key component that can be used to forecast the population-level consequences of any mortality pressure (including fishing). There is no information on the heritability of chronotypes in marine fish. However, Helm & Visser (2010) quantified the heritability of the chronotypes in the great tit, *Parus major* to be 0.86, which is certainly high. In addition, our study is a computational simulation, and it is possible that our results are overestimations because we did not consider other sources of mortality or connectivity; furthermore, we did neither consider other traits that may experience fisheries selection (e.g., size, personality-related behavioural traits, age), nor quantified the fitness in terms of expected reproductive lifetime (i.e., cumulated offspring). The early-life stages of the pearly razorfish are pelagic, and the connectivity of the surrounding non-exploited populations should be integrated to estimate the selection gradients (Alós et al. 2014). Therefore, there is a need to provide empirical data to support our predictions and to develop more complex meta-population dynamics that provide a more accurate view of the strength of the selection gradients on the circadian behavioural variation. Next-generation individual-based ecological models that aim to make predictions in a changing world would help in this task by accounting for spatial and

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temporal resources that merge individual fish and fisher behaviour and bioenergetics with potential micro-evolutionary adaptations (Ayllón et al. 2016).

Conclusions

Our work demonstrates that the timing associated with fleet activity may generate significant selection on fish circadian behavioural traits. In fact, the direct selection acting on chronotypes can indirectly be a mechanism of fishing selection on migration or breeding behaviours (Graham et al. 2017). Therefore, our work proposes a novel view for understanding the selection properties of fishing acting behavioural traits and generates a list of research needs.

First, we should explore how widespread chronotypes are across fish taxa. Adequate technology and approaches used to measure chronotypes in the wild is certainly available (Alós et al. 2017; Helm et al. 2017; Rattenborg et al. 2017), and further work should also consider nocturnal species or species that focus their activity during the crepuscular hours to evaluate the generality of our findings.

Second, there is a need to validate our theoretical predictions by performing selection experiments in the wild, where fish are monitored while they are being exploited by real fishers (Alós et al. 2016b); additionally, this should include different fleet timing dynamics and fish-fishers behavioural interactions. This future work should also help disentangle the synergistic effects of predation risk and fishing from the potential eco-evolutionary dynamics generated by the existence of circadian behavioural variation.

Third, we should identify the mechanisms behind the expression of wild circadian behavioural variation. Chronotypes are the emergent pattern of the interaction between circadian clocks and the environment, which includes potential light entrainment and responses to predation risk, and their study requires a combination of field and laboratory experiments (Helm et al. 2017). In addition, we should explore the plasticity and additive genetic variation (including its heritability) of fish chronotypes to evaluate the potential for evolution in circadian behavioural traits. In a quantitative genetic way, one potential route would be the exploration of candidate genes and polymorphisms linked to chronotypes, such as the CLOCK or the NPAS2 genes (Stuber et al. 2016), and how they are translated across generations (Helm & Visser 2010; Zhang et al. 2017).

Fourth, in our previous study, we found chronotypes as an independent axis of activity as fish personality trait (Alós et al. 2017). However, there is a need to extend our research to other fish personality traits, such as boldness, exploration, aggressiveness or sociability (Conrad et al. 2011), and their feasible interactions. This would help us understand the role of circadian rhythms in the architecture of behavioural variation in fish. In addition, it would be helpful to explore how chronotypes are correlated with individual growth (productivity) or reproductive success, as it has been done with other behavioural traits (Biro & Stamps 2008).

Once this information and population-based approaches become available, we will be able to forecast the relevance of eco-evolutionary consequences of the wild circadian behavioural variation and how human is affecting it. We hope our work stimulates research and debates on this topic.

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References

Adan A, Archer SN, Hidalgo MP, Di Milia L, Natale V, and Randler C. 2012. Circadian typology: a comprehensive review. *Chronobiology International* 29:1153-1175.

Alós J, Cabanellas-Reboredo M, and Lowerre-Barbieri S. 2012a. Diel behaviour and habitat utilisation by the pearly razorfish during the spawning season. *Marine Ecology Progress Series* 460:207-220. 10.3354/meps09755

Alós J, Martorell-Barceló M, and Campos-Candela A. 2017. Repeatability of circadian behavioural variation revealed in free-ranging marine fish. *Royal Society Open Science* 4. 10.1098/rsos.160791

Alós J, Palmer M, and Arlinghaus R. 2012b. Consistent selection towards low activity phenotypes when catchability depends on encounters among human predators and fish. *PLoS ONE* 7:e48030.

Alós J, Palmer M, Balle S, and Arlinghaus R. 2016a. Bayesian state-space modelling of conventional acoustic tracking provides accurate descriptors of home range behavior in a small-bodied coastal fish species. *PLoS ONE* 11:e0154089. 10.1371/journal.pone.0154089

Alós J, Palmer M, Catalan IA, Alonso-Fernández A, Basterretxea G, Jordi A, Buttay L, Morales-Nin B, and Arlinghaus R. 2014. Selective exploitation of spatially structured coastal fish populations by recreational fishers may lead to evolutionary downsizing of adults. *Marine Ecology Progress Series* 503:219-233. 10.3354/meps10745.

Alós J, Palmer M, Rosselló R, and Arlinghaus R. 2016b. Fast and behavior-selective exploitation of a marine fish targeted by fishers. *Scientific reports* 6:38093. 10.1038/srep38093.

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Ayllón D, Railsback SF, Vincenzi S, Groeneveld J, Almodóvar A, & Grimm V. 2016. InSTREAM-Gen: Modelling eco-evolutionary dynamics of trout populations under anthropogenic environmental change. *Ecological Modelling* 326: 36-53.

Allendorf FW, and Hard JJ. 2009. Human-induced evolution caused by unnatural selection through harvest of wild animals. *Proceedings of the National Academy of Sciences of the United States of America* 106:9987-9994.

Arlinghaus R, Alós J, Klefoth T, Laskowski K, Monk CT, Nakayama S, and Schröder A. 2016. Consumptive tourism causes timidity, rather than boldness, syndromes: a response to Geffroy et al. *Trends in Ecology & Evolution*, 31: 92-94.

Arlinghaus R, Laskowski KL, Alós J, Klefoth T, Monk CT, Nakayama S, and Schröder A. 2017. Passive gear-induced timidity syndrome in wild fish populations and its potential ecological and managerial implications. *Fish and Fisheries* 18:360-373. 10.1111/faf.12176

Audzijonyte A, Kuparinen A, Gorton R, and Fulton EA. 2013. Ecological consequences of body size decline in harvested fish species: positive feedback loops in trophic interactions amplify human impact. *Biology Letters* 9. 10.1098/rsbl.2012.1103

Auger-Méthé M, Derocher AE, Plank MJ, Codling EA, and Lewis MA. 2015. Differentiating the Lévy walk from a composite correlated random walk. *Methods in Ecology and Evolution* 6:1179-1189. 10.1111/2041-210X.12412

Barbier M, and Watson JR. 2016. The Spatial Dynamics of Predators and the Benefits and Costs of Sharing Information. *PLOS Computational Biology* 12:e1005147. 10.1371/journal.pcbi.1005147

Bell AM, Hankison SJ, Laskowski KL 2009. The repeatability of behaviour: a meta-analysis. *Animal Behaviour* 77: 771-783.

Benhamou S. 2014. Of scales and stationarity in animal movements. *Ecology Letters* 17:261-272. 10.1111/ele.12225

Biro PA, and Sampson P. 2015. Fishing directly selects on growth rate via behaviour: implications of growth-selection that is independent of size. *Proceedings of the Royal Society B: Biological Sciences* 282. 10.1098/rspb.2014.2283

Biro PA, and Stamps JA. 2008. Are animal personality traits linked to life-history productivity? *Trends in Ecology & Evolution* 23:361-368.

Bloch G, Barnes BM, Gerkema MP, and Helm B. 2013. Animal activity around the clock with no overt circadian rhythms: patterns, mechanisms and adaptive value. *Proceedings of the Royal Society of London B: Biological Sciences* 280. 10.1098/rspb.2013.0019

Börger L, Franconi N, De Michele G, Gantz A, Meschi F, Manica A, Lovari S, and Coulson TIM. 2006. Effects of sampling regime on the mean and variance of home range size estimates. *Journal of Animal Ecology* 75:1393-1405. 10.1111/j.1365-2656.2006.01164.x.

Canty A., and Ripley B. 2017. boot: Bootstrap R (S-Plus) Functions. R-package version 1.3-20.

Castriota L, Scarabello MP, Finoia MG, Sinopoli M, and Andaloro F. 2005. Food and feeding habits of pearly razorfish, Xyrichtys novacula (Linnaeus, 1758), in the southern Tyrrhenian Sea: variation by sex and size. *Environmental Biology of Fishes* 72:123-133. 10.1007/s10641-004-6576-0

Conrad JL, Weinersmith KL, Brodin T, Saltz JB, and Sih A. 2011. Behavioural syndromes in fishes: a review with implications for ecology and fisheries management. *Journal of Fish Biology* 78:395-435.

Diaz Pauli B, and Sih A. 2017. Behavioural responses to human-induced change: Why fishing should not be ignored. *Evolutionary Applications* 10:231-240. 10.1111/eva.12456

Dingemanse NJ, and Dochtermann NA. 2013. Quantifying individual variation in behaviour: mixed-effect modelling approaches. *Journal of Animal Ecology* 82:39-54. 10.1111/1365-2656.12013

Dominoni DM, Helm B, Lehmann M, Dowse HB, and Partecke J. 2013. Clocks for the city: circadian differences between forest and city songbirds. *Proceedings of the Royal Society B: Biological Sciences* 280. 10.1098/rspb.2013.0593

Eikeset AM, Richter A, Dunlop ES, Dieckmann U, and Stenseth NC. 2013. Economic repercussions of fisheries-induced evolution. *Proceedings of the National Academy of Sciences* 110:12259–12264. 10.1073/pnas.1212593110

Graham JL, Cook NJ, Needham KB, Hau M, and Greives TJ. 2017. Early to rise, early to breed: a role for daily rhythms in seasonal reproduction. *Behavioral Ecology* 28:1266-1271. 10.1093/beheco/arx088

Härkönen L, Hyvärinen P, Paappanen J, and Vainikka A. 2014. Explorative behavior increases vulnerability to angling in hatchery-reared brown trout (*Salmo trutta*). *Canadian Journal of Fisheries and Aquatic Sciences* 71:1900-1909. 10.1139/cjfas-2014-0221

Heino M, Pauli BD, and Dieckmann U. 2015. Fisheries-induced evolution. *Annual Review of Ecology, Evolution, and Systematics* 46:null. doi:10.1146/annurev-ecolsys-112414-054339

Helm B, and Visser ME. 2010. Heritable circadian period length in a wild bird population. *Proceedings of the Royal Society of London B: Biological Sciences* 277:3335-3342. 10.1098/rspb.2010.0871

Helm B, Visser ME, Schwartz W, Kronfeld-Schor N, Gerkema M, Piersma T, and Bloch G. 2017. Two sides of a coin: ecological and chronobiological perspectives of timing in the wild. *Philosophical Transactions of the Royal Society B: Biological Sciences* 372. 10.1098/rstb.2016.0246

Hereford J, Hansen TF, and Houle D. 2004. Comparing strengths of directional slection: how strong is strong? *Evolution* 58:2133-2143. 10.1111/j.0014-3820.2004.tb01592.x

Hussey NE, Kessel ST, Aarestrup K, Cooke SJ, Cowley PD, Fisk AT, Harcourt RG, Holland KN, Iverson SJ, Kocik JF, Mills Flemming JE, and Whoriskey FG. 2015. Aquatic animal telemetry: A panoramic window into the underwater world. *Science* 348:9. 10.1126/science.1255642

Jørgensen C, Enberg K, Dunlop ES, Arlinghaus R, Boukal DS, Brander K, Ernande B, Gådmark AG, Johnston F, Matsumura S, Pardoe H, Raab K, Silva A, Vainikka A, Dieckmann U, Heino M, and Rijnsdorp AD. 2007. Managing evolving fish stocks. *Science* 318:1247-1248. 10.1126/science.1148089

Klefoth T, Kobler A, and Arlinghaus R. 2011. Behavioural and fitness consequences of direct and indirect non-lethal disturbances in a catch-and-release northern pike (*Esox lucius*) fishery. *Knowledge and Management of Aquatic Ecosystems*:11.

Kreitzman L, and Foster R. 2005. Rhythms of Life: The Biological Clocks That Control the Daily Lives of Every Living Thing. Yale University Press, Connecticut, New Haven, USA.

Krumme U. 2009. Diel and Tidal Movements by Fish and Decapods Linking Tropical Coastal Ecosystems. In: Nagelkerken I, ed. *Ecological Connectivity among Tropical Coastal Ecosystems*: Springer Netherlands, 271-324.

Koeck B, Alós J, Caro A, Neveu R, Crec'hriou R, Saragoni G, and Lenfant P. 2013. Contrasting fish behavior in artificial seascapes with implications for resources conservation. *PLoS ONE* 8:e69303. 10.1371/journal.pone.0069303

Langrock R, Hopcraft JGC, Blackwell PG, Goodall V, King R, Niu M, Patterson TA, Pedersen MW, Skarin A, and Schick RS. 2014. Modelling group dynamic animal movement. *Methods in Ecology and Evolution* 5:190-199. 10.1111/2041-210X.12155

Laugen AT, Engelhard GH, Whitlock R, Arlinghaus R, Dankel DJ, Dunlop ES, Eikeset AM, Enberg K, Jørgensen C, Matsumura S, Nusslé S, Urbach D, Baulier L, Boukal DS, Ernande B, Johnston FD, Mollet F, Pardoe H, Therkildsen NO, Uusi-Heikkilä S, Vainikka A, Heino M, Rijnsdorp AD, and Dieckmann U. 2014. Evolutionary impact assessment: accounting for evolutionary consequences of fishing in an ecosystem approach to fisheries management. *Fish and Fisheries* 15:65-96. 10.1111/faf.12007

Lennox RJ, Aarestrup K, Cooke SJ, Cowley PD, Deng ZD, Fisk AT, Harcourt RG, Heupel M, Hinch SG, Holland KN, Hussey NE, Iverson SJ, Kessel ST, Kocik JF, Lucas MC, Flemming JM, Nguyen VM, Stokesbury MJW, Vagle S, VanderZwaag DL, Whoriskey FG, and Young N. 2017a. Envisioning the future of aquatic animal tracking: technology, science, and application. *Bioscience*:bix098-bix098. 10.1093/biosci/bix098

Lennox RJ, Alós J, Arlinghaus R, Horodysky A, Klefoth T, Monk CT, and Cooke SJ. 2017b. What makes fish vulnerable to capture by hooks? A conceptual framework and a review of key determinants. *Fish and Fisheries*:n/a-n/a. 10.1111/faf.12219

Lowerre-Barbieri S, DeCelles G, Pepin P, Catalán IA, Muhling B, Erisman B, Cadrin SX, Alós J, Ospina-Alvarez A, Stachura MM, Tringali MD, Burnsed SW, and Paris CB. 2017. Reproductive resilience: a paradigm shift in understanding spawner-recruit systems in exploited marine fish. *Fish and Fisheries* 18:285-312. 10.1111/faf.12180

Matsumura S, Arlinghaus R, and Dieckmann U. 2011. Assessing evolutionary consequences of size-selective recreational fishing on multiple life-history traits, with an application to northern pike (*Esox lucius*). *Evolutionary Ecology* 25:711-735.

Matsumura S, Arlinghaus R, and dieckmann U. 2012. Standardizing selection strengths to study selection in the wild: A critical comparison and suggestions for the future. *Bioscience* 62:1039–1054.

Michelot T, Langrock R, and Patterson TA. 2016. moveHMM: An R package for the statistical modelling of animal movement data using hidden Markov models. *Methods in Ecology and Evolution* 7:1308-1315.

Mittelbach GG, Ballew NG, and Kjelvik MK. 2014. Fish behavioral types and their ecological consequences. *Canadian Journal of Fisheries and Aquatic Sciences* 71:927-944. 10.1139/cjfas-2013-0558

Monk CT, and Arlinghaus R. 2017. Perch, Perca fluviatilis, spatial behaviour determines vulnerability independent of fisher skill in a whole-lake reality mining experiment. *Canadian Journal of Fisheries and Aquatic Sciences*. 10.1139/cjfas-2017-0029

Nakagawa S, and Schielzeth H. 2010. Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. *Biological Reviews* 85:935-956.

Olsen EM, Heupel MR, Simpfendorfer CA, and Moland E. 2012. Harvest selection on Atlantic cod behavioral traits: implications for spatial management. *Ecology and Evolution* 2:13.

Patterson TA, Parton A, Langrock R, Blackwell PG, Thomas L, and King R. 2017. Statistical modelling of individual animal movement: an overview of key methods and a discussion of practical challenges. *AStA Advances in Statistical Analysis*. 10.1007/s10182-017-0302-7

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Price GR. 1970. Selection and Covariance. *Nature* 227:520. 10.1038/227520a0

R Core Team. 2017. R: a language and environment for statistical Computing. *R Foundation for Statistical Computing, Vienna, Austria URL https://wwwR-projectorg/*.

Reebs S. 1992. Sleep, inactivity and circadian rhythms in fish. In: Ali MA, ed. Rhythms in Fishes. Boston, MA: Springer US, 127-135.

Randler C. 2014. Sleep, sleep timing and chronotype in animal behaviour. *Animal Behaviour* 94:161-166. http://dx.doi.org/10.1016/j.anbehav.2014.05.001

Rattenborg NC, de la Iglesia HO, Kempenaers B, Lesku JA, Meerlo P, and Scriba MF. 2017. Sleep research goes wild: new methods and approaches to investigate the ecology, evolution and functions of sleep. *Philosophical Transactions of the Royal Society B: Biological Sciences* 372. 10.1098/rstb.2016.0251

Roenneberg T, Kuehnle T, Juda M, Kantermann T, Allebrandt K, Gordijn M, and Merrow M. 2007. Epidemiology of the human circadian clock. *Sleep medicine reviews* 11:429-438.

Roenneberg T, Wirz-Justice A, and Merrow M. 2003. Life between clocks: daily temporal patterns of human chronotypes. *Journal of Biological Rhythms* 18:80-90.

Smouse PE, Focardi S, Moorcroft PR, Kie JG, Forester JD, and Morales JM. 2010. Stochastic modelling of animal movement. *Royal Society Philosophical Transactions Biological Sciences* 365:2201-2211.

Steinmeyer C, Schielzeth H, Mueller JC, and Kempenaers B. 2010. Variation in sleep behaviour in free-living blue tits, Cyanistes caeruleus: effects of sex, age and environment. *Animal Behaviour* 80:853-864. http://dx.doi.org/10.1016/j.anbehav.2010.08.005

Stuber EF, Baumgartner C, Dingemanse NJ, Kempenaers B, and Mueller JC. 2016. Genetic Correlates of Individual Differences in Sleep Behavior of Free-Living Great Tits (Parus major). *G3: Genes|Genomes|Genetics* 6:599-607. 10.1534/g3.115.024216

Stuber EF, Dingemanse NJ, Kempenaers B, and Mueller JC. 2015. Sources of intraspecific variation in sleep behaviour of wild great tits. *Animal Behaviour* 106:201-221. http://dx.doi.org/10.1016/j.anbehav.2015.05.025

Stuber EF, Grobis MM, Abbey-Lee R, Kempenaers B, Mueller JC, and Dingemanse NJ. 2014. Perceived predation risk affects sleep behaviour in free-living great tits, *Parus major*. *Animal Behaviour* 98:157-165. http://dx.doi.org/10.1016/j.anbehav.2014.10.010

Sullivan AP, Bird DW, and Perry GH. 2017. Human behaviour as a long-term ecological driver of non-human evolution. *Nature Ecology & Evolution* 1:0065.

Sutter DAH, Suski CD, Philipp DP, Klefoth T, Wahl DH, Kersten P, Cooke SJ, and Arlinghaus R. 2012. Recreational fishing selectively captures individuals with the highest fitness potential. *Proceedings of the National Academy of Sciences* 109:6. 10.1073/pnas.1212536109

Schmidt MH. 2014. The energy allocation function of sleep: A unifying theory of sleep, torpor, and continuous wakefulness. *Neuroscience & Biobehavioral Reviews* 47:122-153. http://dx.doi.org/10.1016/j.neubiorev.2014.08.001

Siegel JM. 2008. Do all animals sleep? *Trends in Neurosciences* 31:208-213. http://dx.doi.org/10.1016/j.tins.2008.02.001

Tillotson MD, and Quinn TP. 2017. Selection on the timing of migration and breeding: A neglected aspect of fishing-induced evolution and trait change. *Fish and Fisheries*:in press. 10.1111/faf.12248

Tintoré J, Vizoso G, Casas B, Heslop E, Pascual A, Orfila A, Ruiz S, Martínez-Ledesma M, Torner M, and Cusí S. 2013. SOCIB: The Balearic Islands coastal ocean observing and forecasting system responding to science, technology and society needs. *Marine Technology Society Journal* 47:101-117.

Uusi-Heikkilä S, Whiteley AR, Kuparinen A, Matsumura S, Venturelli PA, Wolter C, Slate J, Primmer CR, Meinelt T, Killen SS, Bierbach D, Polverino G, Ludwig A, and Arlinghaus R. 2015. The evolutionary legacy of size-selective harvesting extends from genes to populations. *Evolutionary Applications*:n/a-n/a. 10.1111/eva.12268

Uusi-Heikkilä S, Wolter C, Klefoth T, and Arlinghaus R. 2008. A behavioral perspective on fishing-induced evolution. *Trends in Ecology & Evolution* 23:419-421.

Vermard Y, Rivot E, Mahévas S, Marchal P, and Gascuel D. 2010. Identifying fishing trip behaviour and estimating fishing effort from VMS data using Bayesian Hidden Markov Models. *Ecological Modelling* 221:1757-1769.

Walker E, and Bez N. 2010. A pioneer validation of a state-space model of vessel trajectories (VMS) with observers' data. *Ecological Modelling* 221:2008-2017.

Walsh MR, Munch SB, Chiba S, and Conover DO. 2006. Maladaptive changes in multiple traits caused by fishing: impediments to population recovery. *Ecology Letters* 9:142-148.

Watkins KS, and Rose KA. 2017. Simulating individual-based movement in dynamic environments. *Ecological Modelling* 356:59-72. http://dx.doi.org/10.1016/j.ecolmodel.2017.03.025

Wicht H, Korf H-W, Ackermann H, Ekhart D, Fischer C, and Pfeffer M. 2014. Chronotypes and rhythm stability in mice. *Chronobiology International* 31:27-36.

Zhang S, Xu X, Wang W, Yang W, and Liang W. 2017. Clock gene is associated with individual variation in the activation of reproductive endocrine and behavior of Asian short toed lark. *Scientific reports*, 7(1), 15002.

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