Fitness consequences of fish chronotypes in marine exploited environments (#24612)

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Fitness consequences of fish chronotypes in marine exploited environments

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The selective properties of fishing acting on behavioural traits have recently gained interest. Recent acoustic tracking experiments have revealed consistent among-individual differences on circadian behavioural traits across time and ecological contexts generating different chronotypes on marine fish. We have hypothesized here that fishing directional selection operates on these wild circadian behavioural variation acting against certain individuals of the same population that differ in traits like awakening time or rest onset. We have developed a spatially-explicit social-ecological Individual-Based Model (IBM) to test this hypothesis. The parametrization of our IBM was fully based on empirical data, and represent a fishery formed by patchily distributed resident fish that are exploited by a fleet of mobile boats (any bottom fisheries). We run 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 open a new dimension understanding the selective properties of fishing by bridging gaps between three traditionally separated fields: fisheries science, behavioural ecology and chronobiology. We derive some general predictions of our theoretical findings and outline a list of research needs to understand the consequences of circadian behavioural variation in marine exploited environments.

Fitness consequences of fish chronotypes in marine exploited environments

Running title: Marine fish chronotypes

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Abstract

The selective properties of fishing acting on behavioural traits have recently gained interest. Recent acoustic tracking experiments have revealed consistent among-individual differences on circadian behavioural traits across time and ecological contexts generating different chronotypes on marine fish. We have hypothesized here that fishing directional selection operates on these wild circadian behavioural variation acting against certain individuals of the same population that differ in traits like awakening time or rest onset. We have developed a spatially-explicit social-ecological Individual-Based Model (IBM) to test this hypothesis. The parametrization of our IBM was fully based on empirical data, and represent a fishery formed by patchily distributed resident fish that are exploited by a fleet of mobile boats (any bottom fisheries). We run 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 open a new dimension understanding the selective properties of fishing by bridging gaps between three traditionally separated fields: fisheries science, behavioural ecology and chronobiology. We derive some general predictions of our theoretical findings and outline a list of research needs to understand the consequences of circadian behavioural variation in marine exploited environments.

Keywords

Chronotypes, circadian behavioural traits, fisheries induced-evolution, individual-based model, selection gradient

Introduction

Humans exploit fish populations through trait-selective harvesting since the origin of our species (Allendorf & Hard 2009). Fishing is in fact widely recognized today as a major driver of contemporaneous evolution and trait change in wild fish populations (Sullivan et al. 2017). 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 change either in commercial and recreational fisheries. There is substantial evidence that positive size-selective harvesting (e.g., gear-selectivity) selects for fast life-histories and generates selection gradients in traits like maturation and reproduction investment (Alós et al. 2014; Heino et al. 2015; Laugen et al. 2014; Matsumura et al. 2011). Although the economic consequences of fisheries selection may be addressed by proper fisheries management (Eikeset et al. 2013), they can generate undesirable consequences for ecosystem functioning (Audzijonyte et al. 2013; Jørgensen et al. 2007), may notably slow down the recovery (Uusi-Heikkilä et al. 2015; Walsh et al. 2006) and may decrease the recreational utility of fisheries (Sutter et al. 2012).

What traits make more vulnerable one individual from others is, however, a complex and multi-trait phenomena (Lennox et al. 2017b). Vulnerability may involve not life-history traits, but also physiology, morphological and behavioural traits that usually, but not always, co-vary (Uusi-Heikkilä et al. 2008). In fact, the behavioural dimension of fisheries selection has recently gained interested among fisheries scientists and managers due to two major recent facts (Biro & Sampson 2015; Diaz Pauli & Sih

2017). In one hand, nowadays, there is massive literature demonstrating the existence of consistent (in time and ecological context) among-individual differences on fish behavioural traits like boldness or aggressiveness, leading to the formation of fish behavioural types (Conrad et al. 2011; Mittelbach et al. 2014). In the other hand, with the recent development of aquatic telemetry, fisheries scientists have a powerful tool available to study fish individual heterogeneity and behavioural types in free-living fishes (Hussey et al. 2015; Lennox et al. 2017a). Fish tracking has provided a new and unique opportunity to add realism in the study on how fisheries produce selection in behavioural traits (e.g., Alós et al. 2016b; Monk & Arlinghaus 2017; Olsen et al. 2012). These two facts together have generated today substantial empirical evidence demonstrating that bolder, more aggressive and/or more explorative behavioural types (e.g., Alós et al. 2012b; Biro & Sampson 2015; Härkönen et al. 2014; Klefoth et al. 2011) and/or individuals with larger foraging areas and swimming speeds (e.g., Alós et al. 2016b; Olsen et al. 2012), are more prone to be harvested independently of their body size. Because this reason, the idea of a timidity syndrome for what fish exploited populations are formed by shy, low active and resident individuals (Arlinghaus et al. 2017), is quickly gaining theoretical and empirical support.

Behavioural traits that determine timing have been surprisingly poorly considered in the context of the selective properties of fishing. Recently, Tillotson & Quinn (2017) have proposed timing of migration or breeding as candidate traits target by fisheries selection. Both timing of migration or breeding season have strong impact in the populations dynamics (Lowerre-Barbieri et al. 2017), and selection imposed in these traits would strongly impact the trajectory of the stocks in the long-term. Similarly, an ubiquitous fish timing behaviour 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 leaded the evolution of endogenous circadian clocks across taxa, including fish species (Kreitzman & Foster 2005). Similar to behavioural types, humans and some animals show consistent among-individual variation in different circadian-related behaviours like awakening time or sleep onset that are the result from the interactions between those endogenous individual circadian clocks and the environment, defining chronotypes (Roenneberg et al. 2007).

In animals, the science of circadian rhythms or chronobiology has a long story of studies (Rattenborg et al. 2017), and have demonstrated the ubiquity and high heritability of circadian clocks across taxa (Bloch et al. 2013). For example, Helm & Visser (2010) quantified the heritability of the chronotypes in great tit (*Parus major*) to be 0.86. However, only few studies have demonstrated the existence of chronotypes by exploring the amount of behavioural variation explained by among-individual differences (Randler 2014), mainly on bird species (Dominoni et al. 2013; Steinmeyer et al. 2010; Stuber et al. 2015; Stuber et al. 2014). Recently, Alós et al. (2017) have found the first evidence of the existence of chronotypes on fish facilitated by the abovementioned new tracking facilities. Similar to bird chronotypes, the pearly razorfish, *Xyrichthys novacula*, exhibited a significant proportion of variation in circadian-related behaviours explained by among-individuals differences forming different chronotypes (Fig. 1); early-delayed risers for instance. Thus, when an individual within a population of diurnal or nocturnal fish species starts or finishes its activity, is not just a plastic component of the individual life-history, but consistent differences among-individual exist independently of its personality or environmental variables (Alós et al. 2017).

Far from being anecdotal, chronotypes are frequently linked to many fitness processes (Roenneberg et al. 2003, and see review by Adan et al. 2012) and any directional selection pressure (either natural or human-induced) acting on them could lead trait change on circadian behavioural rhythms (Helm et al. 2017). In fact, there is one recent study that has demonstrated the potential of human-induced selection in circadian clocks with impact on their fitness (Dominoni et al. 2013); city birds start their activity earlier than their forest conspecifics highlighting urban environments (artificial lighting) can significantly modify biologically important rhythms in wild organisms. Similarly, we hypothesized here that early riser fish chronotypes should be more vulnerable to fishing simply due to the odds of enhanced encounters with fishers. According to this idea, the objective of this work was to explore from a theoretical point of view the plausibility of selection acting on fish chronotypes using a spatially-explicit individual-based model (IBM). Our IBM was based in relatively simple movement rules that lead encounters between fish and fishers, it is based in the real properties of a general coastal bottom fishery, and explicitly incorporate social-ecological factors aiming to add realism to our model (and simulations). We aimed to estimate mean-standardized selection gradients in circadian behavioural traits, as a quantitative measure of directional selection, to compare them with previously reported gradients in other traits (Hereford et al. 2004). Our final objective was to make broader predictions about the expected direction of selection on chronotypes and their consequences, stimulate research on the topic and provide a list of research needs for empirical approaches to fully disentangle the fitness consequences of fish chronotypes in exploited environments.

Material and methods

To explore our hypothesis, we have developed a computational IBM where a fish population spatially behaves in a 2-D landscape and it 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 (change the position every min) across the landscape according to different types of movement models. Encounters fish and fishers determined the mortality of the fish. Our model was built under a prototypical bottom fishery where *i*) target fish performed a sedentary spatial behaviour that lead the establishment of a home range (HR) area, *ii*) the centres of activity were patchily distributed forming a patchy landscape (which could be the consequence of a fragmented habitat), and *iii*) fish is exploited by a fleet of fishing mobile boats. Our model was parametrized based on empirical data from a popular recreational fishery located in Mallorca Island (Spain) targeting pearly razorfish (see full details in Alós et al. 2016b), but it is generalizable to any other system displaying these three main properties. Our computational IBM simulation was implemented and run in R (R Core Team 2017) and the R-Code is provided as 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 where 6.4 Km^2 were formed by 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 were attributed to one fish id (initial population = 2,000 individuals, density = 312 individuals per Km^2). Then fish were monitored (for survival) every minute during a whole prototypical fishing season; here 15 full fishing days after the opening of the fishery in September 1st 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 a position (latitude and longitude) of each fish was mechanistically generated according to the movement and the circadian behavioural variation described below.

Fish movement is usually mechanistically explained by different types of random walks (Smouse et al. 2010). Different to the purely random walks that generate standard diffusion across the space, many fish species use a confined area and form stable HR areas (Alós et al. 2016a). The idea behind the HR movement is that an individual moves within a harmonic potential field following random stimuli (random walk) but with a general tendency to remain around a central residence area (Börger et al. 2006). In such cases there is a need for an additional behavioural rule that maintains the individual attracted to a specific core site (Benhamou 2014; Smouse et al. 2010), which can be described by a an Ornstein–Uhlenbeck process defining a Biased Random Walk (BRW) (Alós et al. 2016a).

For the aim of this study, we considered two descriptors of this BRW movement described in Alós et al. (2016a): *i*) the size of the circular HR-*radius* (in metres) that can be interpreted as a surrogate of 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 toward the centre of its HR, which ultimately determines the slope of the curve describing the cumulative space used in function of time (we refer this as *exploration*). We randomly assigned a value of both parameters to our virtual population of fish from 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 R-package. See Fig. 2 to see the realized daily trajectories of a given fish.

Most diurnal fish species show a circadian-related behaviour switching from active during the day-time to resting during the night-time, or vice-versa for nocturnal species (Krumme 2009). Here, we were interested in the individual differences in the daily timing of switching the circadian state, particularly in the repeatability score (*R*) in two behavioral manifestations of circadian rhythms (Fig. 1): *i)* awakening time and *ii)* rest onset (referred as minutes from sunrise or sunset, respectively). *R* assesses the degree of consistency of behaviors shown by individuals over time (Nakagawa & Schielzeth 2010), represents the phenotypic variation attributable to individual heterogeneity and is often used to characterize animal personalities and, in our context, to detect chronotypes (Alós et al. 2017; Dingemanse & Dochtermann 2013; Stuber et al. 2015).

To test our hypothesis, we simulated two *R* simulating scenarios. In the first scenario, the fish population showed significant repeatability in the awakening and rest onset times generating chronotypes (Fig. 1). We randomly assigned to each of the 2,000 fish 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 (i.e., the real circadian behavioural diversity revealed from acoustic tracking was simulated, Fig. 1). In the second scenario, all individuals of the population had an awakening time and rest onset times with the same mean and s.d. (mean = 0 min and 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 were simulated). This second scenario of simulation was used to confirm that potential selection gradients in the circadian behavioral traits obtained in the first scenario were certainly caused by the chronotypes.

Once a set of movement parameters and circadian behaviors was assigned to each fish id, we generated a Markovian Chain of states (active vs. resting) for each fish for the whole fishing season simulated. Therefore, we re-sampled in a daily basis the mean and s.d. of each individual in both traits (i.e., awakening and rest onset times), and generated one value for every day and individual id. Hence, we constructed a Markovian chain of states according to the individual values and the local sunset and sunrise times. Finally, a position to all time-steps in active state was generated for the whole fishing season according to our HR mechanistic model and the individual movement parameters of each fish (Fig. 1 and see SM1). During resting state the individual remained in the same position, but invulnerable to fishing as the fish remained in the shelter (the pearly razorfish remains buried in the sand during the night-time according to Alós et al. 2012a). The complete sequence of time-steps and positions of 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. We considered a total number of 133 fishing boats (spatial fishing effort: 11 boats per km^2) according to the empirical data found in our target fishery (Alós et al. 2016b). However, we run our two simulation scenarios in different fishing effort scenarios to evaluate the strength of the potential selection under different pressures (2, 4, 6, 8, 10 and 12 boats per km^2). The whole fleet exploited the fishery every day for the whole fishing season (here 15 days). At the daily basis, the IBM carefully considered a different time of arrival and leaving of the boats to the fishery (with respect the local sunrise data, to synchronize with the ecological landscape) as this aspect is highly relevant for the aims of our study. Specially, we put effort in reproducing the real daily dynamics of the fishing pressure by assigning a time of arrival and leaving to each boat (Fig. 2); fishers exploited the scenario in a range of 160-460 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 leaving was considered (i.e., each angler arrived to the fishery at the same moment every day), but some individuals arrived earlier than others did similarly to the idea of fish chronotypes.

As fishers arrived to the fishery (depending on their individual arrival time), they spatially behaved accordingly to a movement models based on two states. Individual boat fisher's trajectories are usually composed by different states, mainly three: cruising, searching and fishing (Vermard et al. 2010; Walker & Bez 2010). In our scenario, when fishers have already arrived to the fishery, they performed a classical search pattern formed by two states: fishing and searching (see Fig. 2). Here we considered a relatively simple Hidden Markov Model (HMM) movement with two types of random walks describing each state (Auger-Méthé et al. 2015). HMM are widely used for modelling any type on animal or fishers movement data (Patterson et al. 2017), and a recent R-package have been recently developed (Michelot et al. 2016).

Accordantly, a bi-variate times-series for each fisher composed by step lengths (in m) and turning angles (in rad) were generated to describe its trajectory 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 each 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 fisher spent most of the time fishing to obtain realistic fisher trajectories (see a realized trajectory of the fisher in Fig. 2).

Each state of the sequence was associated to a distinct random walk movement model; a BRW for fishing and a correlated biased random walk (CBRW) for searching to properly reproduce the spatial dynamics of the fleet (Fig. 2). When the fisher was in fishing state, the boat just drifted following the current. While this process is not a random walk, we used the mathematical description of a conventional BRW for simplicity by biasing the angle of the trajectory according to the surface current in the area and adding some noise (see Fig. 2 and SM1). Accordantly, the step-lengths of this state were described by a gamma distribution (as velocity cannot reach negative values) with mean= 1 m and s.d.= 0.5 m, and an angle described by a von Mises distribution of mean equal to the angle of the surface current and concentration= 1.2 rad (noise) to reproduce similar real 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 00:00 in 2016 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 a CBRW model described by Langrock et al. (2014) developed to model group dynamics of animal movement. Accordantly, the searching state was mathematically described by a mixture of a BRW, where the bias was imposed by the social information generating a tendency to move to the centroid of the other boats were fishing (by watching other boats – social information); and a conventional Correlated Random Walk (CRW) where searching was described by a turning angle drawn form a von Mises distribution with mean= 0 and 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 (searching velocity). The peculiarity of the BCRW developed by (Langrock et al. 2014), is the existence of a parameter (η) which specifies the weight of the BRW with respect the CRW part of the BCRW. Here, we considered η=0.7 which generated behaviour of the fleet with a tendency to remain close to the other fisher boats. The full day fisher trajectory was generated according to the Markov chain of the two states (see Fig. 2) and one independent trajectory was generated every day. The initial location in the fishery of each fisher at was randomly generated in the 2D landscape and the first state of the day was searching. For simplicity, no among-fishers variability in the movement was considered.

c) Exploitation model and estimation of selection gradients

The coupled social-ecological landscapes were simulated and the encounters between fish and fishers quantified in the two scenarios of simulations under the different fishing pressures described above (Fig. 2 and see movie in SM1). We defined a successful encounter when *i*) the distance between the fish and a fisher was lower than 5 m (a reasonable distance to assume visual contacts of the fish with the bait) in a given time-step *n*, *ii*) the fish was in a vulnerable state (i.e., active), *iii*) was not encountered before by another fisher (emulating harvest with depletion) and, *iv*) the fisher was in fishing state. When the four conditions were met, the fish id was considered harvested. Once the fishing season simulation finished, we characterized the survival individuals (exploited population) in the terms of their circadian and spatial behavioural variation. We then estimated the selection gradient (*S*) in the two circadian (awakening time and rest onset) and spatial (radius of the HR and exploration) as a measure of selection commonly used in traditional quantitative genetics (Falconer & Mackay 1996). *S* values were mean-standardized (S_μ) to generate a normalized measure of selection strength following (Matsumura et al. 2012) and make them comparable with previously reported data in other traits (Hereford et al. 2004). S_μ is a clean measure of selection strength and allows ranking the strength of selection acting on each of the various behavioral traits independent of the trait's mean and variance. S_μ can be interpreted as an elasticity of fitness to trait change. For example, an $S_\mu = 0.5$ means that doubling the trait value elevates fitness by 50%. We computed the 95% confidential intervals in S_μ for each behavioral by bootstrapping (1,000 iterations) the results of the simulations using the boot function of the R-package.

Results

The first simulation scenario considering real wild circadian variability (observed fish chronotypes) properly reproduced the existence of chronotypes (Fig. 1). *R* scores in this scenario were of 0.43 [0.37-0.6] for awakening time and 0.45 [0.39-0.6] for rest onset, scores similar to those obtained from the real data by Alós et al. (2017). Fish started their activity up to 400 min after sunrise and among-individuals differences in awakening times were clearly recognizable defining early-riser chronotypes (Fig. 1). In contrast, fish finished their activity in a shorter period of time (up to 20 min after the sunset), but some individuals extended their activity few minutes on average according to the real data (Fig. 1).

The mean and standard deviation in the four behavioral 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 formed by individuals with later awakening times, similar rest onsets, smaller HRs and slower exploration (Table 1). These results generated significant mean-standardized selection gradients (S_μ) in awakening time (mean $S_\mu = 0.85$), HR size (mean $S_\mu = -0.52$) and exploration rate (mean $S_\mu = -0.22$, Table 1). These results were consistent along the simulated gradient of fishing effort, and the strength of significant S_μ increased as fishing effort increased (Fig. 3).

In the second simulation scenario, where no fish chronotypes were simulated, the number of survivals was 315 individuals (exploitation rate = 84.2%). In this case, the exploited population was formed by individuals with similar awakening times and rest onsets, and smaller HRs and exploration rates (Table 1). These results only generated significant S_μ for the HR size (mean S_μ= -0.49) and exploration (mean S_μ= -0.36, Table 1), and we discarded significant S_μ for the circadian behavioural traits (Table 1). These results were also consistent across the simulated gradient of fishing effort (Fig. 3). Therefore, we discarded that the observed significant S_μ in awakening time in the observed fish chronotypes simulation scenario was caused by other factors than the circadian behavioural variation.

Discussion

Fish behaviour has emerged as an important component of the selective properties of fisheries (Diaz Pauli & Sih 2017), including timing of migration and breeding behaviours (Tillotson & Quinn 2017). Recently, consistent-among individual's differences in circadian behavioural traits (chronotypes) have been evidenced in fish using novel acoustic tracking technologies and novel models applied to movement data (Alós et al. 2017). Chronotypes have key implications for individual fitness in human and birds, and many eco-evolutionary trends are dependent on the realized expression of circadian rhythms (Roenneberg et al. 2003; Wicht et al. 2014), but nothing is known about the consequences of fish chronotypes. Here we have developed a social-ecological IBM to test some of their potential consequence in exploited environments. IBMs are especially appropriate to formulate and test 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 is a classic example of the emergent population properties from individuals and makes IBMs particularly suited to test our hypothesis. In addition, our novel IBM allowed us to test our working hypotheses in two different simulations and in a wide range of fishing pressure scenarios, by reproducing as well the real dynamics of coastal fisheries using real data (e.g., the actual among-individuals circadian behavioural variation was considered as revealed by acoustic tracking).

Therefore, we feel our results are representative of many other fisheries around the globe, and we propose individual-based circadian behaviours as important drivers in vulnerability of fish to be harvested across oceans.

The results of the first simulation scenario, with real wild circadian variability, revealed a significant selection gradient in 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 be captured by the fleet of boats. This finding adds a new variable into the complex concept of 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 (2 boats per km^2), fishing selection may act in circadian behavioural traits. In fact, the strength of selection was expected to increase as fishing pressure (mortality) increases. In contrast, no evidence for any selective properties was found regarding the rest onset, probably related with the fact that simulated fishing activity was mainly focused during the day-time. In the second scenario, where no wild circadian behavioural variation was simulated, the selection gradient in awakening time was not significant, confirming chronotypes as major drivers of selection force, as it was found in the first and real based data simulation scenario.

The potential for eco-evolutionary changes of chronotypes under human pressure has been recently claimed (Helm et al. 2017). In fact, Dominoni et al. (2013) have demonstrated that city European blackbirds (*Turdus merula*) started their activity earlier and had faster circadian oscillation than their forest con-specifics. The results by Dominoni et al. (2013) therefore suggested that human (thought artificial lightning) have selected individuals favouring large circadian period lengths. In this example, the selective force imposed by artificial acts in the opposite direction of our working hypothesis. In our work, the selective force is imposed by the timing of the fishing pressure (Fig. 2) and, accordantly, should favour small circadian period lengths and small foraging periods. What is relevant in this context is that either artificial lighting in cities or fishing pressure in the sea may impose selection gradients and may act as eco-evolutionary drivers in wild populations that should be further considered (Helm et al. 2017). Our work, in addition, provides the first evidence that fishing may alter the circadian rhythms in oceans.

Our theoretical selection gradients were mean-standardized which allow to be compared with others traits. We, first, have found significant selection gradients in the two spatial behavioural traits considered here suggesting selection against large HRs and fast exploitation rates. Although both were smaller than the 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 on these spatial behavioural traits which makes our IBM robust (Alós et al. 2016b). The strength of the obtained selection gradients in circadian behavioural traits were also stronger when compared with other life history (S_{μ} = 0.66) and morphological (S_{μ} = 0.29) previously reported traits (Hereford et al. 2004). However, the strength of selection may vary according to the morality pressure as revealed by the different fishing effort scenarios. This fact highlights the relevance of estimating selection gradients in real populations exposed to mortality and using realistic set-ups (based in data from the wild). However, our work demonstrates that the potential of selection in circadian behavioural traits certainly exists, and its strength could be stronger than other more classical considered traits.

The selection gradient is, however, only one component addressing trait change and deriving eco-evolutionary trajectories (Price 1970). The heritability, or the degree of variation in a phenotypic trait in a population that is due to genetic variation between individuals, is a key component forecasting the population consequences of any mortality pressure (including fishing). There is no information on the heritability of chronotypes in marine fish, although Helm & Visser (2010) demonstrated the heritability of the chronotypes to be high in birds. In addition, our study is a computational simulation and it is possible that ore results are overestimating because we are not considering other sources of mortality or connectivity, neither other traits under fisheries selection (e.g., size, personality-related behavioural traits, age, etc). The early-life stages of the pearly razorfish are pelagic and the connectivity of surrounded non-exploited populations should be integrated estimating the selection gradients (Alós et al. 2014). Therefore, there is a need to provide empirical data to our predictions and to develop a more complex metapopulation dynamics to provide a more accurate view of the strength of the selection gradients of the circadian behavioural variation.

Although our work is theoretical, we can derive some ecological implications of the selective properties of fishing acting against early riser chronotypes. Chronotypes are ubiquitous across taxa and key determinants of reproductive success; for instance, females choose males with early awakening time (Helm & Visser 2010). We therefore could predict a reduction in the overall population reproductive output due to the absence of high reproductive early riser males. In addition, fish like the pearly razorfish play a key role in the food-web by preying against other taxa (Castriota et al. 2005), and being predated by larger animals like dolphins. A change in the daily timing of the populations in the population of the pearly razorfish could induce behavioural changes in the lower and upper levels of the food-web. We can also speculate that fishing-induced selection against early risers is actually acting today, and the results observed in Alós et al. (2017) are the results of such selective process. We therefore suggest that the negative ecological consequences of the selective properties acting on circadian behavioural traits are plausible but also may be happening already. In all cases, there is a need to deep inside the causes and consequences of fish chronotypes selection and work deeper in their eco-evolutionary consequences (Bloch et al. 2013; Helm & Visser 2010).

Conclusions

Our work demonstrates that, far from being an anecdote, the timing associated to the fleet activity may generate significant selection against early-risers, and they strength may be larger than those imposed by spatial behavioural traits (Alós et al. 2016b). In fact, direct selection acting on chronotypes can indirectly be the mechanism of fishing selection on migration or breeding behaviours (Graham et al. 2017). Our work therefore opens a novel dimension understanding the selective properties on time-related behavioural traits and opens a new field in fish and fisheries science and generates a list of research needs. First, we should explore how widespread are chronotypes across fish taxa and how they are generated from molecular and environmental drivers. The technology and approaches to measure chronotypes in the wild are certainly available (Alós et al. 2017; Helm et al. 2017; Rattenborg et al. 2017). Second, there is a need to validate our theoretical predictions by performing, for example, experiments in the wild. Third, we should provide the genetic variation and heritability of fish chronotypes to evaluate the potential evolution on circadian behavioural traits. In a quantitative genetic way, we should explore genes and their polymorphisms like the CLOCK or the NPAS2 (Stuber et al. 2016), and study how they are translated across generations (Helm & Visser 2010). Fourth, in our previous study we found chronotypes as independent axis of the fish personality (Alós et al. 2017). However, there is need to extend our research to other personality traits like boldness, aggressiveness or sociability (Conrad et al. 2011). This would help to understand the role of the circadian rhythms in the architecture of the behavioural variation of fish. In addition, there is need to study what are the fitness consequences of fish chronotypes. For example, how chronotypes correlates with the individual growth (productivity) or reproductive success as other behavioural traits do (Biro & Stamps 2008). Fifth and finally, there is need to improve our knowledge in the role of fish chronotypes in ecosystem functioning and in what services can be derived from them. Once this information would be available, we will be able to forecast the eco-evolutionary consequences of human selection against circadian behavioural traits. We hope our work stimulates research and debate on this topic.

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Figure 1(on next page)

Figure 1

Repeatability (*R*) of the wild behavioural variation in awakening time (moment of initiation of the active phase minutes relative to the sunrise) and rest onset (moment of initiation of the resting phase as minutes relative to the sunset) observed in the pearly razorfish, *Xyrithchys novacula*. Sunset and sunrise are denoted by dashed red line. (a) Density and histogram plots showing the distribution in awakening time and rest onset from 25 randomly selected individuals from the simulated population. (b) Daily awakening time and rest onset (each colour represent a fish Id) across 15 days of simulated exploitation. The R scores and their confidential interval are plotted for each trait. (c) Individual violin plots showing the within- and among-individuals variability (the individual mean is plotted as a black dot) in awakening and rest onset describing different types of chronotypes (e.g., early risers). Simulated data showed is based on the empirical work by Alós et al. (2017).

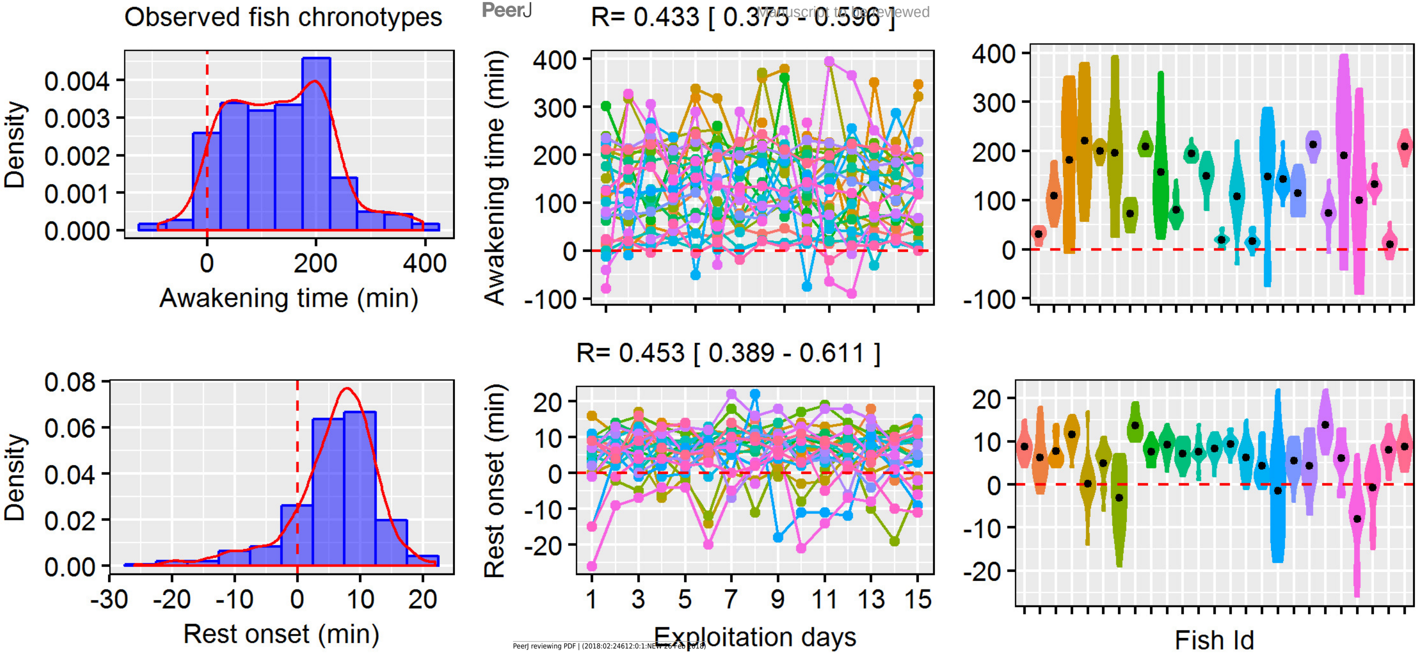
Observed fish chronotypes
Density
0.004
0.003
0.002
0.001
0.000
0
200
400
Awakening time (min)
R= 0.433 [0.375 - 0.596]
Awakening time (min)
400
300
200
100
0
-100
400
300
200
100
0
-100
Density
0.08
0.06
0.04
0.02
0.00
-30
-20
-10
0
10
20
Rest onset (min)
R= 0.453 [0.389 - 0.611]
Rest onset (min)
20
10
0
-10
-20
1
3
5
7
9
11
13
15
Exploitation days
20
10
0
-10
-20
Fish Id

Figure 2(on next page)

Figure 2

Properties of the spatially-explicit individual based model (IBM) developed here. (a) The 2-D landscape simulated here composed by different types of habitats (land, satellite seawater as the preferred fish habitat, seagrass in green and gravels in light brown). The centres of activity of each simulated fish (2,000 individuals) are shown in red. (b) Number of boats in the virtual scenario every day aggregated in 15 min slots since the sunrise (the real data obtained using visual census is plotted in blue and the simulated data is plotted in green). The dashed red line represents the sunrise. (c) Trajectory (positions every minute) of one fish in two different days. Red dots represent the first and the last positions of the active diurnal phase. (d) Trajectory of one fisher in two different days. Red dots represent the positions were the fisher was fishing while blue dots represents the positions were the fisher was searching according to the two-state movement pattern. The IBM was developed according to the real characteristics of the fishery developed in the waters of Mallorca Island (NW Mediterranean targeting the pearly razorfish, *Xyrithchys novacula*, (Alós et al. 2016b).

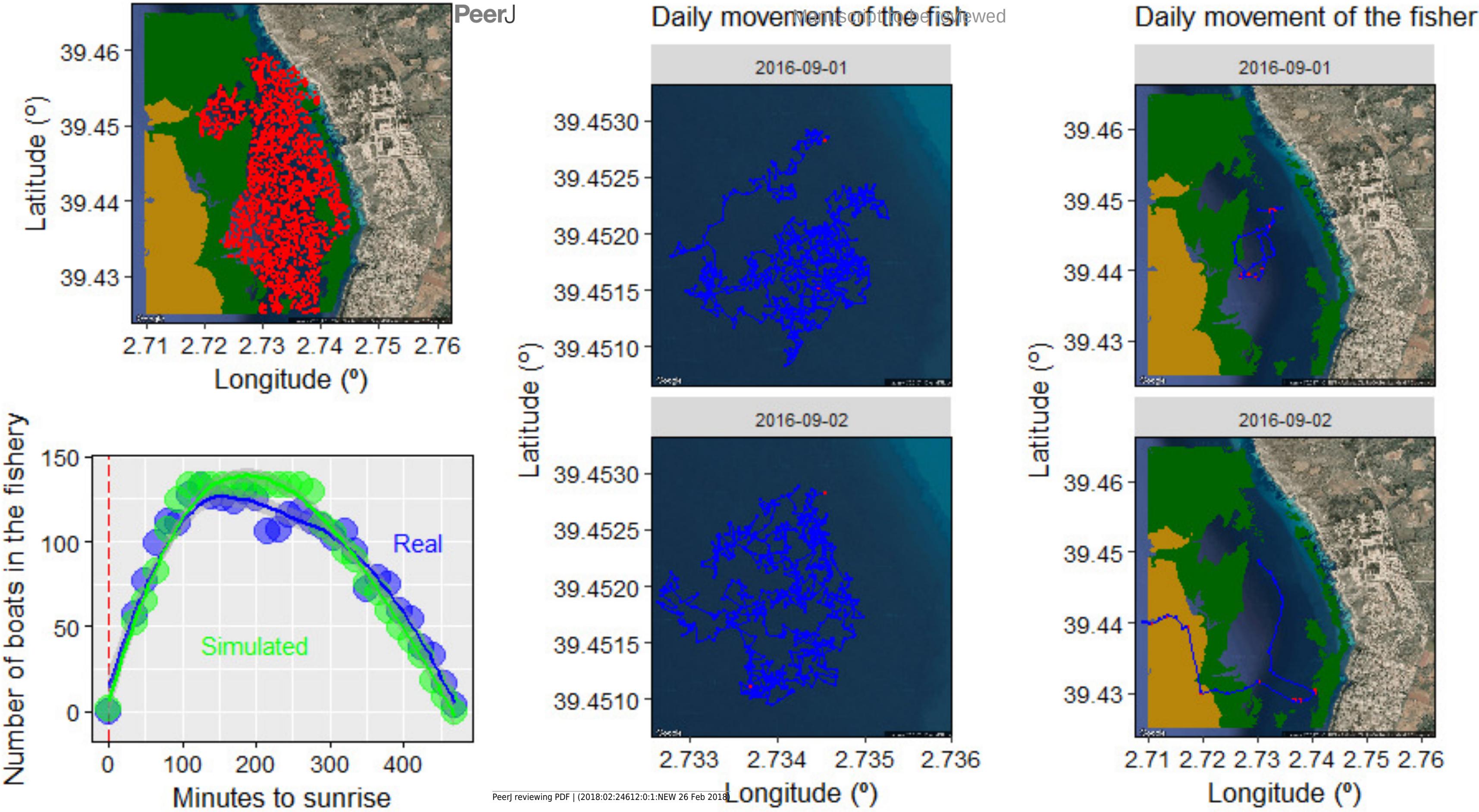
Latitude (º)
39.46
39.45
39.44
39.43
2.71
2.72
2.73
2.74
2.75
2.76
Longitude (º)
Number of boats in the fishery
150
100
50
0
Real
Simulated
0
100
200
300
400
Minutes to sunrise
Daily movement of the fish
2016-09-01
2016-09-02
39.4530
39.4525
39.4520
39.4515
39.4510
Latitude (º)
2.733
2.734
2.735
2.736
Longitude (º)
Daily movement of the fisher
2016-09-01
2016-09-02
39.46
39.45
39.44
39.43
Latitude (º)
2.71
2.72
2.73
2.74
2.75
2.76
Longitude (º)

Figure 3(on next page)

Figure 3

Mean-standardized selection gradients ( ) and their confidential interval (CI) obtained in the two simulation scenarios (observed fish chronotypes vs. no fish chronotypes) in a gradient of fishing effort (defined as number of boats per km^2 per exploitation day) in the four behavioural traits considered: awakening time (as min relative to the sunrise), rest onset (as min relative to the sunset), the home range of the individual (defined as the radius of the circular home range in m) and the level of the exploration of the home range (as min^{-1}). We considered significant when the CI didn’t overlapped with the non-directional selection scenario (plotted as a dashed blue line).

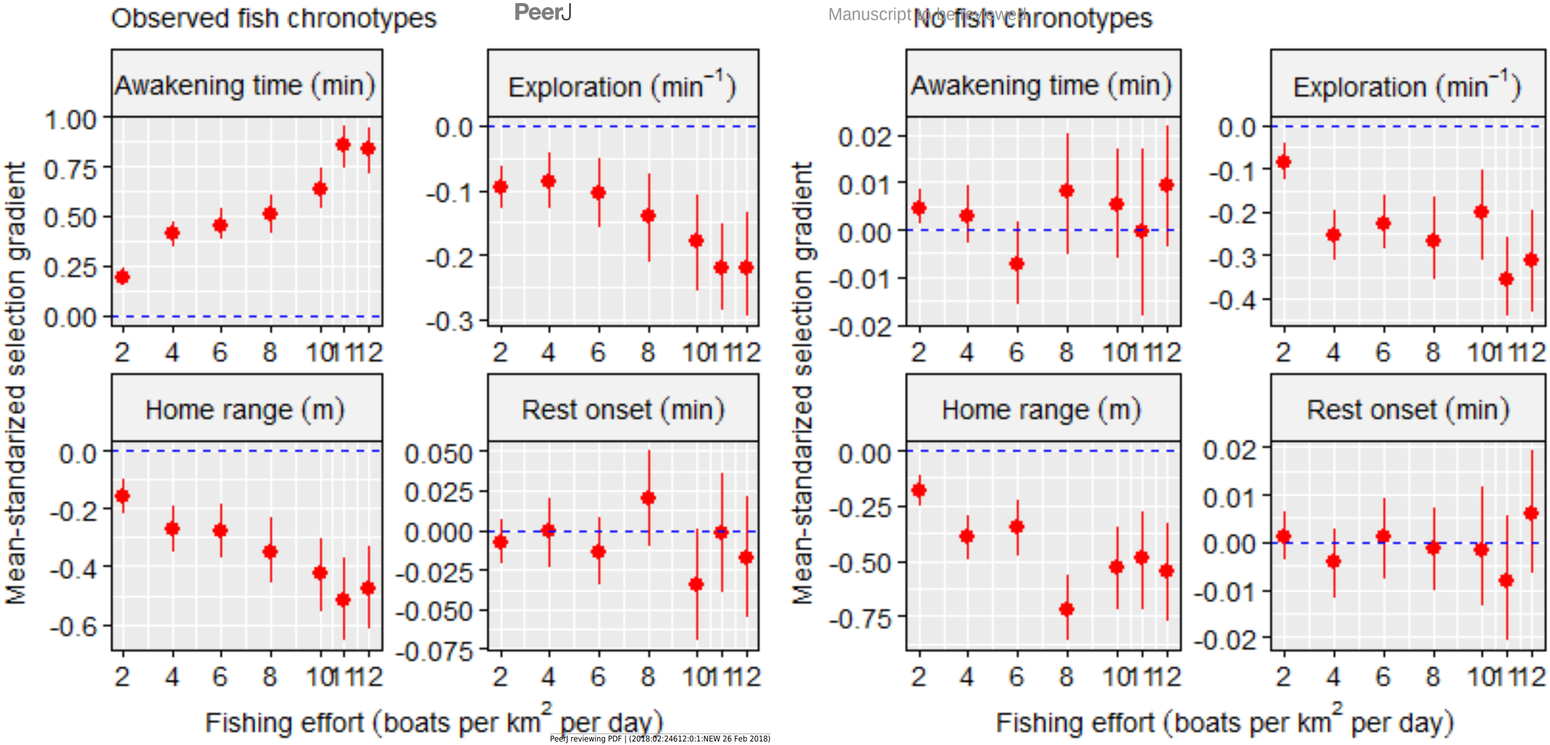
Observed fish chronotypes
No fish chronotypes
Awakening time (min)
Exploration (min^{-1})
Home range (m)
Rest onset (min)
Mean-standarized selection gradient
Fishing effort (boats per km^2 per day)
1.00
0.75
0.50
0.25
0.00
0.0
-0.1
-0.2
-0.3
-0.4
-0.6
0.050
0.025
0.000
-0.025
-0.050
-0.075
0.02
0.01
-0.01
-0.02
-0.25
-0.50
-0.75
2
4
6
8
10
11
12

Table 1(on next page)

Table 1

Mean and standard deviation (s.d.) in the initial and exploited populations of the four behavioural traits studied here resulting from the simulation scenario where wild fish chronotypes were and fishing effort was 11 boats per km^2 per exploitation day. Mean and s.d. of the mean-standardized selection gradients (*S*) and their confidential interval (CI) resulting from the 1,000 bootstrap iterations. *S* in bold were considered significant.

Table 1

Observed fish chronotypes	Initial (n=2,000)		Exploited (n=650)		S_{μ}			
	Mean	s.d.	Mean	s.d.	Mean	s.d.	CI-low	CI-high
Home range size (m)	203	90	183	79	**-0.52**	**0.07**	**-0.65**	**-0.37**
Exploration (min^{-1})	0.006	0.005	0.005	0.005	**-0.22**	**0.03**	**-0.29**	**-0.15**
Awakening time (min)	139	73	165	68	**0.85**	**0.05**	**0.74**	**0.95**
Rest onset (min)	4	7	4.2	6.8	-0.002	0.019	-0.039	0.035
No fish chronotypes	Initial (n=2,000)		Exploited (n=315)					
Home range size (m)	204	88	185	83	**-0.49**	**0.11**	**-0.72**	**-0.28**
Exploration (min^{-1})	0.006	0.005	0.004	0.004	**-0.36**	**0.05**	**-0.44**	**-0.26**
Awakening time (min)	0.7	3.8	0.7	3.8	-0.0003	0.01	-0.02	0.02
Rest onset (min)	-0.5	3.9	-0.3	4	-0.008	0.007	-0.021	0.006