ICES Journal of
Marine Science

ICES Journal of Marine Science (2019), 76(2), 489–500. doi:10.1093/icesjms/fsy172

Contribution to the Themed Section: '*Plugging spatial ecology into sustainable fisheries and EBM*'

Original Article

A modelling approach to evaluate the impact of fish spatial behavioural types on fisheries stock assessment

Josep Alós[1] *, Andrea Campos-Candela[1,2], and Robert Arlinghaus[3,4]

[1]*Department of Marine Ecology, Instituto Mediterráneo de Estudios Avanzados, IMEDEA (CSIC-UIB), C/Miquel Marqués 21, 07190 Esporles, Illes Balears, Spain*
[2]*Department of Marine Sciences and Applied Biology, University of Alicante, C/San Vicente del Raspeig, s/n, 03690, Alicante, Spain*
[3]*Department of Biology and Ecology of Fishes, Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310, 12587 Berlin, Germany*
[4]*Division of Integrative Fisheries Management, Faculty of Life Sciences and Integrative Research Institute on Transformations of Human-Environmental Systems, Humboldt-Universität zu Berlin, Invalidenstrasse 42, 10155 Berlin, Germany*

**Corresponding author: tel: +34 971 61 18 68; e-mail: alos@imedea.uib-csic.es.*

Alós, J., Campos-Candela, A., and Arlinghaus, R. A modelling approach to evaluate the impact of fish spatial behavioural types on fisheries stock assessment. – ICES Journal of Marine Science, 76: 489–500.

Received 15 March 2018; revised 8 October 2018; accepted 19 October 2018; advance access publication 27 November 2018.

Spatial behavioural types (SBTs) arise from between-individual differences in behavioural traits that foster spatial behavioural patterns that are consistent over time and ecological contexts. Fish stocks are regularly assessed using catch per unit effort (CPUE) as input data that may non-linearly co-vary with the underlying abundance (*N*) of the exploited stock when SBT affect catchability. We hypothesized that SBT promote characteristic changes in catchability within harvesting seasons that affect catch rates and in turn catch-based fish stock assessments. To test this hypothesis, we developed a spatially explicit agent-based simulation where we measured encounters between fish and fishers and estimated the shape of the CPUE–*N* relationship. We ran the simulation in a prototypical fish–fisher encounter-leads-to-catch-type fishery and systematically studied outcomes in the presence or absence of SBTs. It was revealed that the existence of SBTs leads to CPUE inevitably declining faster than *N* (a process known as hyperdepletion) when compared with a simulation lacking SBTs. This finding was consistent in a wide range of fishing effort scenarios. The emergent hyperdepletion of catch rates was caused by fast and behavioural-selective exploitation of vulnerable SBT that encompassed the mobile component of the fish stock. The theoretical predictions received support from field data from a coastal recreational fishery. Our work suggests that the consideration of SBT when interpreting trends in CPUE data may notably improve stock assessments by providing a more reliable CPUE–*N* relationship.

Keywords: CPUE, hook-and-line fisheries, hyperdepletion, hyperstability, spatial behavioural types, stock assessment.

Introduction

Individual fish often behave in a way that distinguishes them from other members of their species of the same sex and age (Sih *et al.*, 2004; Réale *et al.*, 2007). When behavioural differences are consistent over time in traits, such as boldness, aggressiveness, exploration, sociability, or activity, they are referred to as fish personalities (Conrad *et al.*, 2011). Fish personalities can lead to systematic variation in spatial movement dynamics of individual fish (e.g. more active fish explore a larger space per unit time), which affects a range of ecological processes such as dispersal or interaction strength among individuals and among predators and prey (Harrison *et al.*, 2014; Spiegel *et al.*, 2017). Consistent and systematic variation in space use can also affect encounters among fish and fishers and promote changes in catchability (Alós *et al.*, 2012). Empirical evidence demonstrating the existence of consistent variation in spatial behavioural traits in the wild has increased in recent years facilitated by the development of fine-scale acoustic telemetry (e.g. Olsen and Moland, 2011; Nakayama *et al.*, 2016; Alós *et al.*, 2016b; Villegas-Ríos *et al.*, 2017; Monk and Arlinghaus, 2018), demonstrating that the pattern seems to be widespread across fish taxa including those exploited by fisheries (Arlinghaus *et al.*, 2016, 2017; Spiegel *et al.*, 2017). For simplifying the interpretation of such consistent variation in spatial behavioural traits, we focus here on two contrasting spatial behavioural types (SBT): mobile-SBT and resident-SBT. There is ample evidence that fish populations are composed of these extreme forms of mobility (Radinger and Wolter, 2014).

SBTs affect a range of ecological processes (Spiegel *et al.*, 2017). For instance, bio-geographical processes such as dispersal and range expansion or population connectivity patterns crucially depend on decisions made by mobile-SBT (Cote *et al.*, 2010; Radinger and Wolter, 2014; Canestrelli *et al.*, 2016). Mobile-SBTs are also more likely to disperse after introduction, thus enhancing invasion success (Rehage and Sih, 2004). Additionally, the ecological context defines the patterns of personality-dependent dispersal (or other personality-dependent space-use patterns) and the selection patterns selecting for optimal strategies, which implies that SBTs vary in fitness depending on ecological contexts. For example, dispersal may be associated with asocial personalities at high densities but this personality-dependent dispersal is negated with predation risk (Cote *et al.*, 2010, 2013). As another example, mobile-SBTs have been shown to have a lower fitness than resident-SBTs in exploited environments (Olsen and Moland, 2011; Wiig *et al.*, 2013; Alós *et al.*, 2016b), while offering similar fitness in unexploited conditions (Kobler *et al.*, 2009). Such patterns are however context and spatial-scale dependent (Parsons *et al.*, 2011). In this context, fisheries constitute an external factor determining the fitness of different SBTs through behavioural-related selectivity (Uusi-Heikkilä *et al.*, 2008; Árnason *et al.*, 2009; Wiig *et al.*, 2013). Vulnerability to fishing has been conceptualized as an internal state where behaviour and personality play an important role (Lennox *et al.*, 2017). Because fisheries are widespread across the globe, harvesting may systematically remove a particular SBT causing an evolutionary trend in the behavioural component of the populations. For instance, when removing consistently the more mobile components of fish populations, fisheries would be causing a "timidity syndrome", which implies forcing fish to evolve or develop behaviours that reduce their exposure to fishing gears (Arlinghaus *et al.*, 2016 2017; Andersen *et al.*, 2017; Claireaux *et al.*, 2018). Such reduction in the exposure to fishing gear might reduce the index value of stock assessments that depend on catch-per-unit-effort (CPUE) data and reduce angler and fisher yield and satisfaction over time, but little research on this topic exists so far in relation to SBTs (Alós *et al.*, 2015b; Arlinghaus *et al.*, 2017).

Catchability represents the efficiency of harvesting, constituting a key link for fishers and managers to know about the status of fish stocks (Arreguín-Sánchez, 1996; Hunt *et al.*, 2011; Villegas-Ríos *et al.*, 2014). Density independent catchability leads to proportionality of fish abundance (N) and CPUE. However, if catchability is density dependent (for which there is substantial evidence in certain fisheries; Peterman and Steer, 1981; Harley *et al.*, 2001; Burgess *et al.*, 2017), the CPUE–N relationship will be non-linear. Two outcomes are then possible: (i) hyperstability or (ii) hyperdepletion of catch rates (Hilborn and Walters, 1992). While hyperstability of the CPUE reflects the idea of a faster decline of N with respect to CPUE, leading to the illusion of plenty (Erisman *et al.*, 2011), the hyperdepletion of the fish stocks reflects a faster decline of the CPUE than N, leading to the false impression of increasingly empty oceans (Alós *et al.*, 2015a). The simplest representation of a model of CPUE and N is of the form $CPUE = qN^{\beta}$, where q is an estimate of the catchability coefficient, N is the true fish abundance, and β is the shape parameter of the CPUE–N relationship (Hilborn and Walters, 1992). Assuming q as constant on average (for which there is some evidence, Pierce and Tomcko, 2003), changing β switches the CPUE–N relationship from hyperstability to hyperdepletion. When $\beta = 1$, CPUE linearly tracks N, when $\beta < 1$, hyperstable catch rate develops; and when $\beta > 1$, hyperdepletion happens (Figure 1). Meta-analysis and empirical studies in selected fisheries (e.g. in recreational fisheries, Post *et al.*, 2003; Ward *et al.*, 2013; Maggs *et al.*, 2016) have suggested hyperstability to be more widespread than hyperdepletion (Harley *et al.*, 2001; Burgess *et al.*, 2017).

Understanding the processes leading to either hyperdepletion or hyperstability is important to improve models of fish stock assessment and to interpret time series in CPUE (Post *et al.*, 2002; Erisman *et al.*, 2011; Burgess *et al.*, 2017). However, beyond a range of phenomenological statistical models, there are few studies describing the detailed mechanisms and processes behind non-linearity among CPUE and N (but see Ward *et al.*, 2013). The few that exist have shown that for example high predictability of spawning aggregations in groupers, tunas, or carangids may maintain CPUE stable over time, while N is actually decreasing, generating hyperstable CPUE (e.g. Hamilton *et al.*, 2016; Maggs *et al.*, 2016; Tidd *et al.*, 2017). In addition, effort sorting due to the less skilled fishers exiting the fishery earlier can explain

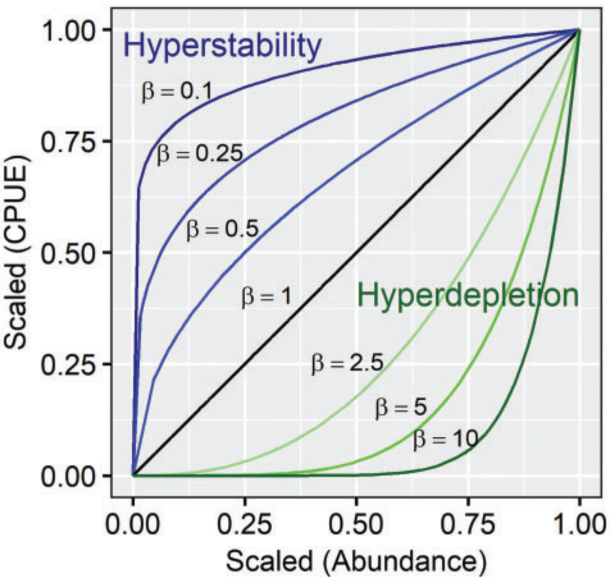

Figure 1. The relationship between CPUE and abundance has been described as possibly non-linear by a power function with parameter β. Hyperstability of the catch rates is generated when CPUEs remain high over time although abundance is declining and produces a non-linear relationship with $\beta < 1$. In contrast, hyperdepletion of the fish stocks is generated when CPUE declines faster than the abundance producing a non-linear relationship with $\beta > 1$. We hypothesized that a quicker removal of mobile SBTs (vulnerable individuals) and, consequently, a lower vulnerability of resident individuals (non-vulnerable individuals), would lead to the hyperdepletion of fish stock whenever behavioural diversity is present in the exploited population.

hyperstability in CPUE in some recreational fisheries (Ward *et al.*, 2013; van Poorten *et al.*, 2016). However, although hyperdepletion may be common in exploited systems with passive fishing gears (Arlinghaus *et al.*, 2017), much less work is available regarding the processes behind it. The few empirical studies that exist show that fish behaviour plays a key role in the process of hyperdepletion (Alós *et al.*, 2015a). In fact, the behaviour of fish species should be strongly involved in both hyperstable and hypedepleted CPUEs, but how within species behavioural differences affects outcomes is largely unknown, particularly regarding the existence of SBTs that affect encounters with fishers.

We hypothesize that SBTs mechanistically explain hyperdepletion of catch rates when catchability is driven by encounters among fish and fishers (Alós *et al.*, 2012). Our argument is based on the recent evidence suggesting that mobile-SBTs (larger foraging areas and larger exploration rates) are more vulnerable to many fishing gear types, particularly recreational gear using hook-and-line and other passive gear (Alós *et al.*, 2016b; Lennox *et al.*, 2017; Monk and Arlinghaus, 2018). Although encounters between fish and fishers do not always predict harvest when artificial bait is used (where other behavioural traits than spatial traits become more important in the capture process, e.g. Monk and Arlinghaus, 2017; Monk and Arlinghaus, 2018), encounters are among the most important components of the vulnerability of most fishes (Lennox *et al.*, 2017). Following our recent empirical work in Alós *et al.* (2016b), we hypothesize that selective removal of more vulnerable mobile-SBTs can lead to a faster decline of the CPUE than *N*, mechanistically explaining hyperdepletion of fish stocks. To test this hypothesis, we developed a spatially explicit agent-based simulation where fish and fishers (agents) spatially interact in a prototypical coastal fishery in a range of fishing effort scenarios. Our theoretical predictions were contrasted with an empirical experiment on fishing catches in a coastal site in the Mediterranean Sea, collectively suggesting that behaviour-selective harvesting foster hyperdepletion in the coastal fishery we examined.

Material and methods

We developed a spatially explicit agent-based simulation of a fish population and a fleet of mobile fishery boats that spatially interact in a 2D landscape during a prototypical fishing season (Figure 2). We measured exploitation by means of encounters between fish and fishers (Alós *et al.*, 2012) and quantified the realized CPUE and *N* in the presence or absence of SBT. Our simulation was built to recreate a prototypical bottom fishery targeting non-migratory fish species that perform a spatially confined behaviour (i.e. home range behaviour, HR) whose centres of activity are patchily distributed (due to for example fragmented habitat) resulting in a behavioural-related ecological landscape. The fishery is exploited by a fleet of mobile boats, which covers an area larger than an individual HR area while fishing. Our simulation was initially parameterized based on empirical data from a popular recreational fishery located in Mallorca Island (Spain) targeting pearly razorfish, *Xyrichtys novacula*. The pearly razorfish is a small omnivorous labrid (common length around 20 cm) that do not form schools, inhabit most of the soft habitats of temperate areas and is highly exploited in the NW Mediterranean by recreational fisheries (see more details in Alós *et al.*, 2016b). However, we content that the simulation outcomes are generalizable to other systems displaying the main properties described above: (i) non-migratory fish exhibiting HR behaviours; (ii) patchy distribution of the individual centres of activity or centres of HR; and (iii) harvesting by a mobile fleet of boats covering an area longer than an individual HR area.

The spatially explicit agent-based simulation was implemented and run in R (R Core Team, 2018). First, two scenarios, with and without the existence of SBTs in the fish stock were initially simulated. Second, we ran the simulations for a total of 32 scenarios characterized by different fishing efforts and different proportion of both SBTs aiming to disentangle the relative weight of these variables in the emerging patterns (we used this second set of simulations also for sensitivity analyses, see "Sensitivity analysis" section).

Movement of the fish and spatial behavioural types

Unlike standard dispersal models that generate standard diffusion across space, many fish species use a confined area and form stable HR areas (Alós *et al.*, 2016a; Campos-Candela *et al.*, 2018). 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.*, 2008). In such a case, an additional behavioural rule may maintain the individual attracted to a specific core site (Smouse *et al.*, 2010; Benhamou, 2014), which can be described by an Ornstein–Uhlenbeck (OU) process (Alós *et al.*, 2016a).

To simulate the fish movement, we considered the derivation of the HR movement model described by an OU process developed in Alós *et al.* (2016a), which is based on two main parameters: *radius* and *exploration* rate. Briefly, the *radius* parameter describes the size of the circular area of the HR (in metres), which can be interpreted as a surrogate of the total foraging area and activity space of a given individual. The *exploration rate* parameter corresponds to the harmonic force, k (in min^{-1}) describing how strongly a fish is attracted toward the centre of its HR, which eventually determines the slope describing the cumulative space used as a function of time (i.e. for a given *radius* of HR, how much time is needed to cover the whole HR).

For simulations, in a virtual 2D scenario with open boundaries ($12.14\,\text{km}^2$ of seawater where $6.4\,\text{km}^2$ was sand, the preferred habitat of pearly razorfish, Figure 2), we first randomly distributed the centres of activity of 2000 individual fish (initial *N* of the population = 2000 individuals, initial density = 312 individuals per km^2). By distributing the centres of activity within the preferred habitat of the pearly razorfish, a realistic patchy distribution of individual fish and overall fish densities in line with the species' ecology as assessed previously with underwater video-recording (Figure 2, unpublished data) was created. Each of the centres of activity was attributed to one fish ID that was monitored (for survival) every minute during the fishing season *in silico*. We assumed 15 full fishing days since the opening of the fishery (i.e. after a previous seasonal closure). The agent-based simulation was discretized on time (by 1 min), had 21 600 time-steps (n), and a position (latitude and longitude) of each fish was mechanistically generated according to the spatial behavioural variation described above.

To test the hypothesis of the present work, we initially simulated two scenarios: with and without the existence of SBT. Accordingly, in the first scenario (with-SBT) we randomly assigned a value of both behavioural parameters *radius* and *exploration rate* (as both are independent, Alós *et al.*, 2016b) to our virtual fish population

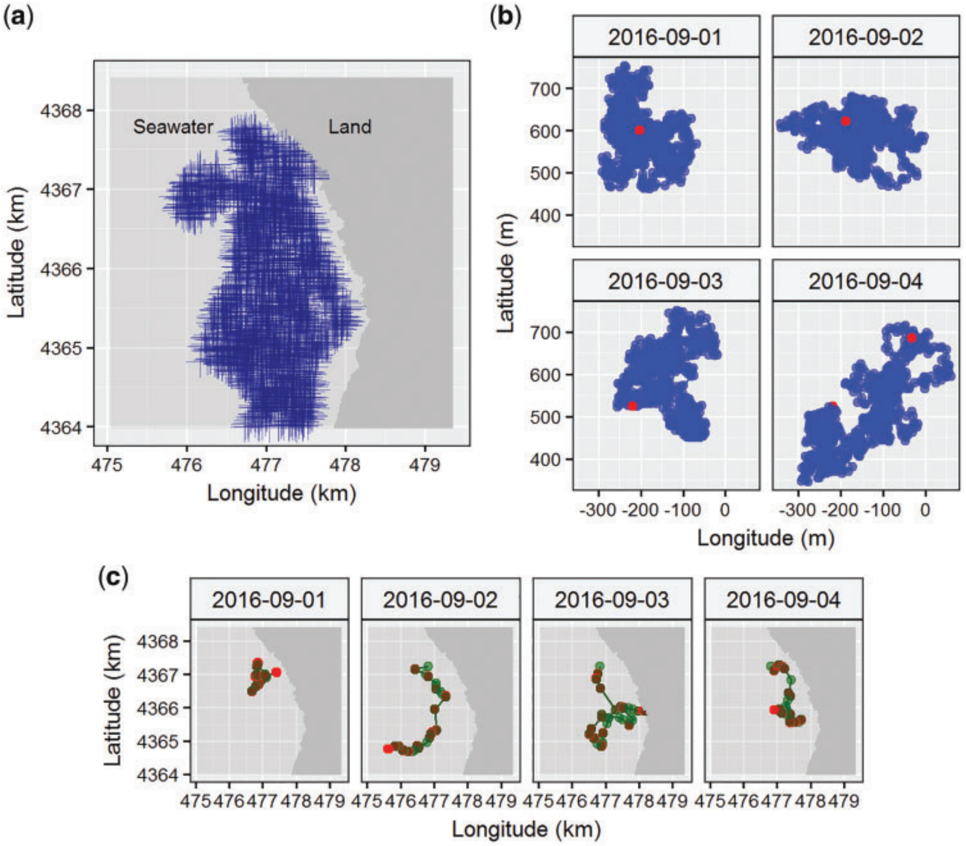

Figure 2. Properties of the spatially explicit agent-based simulation. (a) The 2D landscape simulated was composed by seawater and land where the centre of activity (crosses) of 2000 individuals were distributed forming a patchy landscape. (b) Trajectory (positions every minute) of one fish in four different days. Highlighted dots represent the first and the last positions of the active diurnal phase. (c) Trajectory (positions) of one fisher in four different days according to the two-state movement pattern considered here. The number of encounters (distance between fish and fisher lower than 5 m) was quantified to simulate encounter-based exploitation in a prototypical fishing season representing a pearly razorfish fishery near Mallorca.

drawn from distributions measured in reality in pearly razorfish (range for *radius*: 67–470 m and *k*: 0.0005–0.025 min^{-1}, Alós *et al.*, 2016a) using the function *sample* of the R package. In the agent-based simulation, SBT properly emerged (Figure 3), and therefore included the behavioural axis from mobile- to resident-SBT. In the second scenario (no-SBT), we simulated the absence of between-individual differences in spatial behavioural traits by assigning the same average *radius* and *exploration* in all fish of the population (*radius*: 204.6 m and *k*: 0.006 min^{-1}, mean values of the real population, Alós *et al.*, 2016a). The emerging repeatability score (R) in the first scenario, which measures the consistency of between-individual differences in spatial behaviours (Nakagawa and Schielzeth, 2010), was very high (~0.9, see Figure 3) relative to empirical literature (Bell *et al.* 2009.). This was due to the model-based approach (i.e. each fish had a consistent set of movement parameters) with no environmental noise and no plasticity. To overcome this limitation and explore how our assumption of the repeatability R affected our findings, we performed a range of simulations considering different distribution of SBT (see "Sensitivity analysis" section); ranging from R ~ 0.0 (no-SBT scenario), to R ~ 0.5, following empirical findings of meta-analysis of R in the wild as reported by Bell *et al.* (2009).

Once a set of *radius* and *exploration* values was assigned to each fish, we generated a Markovian chain of states (active during day time/resting during night time, typical for pearly razorfish, Alós *et al.*, 2016b) for the whole fishing season simulated according to a sunrise (7:15 a.m.) and sunset (20:00 p.m.) cycle. The fishery only operated during day time as pearly razorfish are buried in sand during the night and not catchable then. A position at all time-steps in the active movement state was generated using the movement model and assuming the pre-defined individual parameters during the whole fishing season (Figure 2). During the resting state (night time), the individual remained in the same position and was assumed invulnerable to fishing.

Movement of the fleet of boats

A fleet of mobile fishing boats exploited the population of fish, representing recreational boats fishing with natural bait as it is typical for pearly razorfish. We considered a fishing pressure scenario of 2 boats per day and km^2, which is equivalent to a fleet of 25 fishing boats exploiting the fishery. The whole fleet exploited the fishery every day during the whole fishing season (15 days). Similarly to fish, a position of the fisher was generated every time-step (1 min) according to a fisher two-state movement model. Fishing behaviour is usually composed of different states: searching and fishing (Vermard *et al.*, 2010; Walker and Bez, 2010). Our fishers also performed this search pattern (Figure 2).

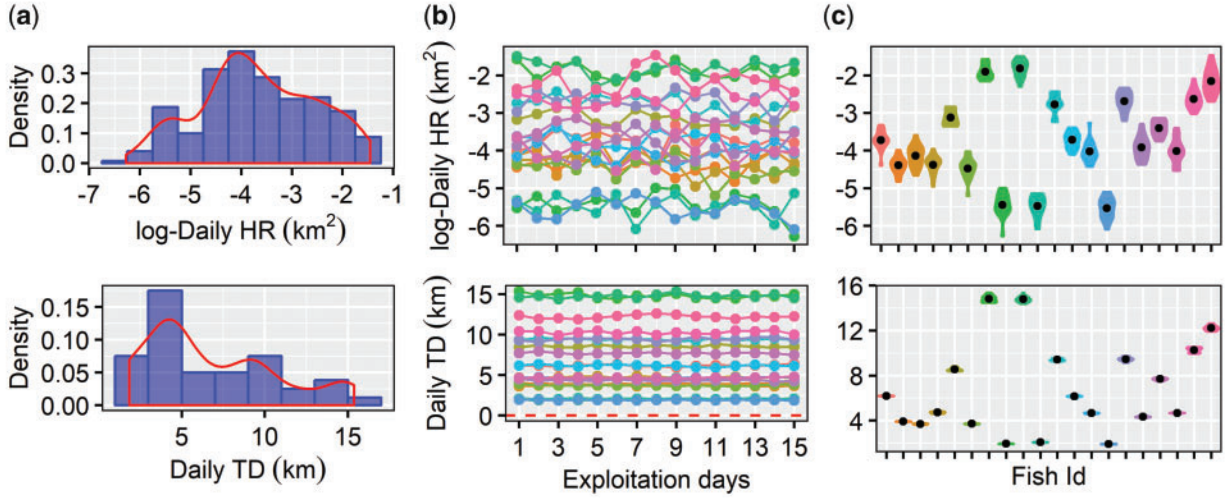

Figure 3. Simulated spatial behavioural diversity of fish: (a) Histogram and density plots showing the distribution in the realized daily home range (defined here as the minimum convex polygon of 100% of the fish positions in a given day) and daily travelled distance (defined here as the accumulated Euclidean distance between all fish positions in a given day). (b) Daily home range (HR) and travelled distance (TD, each group represents a fish ID of 20 simulate d individuals across 15 days of simulated exploitation. (c) Violin plots showing the within- and among-individual variability in the daily home range and travelled distance (the mean individual value is shown by a dot). The consistent among-individuals variability across time describes the existence of mobile SBTs (individuals with large home range and travelled distances means) and resident SBTs. This spatial behavioural diversity was generated according to the empirical data revealed using acoustic tracking found in Alós *et al.* (2016b) for pearly razorfish.

During the fishing state, boats drifted following the surface current (generated by hydrodynamics and local winds), while during the searching state boats showed an active movement.

Each of the two states of the fisher movement was associated with a distinct random walk movement model (Codling *et al.*, 2008), a biased random walk (BRW) for fishing state and a correlated biased random walk (CBRW) for the searching state to properly reproduce the spatial dynamics of the fleet (Figure 2). For simplicity, we used the mathematical description of a conventional BRW to describe the fishing state by biasing the angle of the trajectory according to the surface current in the area plus adding some noise (the mean velocity and SD of drift was 1 and 0.5 m min^{-1}, respectively). To add realism, we used the real observed angle of the surface current for each time-step n obtained from an oceanographic buoy located in the study area by the Balearic Islands Coastal Observing and Forecasting System (www-socib.es, Tintoré *et al.*, 2013).

The searching state was modelled by using a CBRW described by Langrock *et al.* (2014) to model group dynamics of animal movement. Briefly, a mixture of a BRW and a correlated random walk (CRW) composed mathematically the CBRW. In the BRW component of the searching state, the bias was imposed by a social information factor (see below) that generates a tendency to move toward other boats were fishing (i.e. by watching other boats—social information). Added to this, the CRW component described the searching state by a turning angle drawn from a von Mises distribution with mean = 0 and concentration = 5 rad (the mean velocity and SD of searching was 150 and 130 m min^{-1}, respectively). 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 component (movement toward the centre of other fisher boats) with respect to the CRW (diffusion). We considered $\eta = 0.7$, which generated behaviour of the fishers mainly based toward a CRW but with a small tendency to remain close to other fisher boats following our empirical observations of fisher behaviour (Alós, unpublished data).

To describe the daily movement of the fisher, a bi-variate times-series (time-steps separated by 1 min; to be synchronized with the fish movement) for each fisher composed by step lengths (in metres) and turning angles (in radians) were generated. 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 described above (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 $n+1$). We considered that the fisher spent most of the time fishing to obtain similar fisher spatial behaviour than those observed in the real fishery (see a realized trajectory of the fisher in Figure 2, Alós, unpublished data).

The full-day fisher trajectory was generated according to this two-state fisher movement model, and one independent trajectory was generated every day. The initial location in the fishery of each fisher was randomly generated in the 2D scenario, the daily arrival followed a distribution according to the real data (fishers arrived at the fishery at different moments, always in day time and focussed in the morning), and the first state of the day was searching. For simplicity, no between-fishers variability in the movement was considered.

Exploitation model and estimation of realized CPUE–*N* relationship

The resulting trajectories of fish and fishers were coupled and each of the individual simulated fish was monitored for survival, by quantifying encounters between a fish and fishers, every minute during 15 full fishing days in the two scenarios of our simulations (Figure 2). We defined a successful encounter when (i) the distance between the fish and a fisher was smaller than 5 m (a reasonable distance of visual contact between the fish and the gear) in a given time-step n, (ii) the fish was in a vulnerable state (i.e. active), (iii) the fish was not encountered before by another fisher (simulating harvest with depletion), and (iv) the fisher was in fishing state. Whenever these four conditions were met, the fish ID was considered captured and harvested, representing a purely encounter-based harvesting process with depletion.

For every simulated day during the fishing season, we quantified the realized average CPUE (defined as the number of fish caught per boat per day), the daily N (non-harvested fish from the original population remaining that day) and characterized the surviving individuals (non-harvested individuals of the exploited population) in terms of their spatial behavioural parameters (*radius* and *exploration*). We considered the parameter related to the catchability coefficient constant ($q = 1$, meaning all fish were equally vulnerable at the beginning) and focussed our analysis on the shape parameter of the power curve, β (Figure 1). The β was estimated from the realized daily mean CPUE and N (scaled values) data generated in both simulated scenarios (SBT and no-SBT) by using a Bayesian approach with the jags function from the R2jags library of the R package (Plummer *et al.*, 2006). Non-informative priors were described by a uniform prior distribution of the parameter β between 0 and 20. Three Markov chain Monte Carlo (MCMC) models were run. We drew 1000 000 posterior samples, discarded the first 10 000 iterations (burning period) and only 1 out 90 of the remaining iterations were kept to prevent autocorrelation (thinning strategy). The convergence of the MCMC chains of the parameter β was assessed by visual inspection of the chains. The posterior distribution of the parameter β was characterized by the mean and the 2.5% Bayesian credibility interval (BCI). We assumed differences in β between the two simulated scenarios when the BCI of the posterior distribution did not overlap at all.

We additionally estimated the distribution of the spatial behavioural parameters (*radius* and *exploration*) in the exploited population to estimate the selection gradient according to Matsumura *et al.* (2012) as a measure of selection commonly used in traditional quantitative genetics (Falconer and Mackay, 1996). Selection gradient values were mean standardized to generate a normalized measure of selection strength (Matsumura *et al.*, 2012), and we computed their 95% confidential intervals by bootstrapping (1000 iterations) the results of the agent-based simulations using the boot function of the R-package.

Sensitivity analysis

We performed a range of simulations with the purpose of providing a sensitivity analysis for our model. We focussed on the major variables that were expected to significantly affect the CPUE–N relationship: fish abundance, fishers' pressure, and behavioural variability within the population. We performed sets of simulations by combining two opposite levels for abundance of fish (low and high as $n = 1000$ and $n = 2000$ fish), number of fishers (low and high pressure as $n = 25$ and $n = 100$ fishing boats) and duration of the fishing season (short and long as $n = 15$ and $n = 30$ days). Not only the existence of SBTs within an exploited population but also its relative proportion may affect the CPUE–N relationship. To explore how the proportion of SBTs in the simulated scenarios (and therefore different values for R) may affect our findings, within each set of simulations we explored the performance of the model with different proportion of mobile and resident-SBTs: (i) all individuals equal (no-SBT), (ii) 25% resident-SBTs, (iii) 50% resident-SBTs, and (iv) 75% resident-SBTs. Note that when all individuals are equal the R score is approximately 0.0, when the proportion is 50%, an R-score of ~ 0.5 is expected (i.e. 50% of the variance in behaviour can be explained by between-individual differences). Therefore, these four scenarios could represent four different levels of between-individual variability, which translates into different repeatability scores: (i) $R \sim 0.0$, (ii) $R \sim 0.25$, (iii) $R \sim 0.5$, and (iv) $R \sim 0.75$, respectively. In total, 32 scenarios were simulated and the posterior distribution of the parameter β was determined using the approach described above.

Contrasting model results with real data

We contrasted the predictions of our theoretical model with empirical data from an experiment carried out in 2014 where daily CPUE and N of the pearly razorfish were simultaneously measured in a fishery for several days after the opening of the fishing season (see the details of the fishery in Alós *et al.*, 2016b). We randomly selected between 13 and 8 sampling sites within the fishery and deployed an underwater baited camera (UBC) in each site during different days after the opening of the fishery (0 or just before the opening, 3, 10, 17, and 23 days after the opening of the fishery). The UBC were programmed to record a minimum of 28 min (see Alós *et al.*, 2016b for details). Once the sampling season finished, videos were analysed individually to obtain the Max_N, a quantitative measure of the abundance usually used in UBC sampling, which is defined as the maximum number of individuals observed in a single frame during the overall video analysed (Dunlop *et al.*, 2015). It is a reliable method specifically when the abundance of individuals is low (Max_N scores lower than 10 individuals) and allows controlling for the potentially repeated count of the same organisms entering and leaving the focal field of the camera (Alós *et al.*, 2016b). Although we are aware that UBC may produce biased samples of N (Campos-Candela *et al.*, 2018), they are fishery independent and can generate proper absolute abundance estimates of some shallow water fish (Dunlop *et al.*, 2015). To provide a measure of the CPUE, we performed an on-site creel survey to measure the number of fish captured by the recreational boat anglers in the same area where the cameras were deployed. In total, 39 surveys were performed distributed over five different days (opening day, 6, 13, 14, and 19 days after the opening of the fishery). The surveys were carried out from a research vessel by intercepting recreational fishing boats when they were leaving the fishery at the end of the trip. We standardized the effort to number of fish caught per angler per boat. Then, we coupled the daily values of CPUE and N and estimated the parameter β using the same Bayesian approach described above.

Results

Our agent-based simulation considering SBT properly reproduced the existence of spatial behavioural diversity defining a behavioural axis from mobile- to resident-SBT (Figure 3). The simulated exploitation of the fishery resulted in a decrease in the CPUE over time in both simulated scenarios (SBT and no-SBT), but the decrease in the mean CPUE was much stronger when considering the presence of SBT (Figure 4a and b). The

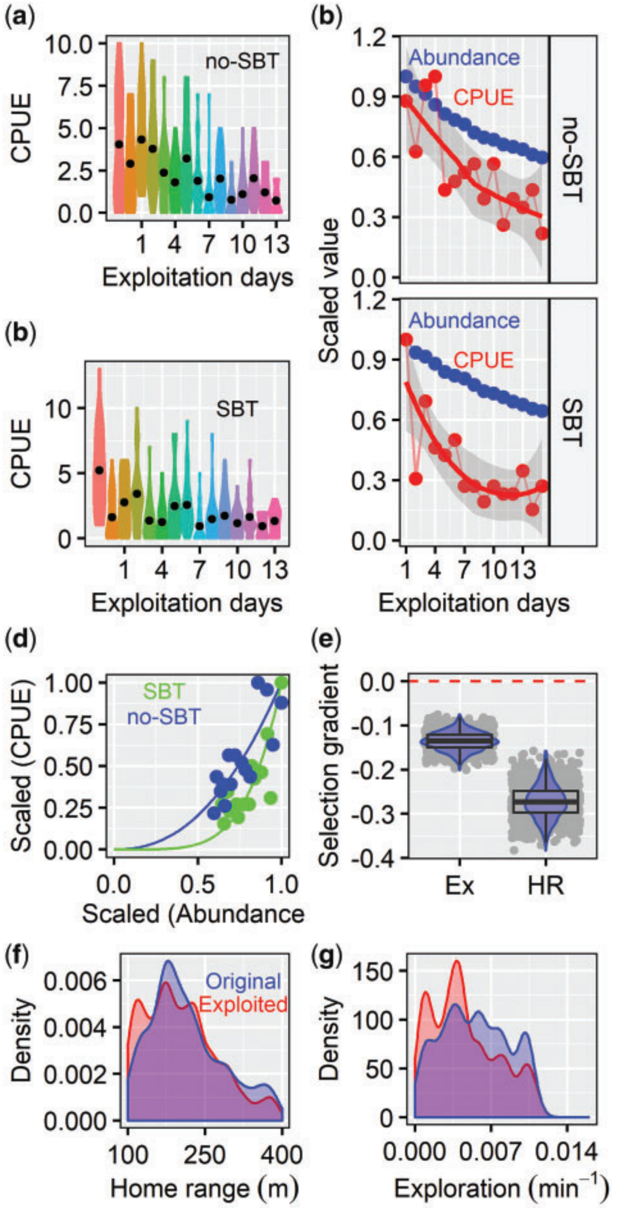

Figure 4. Results of the agent-based simulation considering SBTs or not (no-SBT). (a) Violin plots describing the daily variability in the CPUE (as number of fish per fisher per day) across the exploitation season. The means are shown as black dots. (b) Scaled values of the CPUE and abundance (number of surviving fish) across the exploitation season. A non-linear smoothing fit was applied to the data showing the confidential interval in grey. (c) Relationship between CPUE and abundance (scaled values) in both simulations and (d) the projection of the estimated β using the non-linear catchability model. (e) Mean-standardized selection gradients resulting from the 1000 iterations of our simulation considering SBT in the two spatial behaviours that we considered (the home range size, as radius in metres, and the exploration rate, in min^{-1}). The plot shows the density, the values, and their distribution as a box plot. The dashed line represents the scenario of no selection. (f and g) Distribution of the home range and exploration traits within the original and the exploited population (survivors of the exploited season) resulted from our simulation considering SBT, respectively.

comparison of the scaled values of CPUE and *N* across the exploitation time revealed a faster decrease of the CPUE than *N* in the scenario where SBT where considered (Figure 4b). The estimation of the parameter β of the CPUE–*N* relationship suggested hyperdepletion of the simulated fish stock in both scenarios (no-SBT, $\beta = 2.3$ [1.7–3], Table 1 and Figure 4), but the strength of hyperdepletion was significantly stronger when SBT were considered (SBT, $\beta = 4.96$ [3.7–6.7], Table 1 and Figure 4). The estimation of the mean-standardized selection gradients revealed significant and negative selection in both spatial behavioural traits (radius and exploration rate, Figure 4f and g) as the exploited population was drifting to individuals with increasingly smaller HRs and increasingly lower exploration rates of the HR (i.e. selection favouring resident-SBT, Table 1 and Figure 4f and g). Both, the existence of SBT and the higher vulnerability of the mobile-SBT mechanistically explained the stronger hyperdepletion of the fish stock when behavioural diversity in the fish population was simulated.

Our results were consistent in a range of simulation scenarios as they showed a mismatch between CPUE and *N* ($\beta > 1$) for all cases, and neither the abundance of fish nor days of exploitation generated a difference in our main finding (Figure 5). However, several interesting patterns appeared in Figure 5, which deserve further attention. First, the proportion of SBT notably affected the strength of the mismatch between CPUE and N. When taken as reference the scenario with no-SBT (i.e. a zero proportion of resident-SBT), β increased significantly as the proportion of resident-SBT and therefore the non-vulnerable fraction of the population increased (i.e. hyperdepletion became stronger with an increase in the proportion of resident-SBT in the population) (Figure 5). This pattern suggests that not only the existence of SBT but also their proportion impact stock assessment. Second, greater number of fishers reduced the mismatch between CPUE and *N* as β decreased in scenarios with high fishers' numbers.

Finally, the parameter β of the CPUE–*N* relationship in the real fishery was estimated as 8.5 [4.02–18.2] suggesting an even stronger hyperdepletion in the real fishery relative to the one predicted by the model in the SBT-scenario (Figure 6). However, these differences were not significant because of the overlapping of the BCIs of the data from the real fishery and the simulation with SBT.

Discussion

The existence of consistent between-individual differences in spatial behavioural traits over ecological contexts and time (SBT) have been repeatedly documented across wild fish populations (Harrison *et al.*, 2014; Spiegel *et al.*, 2017). Our spatially explicit agent-based simulations documented how SBTs can promote dynamics in catchability that lead to hyperdepleted catch rates in a wide range of simulation scenarios, which additionally received some empirical support from our field data. We show how SBT shape the relationship (β) between CPUE and *N* and produce stronger hyperdepletion than in a scenario were all individuals are considered equal (no-SBT) in terms of their spatial behaviour. Importantly, the relative proportion of SBT impacted strongly the CPUE–*N* relationship: the more resident SBT compose a population, the stronger is the hyperdepletion effect caused by selective exploitation of mobile SBT.

The absence of either hyperdepletion or hyperstability (i.e. $\beta = 1$) implies that CPUE is recovering the true *N* of a fish

Table 1. Fish harvested (number of fish), exploitation rate, realized shape of the CPUE–*N* relationship (β) and their BCI, means and SD of the original and exploited population (survivors) in the two agent-based simulating scenarios (with and without SBT).

	Fish harvested	Exploitation rate (%)	β	*Radius* (m)	*Radius* (m) survivals	*Exploration* (min^{-1})	*Exploration* (min^{-1}) survivals	Selection gradient *radius*	Selection gradient *exploration*
SBT	744	37.2	4.96 [3.7–6.7]	222.7 ± 93	194 ± 85	0.006 ± 0.005	0.004 ± 0.005	−0.27 [−0.3 to −0.2]	−0.13 [-0.17 to −0.09]
No SBT	824	41.2	2.3 [1.7–3]	204.6	204.6	0.006	0.006	–	–

The table also shows the mean–standardized selection gradients and confidential interval in the scenario where SBT were simulated.

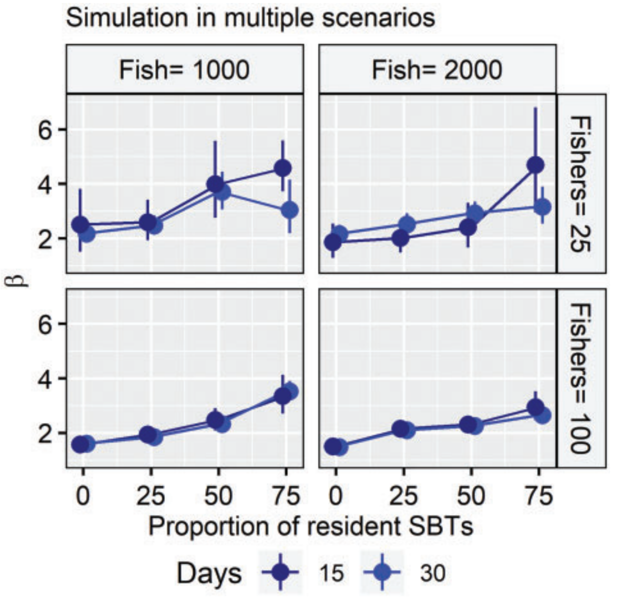

Figure 5. Posterior means (dot) of the parameter β and 2.5% BCI of the relationship between CPUE and *N* resulted from the 32 simulations carried out to the explore the effects of fish abundance, number of fishers exploiting the fishery, and the number of exploitation days in four different scenarios of proportion of resident SBTs; from 0%, which can be interpreted as a scenario without SBTs, to 75% of resident (i.e. 25% of mobile SBTs). Note how the general image of the four panels is similar and BCI generally overlap suggesting low effects of fish abundance, number of fishers or days. In contrast, note how increasing the proportion of resident-SBTs (non-vulnerable individuals) consistently increase the estimation of the parameter β suggesting an increase in the mismatch between CPUE and *N* through hyperdepletion.

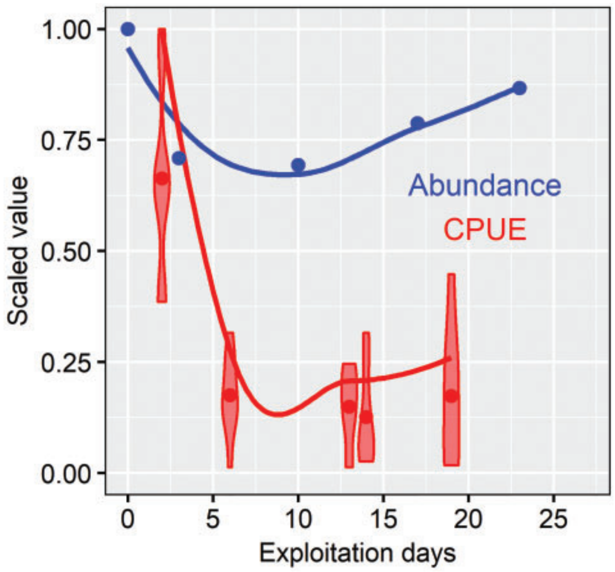

Figure 6. CPUE and abundance data (in scaled values) obtained in the real fishery of the pearly razorfish. The plot shows the mean abundance estimated using underwater video cameras and the distribution CPUE estimated (violin plots) using a creel survey measured several days after the opening of the fishing season. The variability in the CPUE data is shown and a violin plot.

population or, in another words, that it is recovering the stationary distribution of centres of HR (i.e. the true density of fish performing HR behaviour). However, to recover the real density for animals covering the space through a HR behaviour (which has the property of being stationary in time and space at least for a given time and spatial scale, Palmer *et al.*, 2011; Campos-Candela *et al.*, 2018), CPUE data may have important biases difficult to overcome in the field even without behavioural-related selection. β approximates 1 only when the number of fishers is very large and variability of SBTs does not exist (therefore no behavioural-related selection occurs). This observation agrees with the main results from Campos-Candela *et al.* (2018), if we consider fishers as samplers, they will recover the true density of fish whenever they sample enough area to recover the stationary distribution of centres of HR. However, such pattern will not often occur in reality given that spatial SBT seem to be widespread in fish. Another interesting result from our simulations is that the real density of fish in the fishery is not significantly affecting the β value, while the number of fishers and the proportion of resident-SBT in the population did. Interestingly, and within the objectives of this study, we demonstrated that the existence of SBT affects consistently the CPUE–*N* relationship. Such ecolotical context, and the local distribution of resident-mobile phenotypes will exert a strong effect on which hyperdepeletion patterns to expect.

If the stock assessment of our simulated fishery were solely based on raw CPUE data, this would have generated the wrong impression of a nearly empty fishery through a hyperdepletion process after few days of fishing. This situation could be happening in the sampled fishery of pearly razorfish, where β was even higher that the values predicted in Figure 4. Different reasons could explain this observation either the fishers' sample size was too small or the actual non-vulnerable resident-SBT proportion of the wild population was higher than 75%. Independent of the details, our results suggest that in situations where SBT exist and encounters mainly drive exploitation (such as in pearly razorfish fisheries), CPUE will decline faster than abundance and thus CPUE time series may indicate less fish in the sea than there really exists. Consequently, hyperdepletion may decouple the intimate feedback among fishers and fish, which may be widespread in certain passive (hook-and-line, traps) fisheries like the ones considered in our paper (e.g. recreational angling fisheries with natural bait). Eventually, several management-related effects may arise from this hyperdepletion phenomena. For instance, a decrease in the utility of the fishery, dissatisfied anglers, and conflicts between managers and users, may appear when the false perception of overexploitation is established (van Poorten *et al.*, 2011).

In contrast to our findings, recent meta-analysis suggests that most fisheries worldwide exhibit evidence of hyperstable CPUEs (Harley *et al.*, 2001; Burgess *et al.*, 2017). Only a small number of studies have found evidence of hyperdepleted fish stocks, mostly focussed on passive gear like hooks and lures where the odd of capture depends on the active decision of the fish like in our case. For instance, Alós *et al.* (2015a) demonstrated a mismatch between CPUE and *N* based on learning hook-avoidance and selection of bold and aggressive individuals in recreationally exploited coastal fish populations. Tsuboi *et al.* (2015) also provided evidence that heavy historic fishing pressure on a freshwater salmonid has led to a reduction on general vulnerability to capture inducing hyperdepleted mismatches between CPUE and *N*. Moland *et al.* (2013) and Kleiven *et al.* (2012) both reported strong declines in CPUE and consistent low capture probability for European lobster, *Homarus gammarus* when using passive traps. Similar evidence exists for the freshwater fish largemouth bass, *Micropterus salmoides* (Sutter *et al.*, 2012). Further, hook avoidance learning in catch-and-release fisheries can lead to a disjoint of *N* and CPUE (Klefoth *et al.*, 2013; van Poorten *et al.*, 2016), eventually leading to hyperdepletion as some fish may die due to hooking mortality (Arlinghaus *et al.*, 2007). Therefore, although hyperstable catch rates have been reported to be far more widespread than hyperdepleted catch rates, the situation seems to be dependent on the type of gear, whether it is passive or active and whether the bait is natural or artificial. In species that are not aggregating (aggregations are one of the most important predictor of hyperstable catch rates, Erisman *et al.*, 2011) and when the encounters are dependent on behavioural traits and imply high probability of capture and harvest at local scales, local hyperdepletion should be widespread according to the results of our model and empirical findings.

We suggest that hyperdepletion in catch rates may be predominantly explained by between-individual differences in behaviour or SBT. In our work, hyperdepletion emerged from simple rules leading to encounters between fish and fishers, but because variability in the movement existed (i.e. SBT) a differential selection pressures occurred on different SBT. Therefore, a fraction of the biomass was vulnerable to be harvested while another fraction remained largely invulnerable to the fishing gear partially ensuring the survival of a fraction of the stock. In fact, decreasing the proportion of vulnerable mobile-SBTs produced stronger and more evident hyperdepletion of the fish stock. This effect could be stronger if we consider other fish personality traits such as boldness or aggressiveness that have been linked to a higher vulnerability to fishing (Biro and Post, 2008; Sutter *et al.*, 2012; Klefoth *et al.*, 2013, 2017; Monk and Arlinghaus, 2017), which may increase the strength of the observed patterns by enhancing differences in the individual vulnerability to harvest once the encounter has happened. This fact has two implications for fisheries management.

First, the fraction of biomass harder to catch could confer resilience to the population, although this hypothesis requires further attention in a population dynamic model. In fact, the existence of mobile- and resident-SBT not only plays a role in ecosystem functioning (Spiegel *et al.*, 2017), but may also guarantee the conservation of a reproducing biomass invulnerable to fishing over time (the resident-SBT, Alós *et al.*, 2015a, 2016b). The selective properties of harvesting on behavioural traits could also indirectly contribute to a reduction of the productivity of the fishery (Arlinghaus *et al.*, 2017). Although this could not be the general rule (e.g. Cardinale *et al.*, 2017), traditionally assumed depleted stocks may be affected from similar phenomena observed here and, at least, deserves further attention. Additionally, one can speculate that the alteration of the behavioural features of the surviving portion of the adults could induce both top-down and bottom-up ecological effects, whenever the exploited species plays a significant role in the food web (Ward *et al.*, 2016). Moreover, behavioural traits, such as exploration, are usually positively correlated with productivity life-history traits such as growth rates at individual level (Biro and Post, 2008). Therefore, the selective properties of harvesting on behavioural traits should also indirectly contribute to a reduction of the productivity of the fishery (Alós *et al.*, 2014).

Second, knowledge of the mechanism underpinning hyperdepletion in catch rates provides an opportunity to improve the assessments of the stocks that are solely or mainly based on CPUE data. By coupling the study of the spatial behavioural diversity (i.e. knowing the fraction of the vulnerable and non-vulnerable individuals), we can provide more reliable estimates of *N* to be incorporated in classical population dynamic models based on CPUE data and the estimation of the shape of the relationship of *N* and CPUE (β). Therefore, our work provides concrete directions in how fish spatial behaviour can improve stock fisheries assessments and management (Crossin *et al.*, 2017).

We demonstrate the emergence of hyperdepletion from SBT using a coupled theoretical and empirical approach. The number of fishing experiments demonstrating either hyperstability or hyperdepletion of CPUEs is limited, mainly due to the difficulties of obtaining a reliable estimate of true abundance at the same time and site where CPUE data are collected. Most works have used fishery independent methods like entrapment, trawl surveys, or systematic underwater visual census to approximate *N* (e.g. Erisman *et al.*, 2011; Robinson *et al.*, 2015; Hamilton *et al.*, 2016), but certainly a perfect experiment with real *N* is so far not available. Our approach, however, took the advantages offered by the recent advance of underwater video-recording systems and developed methods to estimate absolute densities, which supported our hypothesis that the hyperdepletion was revealed in a fish stock where SBT have been widely identified (Alós *et al.*, 2016b). However, our data set had limitations (e.g. there is no replication of the fishing experiment, the sample size is limited) and the results can thus not be easily generalized. In fact, the BCI of the estimation of the β was quite large. In addition, the field method we used to estimate *N* may imply some behavioural-related bias as well, which can be overestimating the true density in the field (fraction vulnerable and non-vulnerable together). Such a bias could have been avoided by using un-baited underwater video-recording methods to estimate behavioural independent *N* (Campos-Candela *et al.*, 2018). We recommend further empirical experiments to provide a broader support to our theoretical and empirical predictions and the use of underwater video-recording while simultaneously measuring CPUE to provide more comprehensive data. This future work should also consider other fisheries, including these performed with active gear (e.g. purse seining or trawling).

Notwithstanding these limitations, the actual local hyperdepletion observed in the real fish stock was found to be even stronger than the one found *in silico*, suggesting that other mechanisms may play a role and affect catchability independent of encounters with the gear. For instance, among the factors outlined above, learning to avoid capture (hook avoidance, Klefoth *et al.*, 2013; Wegener *et al.*, 2018) is an important contributor to altered behaviours levels in fish and could partially explain the differences between the shape between the CPUE and *N* from our model and the empirical data. The rapid acquisition of gear avoidance, through individual or social learning, has been widely reported across exploited fish species (Raat, 1985; Askey *et al.*, 2006; Klefoth *et al.*, 2013; Alós *et al.*, 2015b), and it may play an important role in the fast decline of the CPUE as an additive effect to be imposed by SBT. Additionally, the existence of cryptic habitat or other environmental factors constraining the fishing gears to efficiently operate could also produce a fraction of the stock unavailable to the gear and contribute to the fast decline of the CPUE as suggested in the fishery of the squid, *Loligo gahi* (Roa-Ureta, 2012). However, the pearly razorfish inhabit large or relatively large extensions of homogeneous sandy and soft habitats (Katsanevakis, 2005), which limits this hypothesis for our case study. An additional sampling using fishing gear in different types of habitats to evaluate learning and gear recognition (i.e. by exposing fishing gear to fish in a video-recording setup, Alós *et al.*, 2015a) while simultaneously measuring CPUE–*N* relationships would help in disentangling the role of hook avoidance and habitat effects in further empirical assessments.

Finally, one general prediction in the CPUE–*N* relationship in recreational fisheries is fishing effort sorting due to the less skilled fishers (in our case skipper-boat drivers) exiting the fishery earlier, in turn leading to higher-skilled anglers maintaining high hyperstable CPUE even at low fish densities (Ward *et al.*, 2013; van Poorten *et al.*, 2016). In our agent-based simulation we did not include either variability in the fishers' movement characteristics (which may include different optimal search patterns to improve encounter with fish, Alós *et al.*, 2012) or the variability in fishing skills, factors that could collectively explain hyperstable catch rates in fisheries (van Poorten *et al.*, 2016). However, from the empirical data, there was no evidence of effort sorting in the pearly razorfish fishery, instead, all fishers start giving up when the catch rates drop after a few days (Alós *et al.*, 2016b). The strong decrease in the fishing pressure after 2 or 3 weeks since the opening of the fishing season is probably caused by a decrease in the utility of this specific fishery (which is a consumptive fishery and CPUE is the main driver of satisfaction). Actually, the pearly razorfish fishery is a low-skilled fishery based on natural bait which probably means that the angler-skill effect is smaller than in other fisheries where specialization skills may produce larger CPUEs (Ward *et al.*, 2013; van Poorten *et al.*, 2016). However, at a broader scale or at the whole fishery system the results may change because the patterns of hyperstability or hyperdepeletion may be scale dependent. In fact, the rapid exit behaviour of most pearly razorfish anglers to other fisheries may maintain relatively high CPUEs in other stocks by exploiting the fraction of mobile-SBT in several sites. These reflexions highlight the need of developing more complex social-ecological agent-based simulations not only considering one particular fishery (e.g. including other types of fisheries like those performed in spawning aggregations or isolated or semi-isolated populations) but also considering a landscape of angler-linked fisheries. In addition, our model is based on an exploited population. Further work should evaluate the emergent patterns in the relationship between *N* and CPUE when pristine or non-exploited populations are considered. In such populations, behavioural variability as well as *naïveté* of fish (Alós *et al.*, 2015b) should be enhanced and the mismatch between *N* and CPUE could be enhanced.

Acknowledgements

This study was funded by the research project PHENOFISH (grant no. CTM2015-69126-C2-1-R) funded by the Spanish Ministry of Economy and Competiveness and a Marie Curie grant (FP7-PEOPLE-2012-IEF, grant no. 327160) funded by the European Union. JA was supported by a JdC post-doc grant funded by the Spanish Ministry of Economy, Industry and Competitiveness (ref. IJCI-2016-27681). AC-C was supported by a FPU pre-doctoral fellowship (ref. FPU13/01440) from the Spanish Ministry of Education, Culture and Sports. We thank reviewers for constructive feedback.

References

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

Alós, J., Palmer, M., Catalan, I. A., Alonso-Fernández, A., Basterretxea, G., Jordi, A., and Buttay, L., *et al.* 2014. Selective exploitation of spatially structured coastal fish populations by recreational anglers may lead to evolutionary downsizing of adults. Marine Ecology Progress Series, 503: 219–233.

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.

Alós, J., Palmer, M., Rosselló, R., and Arlinghaus, R. 2016b. Fast and behavior-selective exploitation of a marine fish targeted by anglers. Scientific Reports, 6: 38093.

Alós, J., Palmer, M., Trías, P., Díaz-Gil, C., and Arlinghaus, R. 2015a. Recreational angling intensity correlates with alteration of vulnerability to fishing in a carnivorous coastal fish species. Canadian Journal of Fisheries and Aquatic Sciences, 72: 217–225.

Alós, J., Puiggrós, A., Díaz-Gil, C., Palmer, M., Rosselló, R., and Arlinghaus, R. 2015b. Empirical evidence for species-specific export of fish naïveté from a no-take marine protected area in a coastal recreational hook and line fishery. PLoS One, 10: e0135348.

Andersen, K. H., Marty, L., and Arlinghaus, R. 2017. Evolution of boldness and life history in response to selective harvesting. Canadian Journal of Fisheries and Aquatic Sciences, 75: 271–281.

Arlinghaus, R., Alós, J., Klefoth, T., Laskowski, K., Monk, C. T., 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., Cooke, S. J., Lyman, J., Policansky, D., Schwab, A., Suski, C., and Sutton, S. G. 2007. Understanding the complexity of catch-and-release in recreational fishing: an integrative synthesis of global knowledge from historical, ethical, social, and biological perspectives. Reviews in Fisheries Science, 15: 75–167.

Arlinghaus, R., Laskowski, K. L., Alós, J., Klefoth, T., Monk, C. T., 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.

Árnason, E., Hernandez, U. B., and Kristinsson, K. 2009. Intense habitat-specific fisheries-induced selection at the molecular Pan I locus predicts imminent collapse of a major cod fishery. PLoS One, 4: e5529.

Arreguín-Sánchez, F. 1996. Catchability: a key parameter for fish stock assessment. Reviews in Fish Biology and Fisheries, 6: 221–242.

Askey, P. J., Richards, S. A., Post, J. R., and Parkinson, E. A. 2006. Linking angling catch rates and fish learning under catch-and-release regulations. North American Journal of Fisheries Management, 26: 10.

Bell, A. M., Hankison, S. J., and Laskowski, K. L. 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.

Biro, P. A., and Post, J. R. 2008. Rapid depletion of genotypes with fast growth and bold personality traits from harvested fish populations. Proceedings of the National Academy of Sciences of the United States of America, 105: 2919–2922.

Börger, L., Dalziel, B. D., and Fryxell, J. M. 2008. Are there general mechanisms of animal home range behaviour? A review and prospects for future research. Ecology Letters, 11: 637–650.

Burgess, M. G., Costello, C., Fredston-Hermann, A., Pinsky, M. L., Gaines, S. D., Tilman, D., and Polasky, S.. 2017. Range contraction enables harvesting to extinction. Proceedings of the National Academy of Sciences of the United States of America, 114: 3945–3950.

Campos-Candela, A., Palmer, M., Balle, S., and Alós, J. 2018. A camera-based method for estimating absolute density in animals displaying home range behaviour. Journal of Animal Ecology, 87: 825–837.

Canestrelli, D., Bisconti, R., and Carere, C. 2016. Bolder takes all? The behavioral dimension of biogeography. Trends in Ecology & Evolution, 31: 35–43.

Cardinale, M., Svenson, A., and Hjelm, J. 2017. The "easy restriction" syndrome drive local fish stocks to extinction: the case of the management of Swedish coastal populations." Marine Policy, 83: 179–183.

Claireaux, M., Jørgensen, C., and Enberg, K. 2018. Evolutionary effects of fishing gear on foraging behavior and life-history traits. Ecology and Evolution, in press.

Codling, E. A., Plank, M. J., and Benhamou, S. 2008. Random walk models in biology. Journal of the Royal Society Interface, 5: 813–834.

Conrad, J. L., Weinersmith, K. L., Brodin, T., Saltz, J. B., and Sih, A. 2011. Behavioural syndromes in fishes: a review with implications for ecology and fisheries management. Journal of Fish Biology, 78: 395–435.

Cote, J., Clobert, J., Brodin, T., Fogarty, S., and Sih, A. 2010. Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations. Philosophical Transactions of the Royal Society: Biological Sciences, 365: 4065–4076.

Cote, J., Fogarty, S., Tymen, B., Sih, A., and Brodin, T.. 2013. Personality-dependent dispersal cancelled under predation risk. Proceedings of the Royal Society: Biological Sciences, 280: 20132349–20132349.

Crossin, G. T., Heupel, M. R., Holbrook, C. M., Hussey, N. E., Lowerre-Barbieri, S. K., Nguyen, V. M., and Raby, G. D. 2017. Acoustic telemetry and fisheries management. Ecological Applications, 27: 1031–1049.

Dunlop, K. M., Ruxton, G. D., Scott, E. M., and Bailey, D. M. 2015. Absolute abundance estimates from shallow water baited underwater camera surveys; a stochastic modelling approach tested against field data. Journal of Experimental Marine Biology and Ecology, 472: 126–134.

Erisman, B. E., Allen, L. G., Claisse, J. T., Pondella, D. J., Miller, E. F., and Murray, J. H. 2011. The illusion of plenty: hyperstability masks collapses in two recreational fisheries that target fish spawning aggregations. Canadian Journal of Fisheries and Aquatic Sciences, 68: 1705–1716.

Falconer, D. S., and Mackay, T. F. C.. 1996. Introduction to Quantitative Genetics, Ronald Press Co, New York.

Hamilton, R. J., Almany, G. R., Stevens, D., Bode, M., Pita, J., Peterson, N. A., and Choat, J. H. 2016. Hyperstability masks declines in bumphead parrotfish (*Bolbometopon muricatum*) populations. Coral Reefs, 35: 751–763.

Harley, S. J., Myers, R. A., and Dunn, A. 2001. Is catch-per-unit-effort proportional to abundance? Canadian Journal of Fisheries and Aquatic Sciences, 58: 1760–1772.

Harrison, P. M., Gutowsky, L. F. G., Martins, E. G., Patterson, D. A., Cooke, S. J., and Power, M. 2014. Personality-dependent spatial ecology occurs independently from dispersal in wild burbot (*Lota lota*). Behavioral Ecology, 26: 483–492.

Hilborn, R., and Walters, C.. 1992. Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty, Chapman & Hall Inc., New York. 570 pp.

Hunt, L. M., Arlinghaus, R., Lester, N., and Kushneriuk, R. 2011. The effects of regional angling effort, angler behavior, and harvesting efficiency on landscape patterns of overfishing. Ecological Applications, 21: 2555–2575.

Katsanevakis, S. 2005. Habitat use by the pearly razorfish, *Xyrichtys novacula* (Pisces: Labridae). Scientia Marina, 69: 223–229.

Klefoth, T., Pieterek, T., and Arlinghaus, R. 2013. Impacts of domestication on angling vulnerability of common carp (*Cyprinus carpio* L.): the role of learning, foraging behaviour and food preferences. Fisheries Management and Ecology, 20: 12.

Klefoth, T., Skov, C., Kuparinen, A., and Arlinghaus, R. 2017. Toward a mechanistic understanding of vulnerability to hook-and-line fishing: boldness as the basic target of angling-induced selection. Evolutionary Applications, 10: 994–1006.

Kleiven, A. R., Olsen, E. M., and Vølstad, J. H. 2012. Total catch of a red-listed marine species is an order of magnitude higher than official data. PLoS One, 7: e31216.

Kobler, A., Klefoth, T., Mehner, T., and Arlinghaus, R. 2009. Coexistence of behavioural types in an aquatic top predator: a response to resource limitation? Oecologia, 161: 837–847.

Langrock, R., Hopcraft, J. G. C., Blackwell, P. G., Goodall, V., King, R., Niu, M., and Patterson, T. A. 2014. Modelling group dynamic animal movement. Methods in Ecology and Evolution, 5: 190–199.

Lennox, R. J., Alós, J., Arlinghaus, R., Horodysky, A., Klefoth, T., Monk, C. T., and Cooke, S. J. 2017. What makes fish vulnerable to capture by hooks? A conceptual framework and a review of key determinants. Fish and Fisheries, 18: 986–1010.

Maggs, J. Q., Mann, B. Q., Potts, W. M., and Dunlop, S. W. 2016. Traditional management strategies fail to arrest a decline in the catch-per-unit-effort of an iconic marine recreational fishery species with evidence of hyperstability. Fisheries Management and Ecology, 23: 187–199.

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.

Moland, E., Ulmestrand, M., Olsen, E. M., and Stenseth, N. C. 2013. Long-term decrease in sex-specific natural mortality of European lobster within a marine protected area. Marine Ecology Progress Series, 491: 153–164.

Monk, C. T., and Arlinghaus, R. 2017. Encountering a bait is necessary but insufficient to explain individual variability in vulnerability to angling in two freshwater benthivorous fish in the wild. PLoS One, 12: e0173989.

Monk, C. T., and Arlinghaus, R. 2018. Eurasian perch, *Perca fluviatilis*, spatial behaviour determines vulnerability independent of angler skill in a whole-lake reality mining experiment. Canadian Journal of Fisheries and Aquatic Sciences, 75: 417–428.

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

Nakayama, S., Laskowski, K. L., Klefoth, T., and Arlinghaus, R. 2016. Between- and within-individual variation in activity increases with water temperature in wild perch. Behavioral Ecology, 27: 1676–1683.

Olsen, E., and Moland, E. 2011. Fitness landscape of Atlantic cod shaped by harvest selection and natural selection. Evolutionary Ecology, 25: 695–710.

Palmer, M., Balle, S., March, D., Alós, J., and Linde, M. 2011. Size estimation of circular home range from fish mark-release-(single)-recapture data: case study of a small labrid targeted by recreational fishing. Marine Ecology-Progress Series, 430: 87–97.

Parsons, D. M., Morrison, M. A., McKenzie, J. R., Hartill, B. W., Bian, R., and Francis, R. I. C. C. 2011. A fisheries perspective of behavioural variability: differences in movement behaviour and extraction rate of an exploited sparid, snapper (*Pagrus auratus*) (R Hilborn, Ed.). Canadian Journal of Fisheries and Aquatic Sciences, 68: 632–642.

Peterman, R. M., and Steer, G. J. 1981. Relation between sport-fishing catchability coefficients and salmon abundance. Transactions of the American Fisheries Society, 110: 585–593.

Pierce, R. B., and Tomcko, C. M. 2003. Variation in gill-net and angling catchability with changing density of northern pike in a small Minnesota lake. Transactions of the American Fisheries Society, 132: 771–779.

Plummer, M., Best, N., Cowles, K., and Vines, K. 2006. CODA: convergence diagnosis and output analysis for MCMC. R News, 6: 5.

Post, J. R., Sullivan, M., Cox, S., Lester, N. P., Walters, C. J., Parkinson, E. A., Paul, A. J., *et al.* 2002. Canada's recreational fisheries: the invisible collapse? Fisheries, 27: 6–17.

Post, J., Mushens, C., Paul, A., and Sullivan, M. 2003. Assessment of alternative harvest regulations for sustaining recreational fisheries: model development and application to bull trout. North American Journal of Fisheries Management, 23: 22–34.

R Core Team. 2018. R: a language and environment for statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/ (last accessed 7 January 2018).

Raat, A. J. P. 1985. Analysis of angling vulnerability of common carp, *Cyprinus carpio* L., in catch-and-release angling in ponds. Aquaculture Research, 16: 171–187.

Radinger, J., and Wolter, C. 2014. Patterns and predictors of fish dispersal in rivers. Fish and Fisheries, 15: 456–473.

Réale, D., Reader, S. M., Sol, D., McDougall, P. T., and Dingemanse, N. J. 2007. Integrating animal temperament within ecology and evolution. Biological Reviews, 82: 291–318.

Rehage, J. S., and Sih, A. 2004. Dispersal behavior, boldness, and the link to invasiveness: a comparison of four Gambusia species. Biological Invasions, 6: 379–391.

Roa-Ureta, R. H. 2012. Modelling in-season pulses of recruitment and hyperstability-hyperdepletion in the *Loligo gahi* fishery around the Falkland Islands with generalized depletion models. ICES Journal of Marine Science, 69: 1403–1415.

Robinson, J., Graham, N. A. J., Cinner, J. E., Almany, G. R., and Waldie, P. 2015. Fish and fisher behaviour influence the vulnerability of groupers (Epinephelidae) to fishing at a multispecies spawning aggregation site. Coral Reefs, 34: 371–382.

Sih, A., Bell, A., and Johnson, J. C. 2004. Behavioral syndromes: an ecological and evolutionary overview. Trends in Ecology & Evolution, 19: 372–378.

Smouse, P. E., Focardi, S., Moorcroft, P. R., Kie, J. G., Forester, J. D., and Morales, J. M. 2010. Stochastic modelling of animal movement. Philosophical Transactions of the Royal Society: Biological Sciences, 365: 2201–2211.

Spiegel, O., Leu, S. T., Bull, C. M., and Sih, A. 2017. What's your move? Movement as a link between personality and spatial dynamics in animal populations. Ecology Letters, 20: 3–18.

Sutter, D. A. H., Suski, C. D., Philipp, D. P., Klefoth, T., Wahl, D. H., Kersten, P., Cooke, S. J., *et al.* 2012. Recreational fishing selectively captures individuals with the highest fitness potential. Proceedings of the National Academy of Sciences of the United States of America, 109: 6.

Tidd, A., Brouwer, S., and Pilling, G. 2017. Shooting fish in a barrel? Assessing fisher-driven changes in catchability within tropical tuna purse seine fleets. Fish and Fisheries, 18: 808–820.

Tintoré, J., Vizoso, G., Casas, B., Heslop, E., Pascual, A., Orfila, A., Ruiz, S., *et al.* 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.

Tsuboi, J-i., Morita, K., Klefoth, T., Endou, S., and Arlinghaus, R. 2015. Behaviour-mediated alteration of positively size-dependent vulnerability to angling in response to historical fishing pressure in a freshwater salmonid. Canadian Journal of Fisheries and Aquatic Sciences, 73: 461–468.

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.

van Poorten, B. T., Arlinghaus, R., Daedlow, K., and Haertel-Borer, S. S.. 2011. Social-ecological interactions, management panaceas, and the future of wild fish populations. Proceedings of the National Academy of Sciences of the United States of America, 108: 12554–12559.

van Poorten, B. T., Walters, C. J., and Ward, H. G. M. 2016. Predicting changes in the catchability coefficient through effort sorting as less skilled fishers exit the fishery during stock declines. Fisheries Research, 183: 379–384.

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.

Villegas-Ríos, D., Alós, J., Palmer, M., Lowerre-Barbieri, S. K., Bañón, R., Alonso-Fernández, A., and Saborido-Rey, F. 2014. Life-history and activity shape catchability in a sedentary fish. Marine Ecology Progress Series, 515: 239–250.

Villegas-Ríos, D., Réale, D., Freitas, C., Moland, E., and Olsen, E. M. 2017. Individual level consistency and correlations of fish spatial behaviour assessed from aquatic animal telemetry. Animal Behaviour, 124: 83–94.

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.

Ward, H. G. M., Askey, P. J., and Post, J. R. 2013. A mechanistic understanding of hyperstability in catch per unit effort and density-dependent catchability in a multistock recreational fishery. Canadian Journal of Fisheries and Aquatic Sciences, 70: 1542–1550.

Ward, T. D., Algera, D. A., Gallagher, A. J., Hawkins, E., Horodysky, A., Jørgensen, C., and Killen, S. S., *et al.* 2016. Understanding the individual to implement the ecosystem approach to fisheries management. Conservation Physiology, 4: cow005–cow005.

Wegener, M. G., Schramm, H. L., Neal, J. W., and Gerard, P. D. 2018. Effect of fishing effort on catch rate and catchability of largemouth bass in small impoundments. Fisheries Management and Ecology, 25: 66–76.

Wiig, J. R., Moland, E., Haugen, T. O., and Olsen, E. M. 2013. Spatially structured interactions between lobsters and lobster fishers in a coastal habitat: fine-scale behaviour and survival estimated from acoustic telemetry. Canadian Journal of Fisheries and Aquatic Sciences, 70: 1468–1476.

Handling editor: Manuel Hidalgo