

Life-history and activity shape catchability in a sedentary fish

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ABSTRACT: Catchability, a key parameter in stock assessment, is often considered constant in time and space. However, when fishing with passive gears like traps or gillnets, fish behavior determines the odds of encounter with the fishers and thus catchability. Few studies have presented comprehensive empirical evidence of the link between behavior measured in the wild and catchability from a life-history strategy perspective. Here, a suite of different variables, including environmental cues, physiological states, fish activity, home range and catchability, were modeled using a sinusoidal function to describe their seasonality over the year and the degree of coupling among them in a sedentary coastal fish (*Labrus bergylta*). All the variables except the home range size showed a significant variation over the year, following a sinusoidal pattern. The models showed a tight match between the seasonality of catchability and fish activity, with high values of both variables occurring in late spring to early summer, when the highest levels of feeding and the period of reproductive inactivity occurred. Lower catchability values were predicted in late autumn to early winter, coinciding with the spawning season and the associated reduced activity. This integrative research shows that the spatio-temporal dimension of fish life-history strategy has a key role in shaping catchability even in highly sedentary species. Time-varying catchability needs to be incorporated into stock assessment models that aim to accurately describe fish population health and to estimate abundance indices.

KEY WORDS: Feeding · Fish activity · Home range · Movement ecology · Reproduction · Seasonality · Sedentary fish · Vulnerability

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INTRODUCTION

Catchability is a key parameter in fisheries stock assessment and refers to the probability of a single fish being caught by a defined unit of fishing effort (Arreguín-Sánchez 1996). It allows the estimation of stock abundance from catch and effort data, and it ultimately measures the interaction between the resource abundance and the fishing effort. Gear char-

acteristics, environmental effects and the different biological features of the targeted individuals all influence catchability (Wilberg et al. 2009). Particularly, fish size and fish behavior play a key role, especially for passive gears like traps or gillnets, for which catchability depends on the probability of the fish encountering the net (Arreguín-Sánchez 1996, Alós et al. 2012). Therefore, catchability is difficult to estimate and is often left constant in time and space

when modelling stock dynamics (Arreguín-Sánchez 1996), potentially leading to biased estimates of abundance (Ricker 1975, Cooke & Beddington 1984, Wilberg et al. 2009).

Fish behavior may be largely influenced by the life-history strategy of the species, especially the reproductive and energy allocation strategy (reviewed by McBride et al. 2013). In some species, predictable behavior like the formation of spawning aggregations (e.g. shallow water groupers; Coleman et al. 1996) or the realization of large-scale migrations (e.g. blue tuna; Block et al. 2001) for reproductive or feeding purposes allows fishers to increase the probability of encountering fish (Sadovy & Domeier 2005). However, many harvested coastal fishes around the world are sedentary and move within well-defined and relatively small home ranges, within which feeding and reproductive areas overlap (Botsford et al. 2009, March et al. 2010, Palmer et al. 2011). At middle and high latitudes (roughly north to 25°N and south to 25°S), coastal fish are subject to seasonal, sinusoidal-like variations in the environmental conditions (Schmidt-Nielsen 1997, Stoner 2004). These species usually display a life-history strategy characterized by a predominantly capital energy allocation strategy (i.e. reproduction financed with stored energy) and determinate fecundity (i.e. no recruitment of oocytes during the spawning season; Ganius 2013). That is, foraging and reproduction occur within distinct time periods (Houston et al. 2007, McBride et al. 2013). If feeding and reproduction are associated with different behavioral patterns (i.e. active food search versus spawning territoriality) that alter the likelihood of encounter between fishers and fish, then catchability may vary seasonally (Neumann & Willis 1995, Stoner 2004).

Empirical evidence on how life-history and fish behavior influence catchability is still lacking, primarily due to the limitations of studying behavior for long-term periods in the wild. However, the miniaturization and increase of the life-span of telemetry tags have allowed monitoring of the fine-scale movement behavior in fish (Cooke et al. 2004, Krause et al. 2013). In this study, we aimed to get insight into the relationships between time-varying behavior and catchability in a coastal sedentary fish. We selected *Labrus bergylta* as our model species due to its local commercial importance and to the fact that stock assessments are currently lacking for the species, making the results of this research very timely and useful for future management plans. We hypothesized that the fish life-history strategy would induce seasonality in its behavior (in order to adapt to repro-

ductive or feeding requirements) and, as a consequence, seasonality in catchability. Even though spatial models that take into account fish movements have been widely used for migratory species (Hancock et al. 2000, Porch et al. 2001), spatial behavior is often ignored for coastal fish. To the best of our knowledge, the present work is the first study that compiles empirical evidence describing (1) the seasonal behavior using fine-scale telemetry in sedentary fish, (2) the potential drivers of behavioral variability and (3) its implications for stock assessment and fishing vulnerability.

MATERIALS AND METHODS

Data collection

Six variables (i.e. sea surface temperature [SST], the seasonal dependence of the spawning probability (pR ; see 'Data analysis' below), feeding, distance travelled, home range and catchability) derived from 5 different datasets (Table 1) were analyzed for seasonality. SST was used as a general tracer of the environmental seasonality in the study area (Fig. 1). Daily values of SST for the period 2008 to 2012 were obtained from an oceanographic station (www.meteogalicia.es) located in the vicinity of the telemetry study area (Table 1, Fig. 1, see Fig. S1a in Supplement 1 at www.int-res.com/articles/suppl/m515p239_supp/).

Labrus bergylta (Ascanius, 1767) (Fig. 1) is the largest labrid in the NE Atlantic and a valuable resource for both recreational and commercial fisheries (Bañón et al. 2010, Pita 2011). It is a protogynous hermaphrodite (i.e. sex changes from female to male), capital breeder and sedentary species living in spatially stable home ranges smaller than 1.5 km² (Villegas-Ríos et al. 2013a,b). Large, territorial males court and mate with several smaller females within their reproductive groups during the spawning season (Sjölander et al. 1972). Life-history traits (i.e. total weight, total length, gonad weight and gut weight, Table 1) of *L. bergylta* were obtained from a 2 yr (December 2009 to December 2011) monthly biological sampling program at the local fish markets of Galicia, where the artisanal fleet delivers all the catches. A gonadosomatic index (GSI; Fig. S1b in Supplement 1) of females ($n = 1150$) was estimated as the percentage of gonad weight (± 0.01 g) relative to fish gutted weight (± 0.01 g). Histological assessment of the ovaries allowed the classification of each individual as mature or immature and the calculation of the subsequent maturity ogive (for additional details, refer to

Table 1. Summary of the datasets, observed variables and derived variables (i.e. variables of interest modeled for seasonality) used in this study, showing their spatial and temporal coverage

Dataset	Observed variable	Derived variable	Spatial coverage	Temporal coverage
Oceanographic	Sea surface temperature	Sea surface temperature	42° 05.8' N, 8° 55.8' W	2008–2012
Biological sampling	Gonad weight	Seasonal dependence of the spawning probability	Ría de Vigo	Dec 2009–Dec 2011
	Total length		Ría de Vigo	Dec 2009–Dec 2011
	Gutted weight	Ría de Vigo	Jan–Dec 2011	
	Gut weight	Feeding index	Ría de Vigo	Jan–Dec 2011
	Gutted weight		Ría de Vigo	Jan–Dec 2011
Telemetry	Home range	Home range	Cíes Archipelago	Sept 2011–Sept 2012
	Distance travelled	Distance travelled	Cíes Archipelago	Sept 2011–Sept 2012
Catches	Catches	Catchability	Galician coast	1999–2012
Underwater visual census	Abundance index		Ría de A Coruña	2003–2006

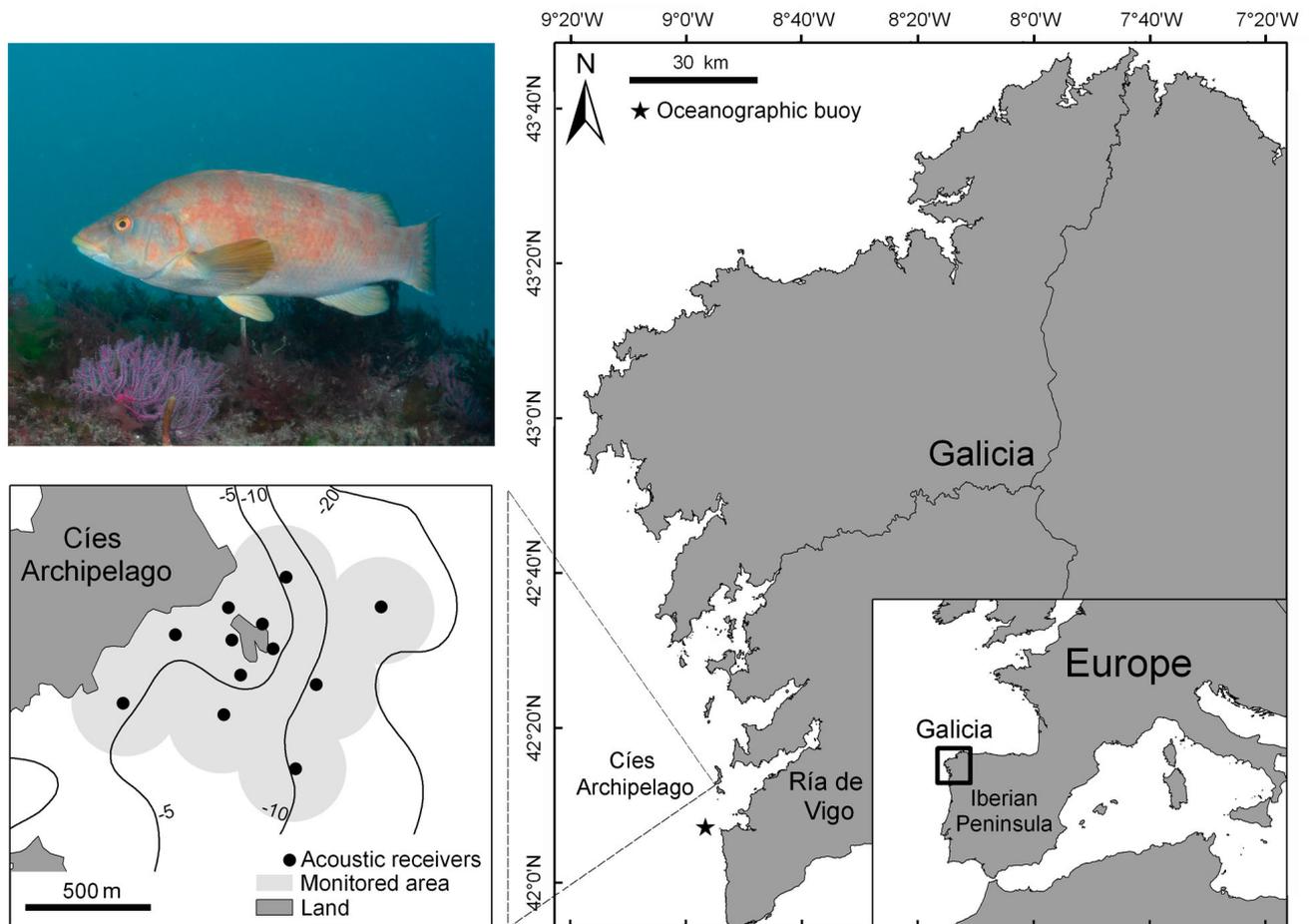


Fig. 1. Map of the study area including a photograph of the study species, *Labrus bergylta* (upper left), and a map of the telemetry array (lower left)

Villegas-Ríos et al. 2013a). Both variables, the GSI and the probability of being mature, were used to estimate the spawning probability (here defined as the probability of belonging to the spawning population, sensu Lowerre-Barbieri et al. 2009) for each

individual, as described in 'Data analysis'. A feeding index, F , was estimated for the individuals sampled in 2011 ($n = 579$) as the percentage of the gut weight (i.e. the weight of the full stomach; ± 0.01 g) divided by the fish gutted weight (± 0.01 g; Fig. S1c). F was

used as an index of feeding intensity (Rikardsen & Sandring 2006). Additional information on the biological sampling used to calculate the GSI and F can be found in Villegas-Ríos et al. (2013a, 2014).

Fine-scale spatio-temporal information was obtained from an acoustic telemetry study of 24 unsexed individuals (size range: 20.5 to 50.5 cm) within an array of 12 Vemco® VR2-W receivers whose detection range largely overlapped (Villegas-Ríos et al. 2013b). Anesthetized individuals were implanted with acoustic transmitters in the body cavity through an incision, and the wound was closed with 2 surgical stitches (Villegas-Ríos et al. 2013b). The study was conducted at the Cíes Archipelago (Fig. 1) and lasted for 12 mo (September 2011 to September 2012), after which the receivers were retrieved and data were downloaded. Fish positions were estimated at 30 min time steps based on detections at multiple receivers as described by Villegas-Ríos et al. (2013b). Mean/average residence index (i.e. the number of days each fish was detected inside the array, divided by the total period of detection) during the study period was 0.99 (Villegas-Ríos et al. 2013b), so movement measurements are based on the assumption that no fish left the study area during the whole period. Home range and horizontal distance travelled (as a proxy of activity) were estimated at 10 d time steps. Home range was calculated using 95% kernel utilization distribution (KUD₉₅, see Supplement 1). The distance travelled in each 10 d time step was estimated by summing the distances between consecutive fish positions within each time step, assuming linear movement routes.

Catch rates of *L. bergylta* were obtained from a long-term artisanal-fishing monitoring program led by the Galician Regional Government (UTPB-Xunta de Galicia). This is a fishery-dependent monitoring program in which scientists on board commercial artisanal boats monitor their catches. The monitored boats are randomly selected among a fleet of ~4000 units operating all over the Galician coast (Fig. 1). *L. bergylta* in this fishery is targeted mainly with gillnets (99.3% of the catches) and secondarily with hook and line or small long lines (R. Bañón pers. obs.). Therefore, we retained only the 3844 gillnet deployments (defined as a gillnet deployment by a single boat in a single day) available in the dataset

between 1999 and 2012. In spite of the local importance as a fishing resource (Villegas-Ríos 2013), *L. bergylta* is not currently subject to stock assessment in the study area. For each gillnet deployment, the following information was recorded: number of *L. bergylta* captured (including zeros, i.e. hauls without captures), position, depth, bottom type, soak time and number of panels (50 m each) composing the gillnet. Previous analyses (data not shown) revealed a saturation of the gillnets for soaking times >24 h, so data were filtered to remove those deployments ($n = 13$). Since this gillnet fishery is not exclusively aimed at targeting *L. bergylta*, data were also filtered to exclude those habitats and depths where the species is known to be absent in the area (depths > 50 m; muddy and sandy bottoms). Therefore, we retained data from 838 gillnet deployments for analyses (Table 2, Figs. S1d & S2 in Supplement 1). Information on the seasonal variation in stock size was derived from the density of *L. bergylta* in Galicia obtained from Pita (2011) and used as a relative index of abundance in the catchability model (see 'Data analysis'). These estimates of fish density were fishery-independent (obtained by underwater visual censuses) and were considered constant for a given season. Underwater visual censuses are considered a precise and reliable method for the estimation of fish density of the Galician fish communities (Pita et al. 2014). Underwater visual censuses were conducted between 2003 and 2006 in Ría de Coruña (43° 22' N; 8° 22' W) at a place ~150 km north of the telemetry study area but with similar biotic and abiotic characteristics (Pita 2011). Since the temporal scale of the

Table 2. Temporal coverage (yearly and monthly distribution) of the gillnet deployments used in this study

Year	Month												Total
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	
1999	–	–	–	–	–	5	–	–	–	–	4	–	9
2000	1	–	5	–	1	5	–	–	–	–	4	–	16
2001	–	4	1	2	9	–	–	–	–	–	–	4	20
2002	–	–	8	6	2	7	4	–	1	–	–	–	28
2003	6	3	4	2	7	9	1	–	1	3	15	30	81
2004	10	12	20	16	23	10	5	–	4	–	4	13	117
2005	13	14	12	16	12	7	10	1	–	–	1	14	100
2006	9	7	10	25	14	9	1	5	2	–	3	4	89
2007	–	2	10	8	8	6	–	2	15	8	5	4	68
2008	4	4	1	11	6	4	–	–	11	–	8	3	52
2009	1	8	5	7	9	5	–	3	10	1	–	5	54
2010	4	4	13	14	13	3	–	6	–	–	10	7	76
2011	–	6	–	1	9	28	–	–	–	1	4	9	58
2012	3	4	9	12	18	18	–	1	–	1	2	2	70
Total	51	68	98	120	131	116	21	18	44	16	60	95	838

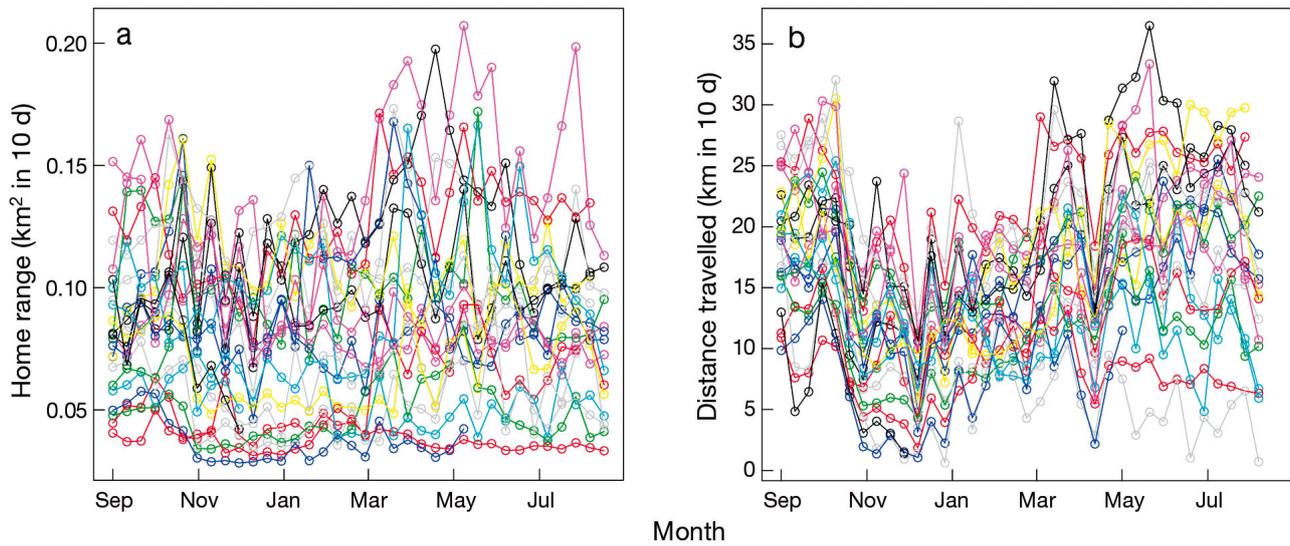


Fig. 2. Raw data of the home range size and distance travelled for each individual fish ($n = 24$) at 10 d time periods, during the telemetry experiment (1 September 2011 to 1 September 2012)

visual census was considerably shorter than the catch time series (4 yr vs. 14 yr), we used the pooled average seasonal values for all the years provided by Pita (2011) and considered them representative for all study years (i.e. we assumed a stable population density across years). Mean ± 1 SD density values for each season were 440.4 ± 385.3 , 256.2 ± 230.2 , 457.7 ± 532.3 and 620.8 ± 566.3 ind. ha^{-1} in spring, summer, autumn, winter, respectively (see details in Pita 2011).

Data analysis

We hypothesized that in seasonal environments, the analyzed variables should follow a sinusoidal variation. Given that cause-and-effect relationships are especially difficult to establish among observational variables experiencing seasonal cycles (Adams 2003), we tested this hypothesis by fitting the data to a sinusoidal function and then estimating and comparing the phase (defined below) of each variable. We assumed that variables showed no interannual variations. A sinusoidal model seemed reasonable according to the raw data (Fig. 2, see Figs. S1 & S2 in Supplement 1). The deterministic part of all the sinusoidal models was the same:

$$S_i = \alpha + \beta_1 \cos(2\pi d_i / 365) + \beta_2 \sin(2\pi d_i / 365) \quad (1)$$

where S_i is the sinusoidal function at day i , d_i is the number of days from a reference date (1 January), α represents the mean of the trend, and the combina-

tion of β_1 and β_2 determines the phase and the amplitude. Specifically, we were interested in estimating the phase φ , i.e. the number of days between the reference date and the maximum of the sinusoidal function, which represents the time of the year when each variable reaches its maximum value:

$$\varphi = (365 / 2\pi) \arctan(\beta_2 / \beta_1) \quad (2)$$

This general model was adapted (see Supplement 2 at www.int-res.com/articles/suppl/m515p239_supp/) to the particularities of each of the 6 variables of interest (i.e. SST, pR, feeding index, distance travelled, home range and catchability).

For SST, the phase of its seasonal cycle was estimated from Eq. (1) but assuming a normally distributed error term plus a first-order autocorrelation term (AR1):

$$T_i = S_i + \rho(T_{i-1} - S_{i-1}) + \varepsilon_i \quad (3)$$

where T_i and T_{i-1} are the temperatures at the days i and $i-1$, ρ is the AR1 coefficient, and ε_i represents a random sample from a normal variate with zero mean.

The spawning probability, i.e. the probability that a given female i belonged to the spawning population at the specific date it was sampled (pS_i), depends not only on the seasonal dependence of the spawning probability (pR_i , which is the variable of interest) but also on the probability that this female was actually mature (pM_i). The challenge here is to estimate the phase of the seasonal cycle of pR (a hidden variable) from the GSI values (currently observed data). Thus, a hierarchical model was used. First, GSI values were

assumed to come from 1 of 2 possible gamma distributions. The parameters of each gamma distribution (*shape_i* and *rate_i*; Supplement 2) can take 1 of only 2 possible values: (1) low-GSI state would correspond to immature females and to mature females outside the spawning season and (2) high-GSI state would correspond to mature females at the spawning season. The value pS_i is the probability that a female was in a reproductive state given its GSI value. Second, pS_i is given by the product of the seasonal dependence of the spawning probability (pR_i) and the probability of being mature (pM_i). Since pR_i was assumed to depend on seasonality, its logit has been modeled using Eq. (1):

$$\text{Logit}(pR_i) = S_i \quad (4)$$

In contrast, pM_i depends on the fish size and fish colour pattern (plain or spotted) and has been estimated from the parameters of the maturity ogive of the total population (Villegas-Ríos et al. 2013a).

For the feeding index, the *F*-values estimated for each sampling date were fitted to the sinusoidal function defined in Eq. (1), assuming *F* to have a gamma distribution. As fish are not randomly sampled, but some of them come from the same haul, haul (i.e. sample) was considered to be a random factor (Supplement 2).

In the case of the home range size and the distance travelled for each 10 d period, the nature of the data imposed a more complex model. First, the observed distance *D* at the time period *i* for the fish *j* (D_{ij}) was modeled as follows:

$$D_{ij} = S_{ij} + \rho(D_{ij-1} - S_{ij-1}) + \varepsilon_i \quad (5)$$

where the second term ($\rho(D_{ij-1} - S_{ij-1}) + \varepsilon_i$) represents an AR1 term (between the successive observations from the same individual), ε_i represents a random sample from a normal variate with zero mean, and S_{ij} is given by the following relation:

$$S_{ij} = \alpha_0 + \alpha_j + \beta_1 \cos(2\pi d_i / 365) + \beta_2 \sin(2\pi d_i / 365) + \beta_3 TL_j \quad (6)$$

Note that Eq. (6) was modified in 2 ways in relation to Eq. (1). First, the size of the fish (TL_j , in cm) was also considered as a new fixed covariate to account for the potential size effect on the spatial ecology of the fish, as suggested by the raw data (Fig. 2) and previous studies (Villegas-Ríos et al. 2013b). Second, the observations from the same fish were structured as a random factor; thus, their mean (α_j , with α_0 being the grand mean) was allowed to vary following a normal distribution.

Finally, to describe seasonality in the catchability of *L. bergylta*, the observed catch (number of fish

accumulated by month) of the month *i* was assumed to come from a Poisson distribution whose mean is given by the product of catchability, q_i , and fish abundance as estimated from the fishery independent survey (Pita 2011). Fish abundance (count data) is assumed to have a Poisson distribution, but the expected mean of this distribution is assumed to have a gamma distribution with the parameters estimated from the empirical data (priors) provided by Pita (2011). Catchability is assumed to follow a sigmoidal curve, and hence, its logit was fitted to Eq. (1) modified to take into account the fishing effort ($EFFORT_i$, i.e. sum of all gillnet panels for each month multiplied by the duration of the corresponding haul in hours):

$$\text{Logit}(q_i) = \log(EFFORT_i) + \alpha + \beta_1 \cos(2\pi d_i / 365) + \beta_2 \sin(2\pi d_i / 365) \quad (7)$$

The parameters of these 6 models were estimated using a Bayesian approach, which accommodates the complexities of hierarchical models and allows combining the observed data with additional information (Clark 2007). The existence of an identifiable sinusoidal pattern was evaluated based on 95 % Bayesian credibility intervals (BCI) of β_1 and β_2 . A sinusoidal pattern was assumed when either β_1 or β_2 were different from zero, i.e. their 95 % BCI did not include zero. Otherwise, a sinusoidal pattern was not assumed. When a seasonal pattern was identified, the 95 % BCI of the phase was used to compare the match-mismatch (i.e. the degree of overlap) between the seasonality of the 6 variables investigated. All the models were fitted using the Bayesian machinery implemented in JAGS (<http://mcmc-jags.sourceforge.net/>) and using the *R2jags* library (Su & Yajima 2011) in R (R Development Core Team 2011). Flat, uninformative priors were used in all cases, except the case of seasonal averaged fish abundance which used priors from Pita (2011) as mentioned above. Conventional tools were used to assess the proper mixing of the Markov chain Monte Carlo chains run in each analysis, the convergence of the algorithm and the lack of autocorrelation by adjusting the burning period, thinning interval, the number of chains and the valid sample size.

RESULTS

SST ranged between 12.2°C and 20.5°C, and as expected, it followed a sinusoidal pattern (Table 3). Predictions for a year period revealed a maximum value (17.2°C) in summer (3 August) and a minimum

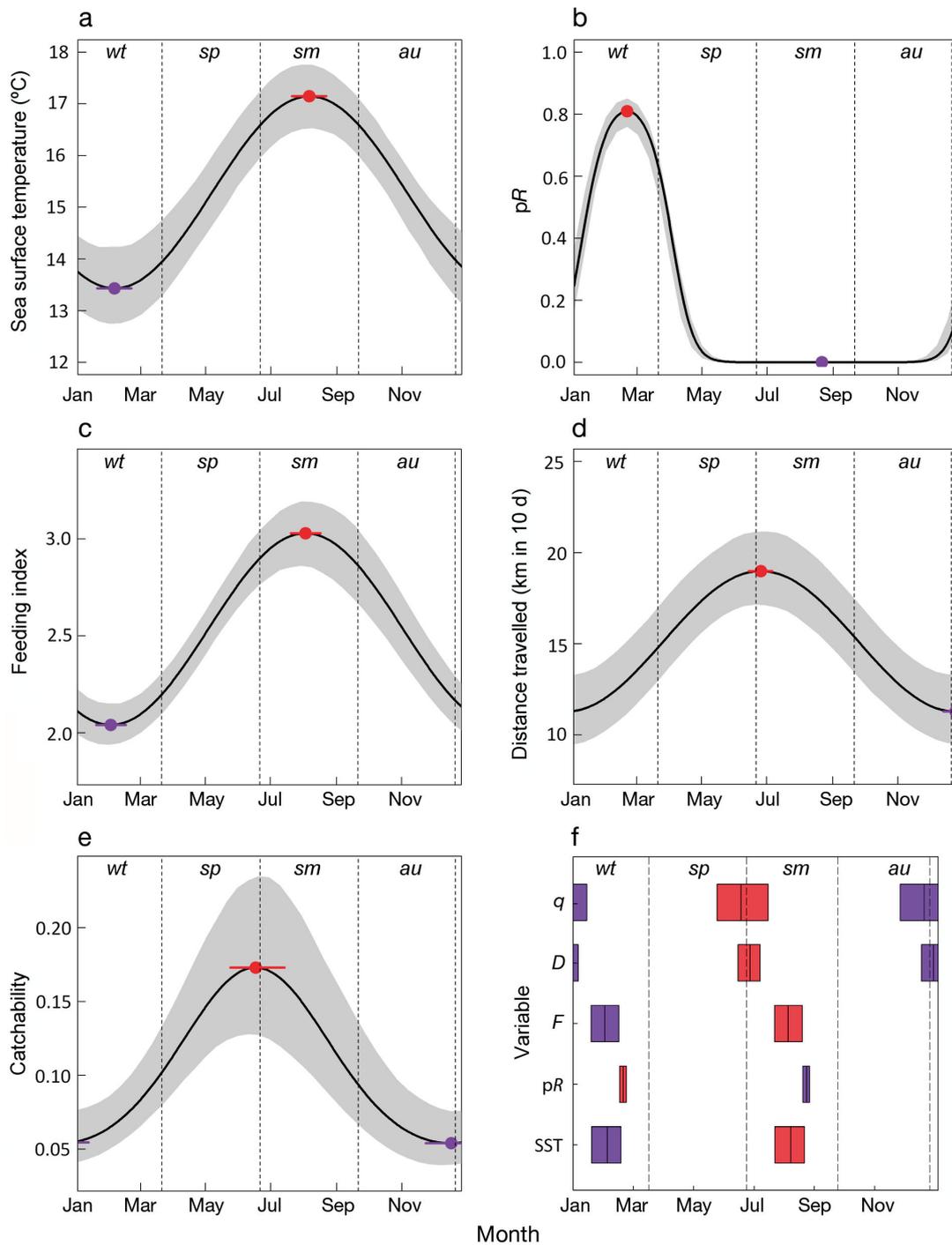


Fig. 3. Model predictions for (a) sea surface temperature (SST), (b) the seasonal dependence of the spawning probability (pR), (c) feeding index (F), (d) distance travelled (D) and (e) catchability (q) of *Labrus bergylta* throughout the year. Grey shading: 95% Bayesian credibility intervals for the predictions. Maximum (red) and minimum (violet) predicted values of each variable are represented with a coloured dot and their credibility interval as a coloured line. Dashed vertical lines: limits between seasons (wt: winter, sp: spring, sm: summer, au: autumn). Maximum and minimum values of each sinusoid are presented together in panel (f)

values (13.5°C) in winter (2 February), with a mean value of 15.3°C (Fig. 3a). The pR followed a sinusoidal pattern too (Table 1). The model predicted a maximum value (0.81) in winter (19 February) and a

minimum value in summer (20 August), but it was virtually zero from May to November (Fig. 3b). A sinusoidal variation over the year was also obtained for the feeding index (Table 3), whose raw values

ranged between 0.32 and 7.81. Modelled feeding index (Fig. 3c) peaked (3.03) in summer (2 August), revealing higher feeding intensity in this season, and decreased until minimum values (2.04) in winter (1 February).

The variation of the home-range size greatly differed among individuals and along the year, ranging between 0.01 km² and 0.21 km². However, the model did not detect a significant sinusoidal pattern for this variable, i.e. both β_1 and β_2 BCI included zero (Table 3). Distance travelled in 10 d periods ranged between 0.62 km and 36.48 km. In this case, the model resulted in a β_1 coefficient different from zero and a β_2 coefficient narrowly including zero (Table 3), therefore assuming a significant sinusoidal pattern. This sinusoidal pattern was, however, dependent on fish size ($\beta_3 \neq 0$; Table 3), with larger distances travelled for smaller fish all over the year, as evidenced by the negative β_3 value. Model predictions for a mean-sized individual (34.7 cm) revealed maximum values (19.03 km) in summer (25 June) and minimum values (11.37 km) in winter (24 December; Fig. 3d). CPUE of *Labrus bergylta* greatly varied among deployments, ranging from 0 (no catches; n = 231) to 0.33 fish gillnet panel⁻¹ h⁻¹. Catchability followed a sinusoidal pattern throughout the year (Table 3, Fig. 3e) with maximum values (0.17) predicted in summer (17 June) and minimum values (0.05) predicted in winter (17 December).

There was a large overlap between the phase BCI of the SST and the feeding index (early August; Fig. 3f) and between distance travelled and catchability (late June; Fig. 3f). The pR was not in phase with any of the other variables analyzed, but it minimized in mid-August, and in general, low probabilities were obtained for the period when the other variables maximized, i.e. June to September. In consequence, the minimum values of SST, the lowest feeding intensity and the maximum values of the pR (the antiphase) overlapped in January to February (Fig. 3f). The distance travelled and the catchability were at the lowest level in late autumn to early winter, a month before the peak of pR. Similarly, there was a lag of 38 d between the maximums of the feeding index and distance travelled and of 54 d in the case of the pR and the distance travelled.

DISCUSSION

This study integrated data from acoustic telemetry, biological sampling, fisheries catches and envi-

Table 3. Summary statistics for the population Bayesian means of the sinusoid patterns for each variable analyzed. For each estimated parameter, the median and the lower and upper 2.5 percentiles of the posterior distribution are shown. pR: seasonal dependence of the spawning probability

Parameters	Bayesian credibility intervals		
	2.5%	50%	97.5%
Sea surface temperature			
α	14.89	15.31	15.70
β_1	-2.02	-1.55	-1.02
β_2	-1.47	-1.01	-0.52
ϕ	200.8	216.5	230.2
pR			
α	-7.43	-5.94	-4.85
β_1	4.03	4.83	5.94
β_2	4.53	5.59	6.98
ϕ^a	228.7	232.4	235.5
Feeding index			
α	2.44	2.53	2.62
β_1	-0.53	-0.42	-0.32
β_2	-0.39	-0.26	-0.13
ϕ	200.4	214.0	228.0
Distance travelled			
α	19.47	28.45	37.62
β_1	-4.57	-3.79	-2.90
β_2	-0.06	0.68	1.51
β_3	-0.64	-0.38	-0.12
ϕ	164.2	176.0	186.0
Home range			
α	-1890.96	20.19	1816.95
β_1	-0.01	0.00	0.01
β_2	-0.02	-0.01	0.01
β_3	-1152.05	-19.60	649.68
Catchability			
α	-10.07	-9.87	-9.65
β_1	-0.91	-0.63	-0.33
β_2	-0.12	0.17	0.43
ϕ	143.2	167.0	194.0

^aTo allow a better comparison of the results, we show the phase plus (365/2), i.e the antiphase

ronmental time series to gain insight into the relationship between fish activity and catchability as well as drivers influencing activity. We hypothesized that the seasonal changes in catchability should be driven by a change in fish behavior (by increasing the probability of encounter between fish and fishers) mediated by shifts between feeding and reproductive behavior, which are ultimately determined by the life-history strategy of the species. These hypotheses were tested on *Labrus bergylta*, a sedentary fish species locally harvested by a gillnet fishery. We used very diverse datasets with different temporal and spatial coverage. This prevented us from including interannual variation in our analyses, which should be taken

into account in future studies. However, our results support our *a priori* hypotheses.

We found a good temporal overlap between SST and the state of the fish (reproductive vs. feeding). At the seasonal scale, it is expected that the fish life-history strategy drives the connection between environmental cues, physiological state and behavior. Fish species have evolved to maximize survival by synchronizing their offspring production and development with the best environmental conditions and food availability (Cushing 1969, Varpe et al. 2009, Lowerre-Barbieri et al. 2011). Therefore, we argue that the seasonal alternation between the feeding and reproductive periods in *L. bergylta* is ultimately determined by its life-history strategy (capital breeding) and the seasonal variation in the environmental cues. First, increased activity during the summer might be related to intensified feeding to recover from the previous spawning effort in winter and to store energy for the next reproductive season (Villegas-Ríos et al. 2014). Second, the reproductive behavior of the species favors reduced movement in winter, when large territorial males court and mate with a group of females during the spawning season (Sjölander et al. 1972). As the social ties relax after spawning, greater mobility is expected, and this is what was observed in this study.

L. bergylta increased its activity by ~67% from winter to summer, when average SST increased from 13.5°C to 17.2°C. The relationship between fish activity and sea temperature is widely recognized both in wild and captive animals (e.g. Claireaux et al. 1995, Ovidio et al. 2002, Topping et al. 2006). Our results adhere to the general pattern of increased activity with increased temperature. However, they represent a novelty to the field because our results are derived from an uninterrupted measurement of fish behavior in the wild during a whole year. Although we found increased activity with the summer season and warmer temperatures, we did not detect a seasonal pattern in home range size. The home range behavior has a complex nature, and many environmental and biological factors can influence it (Börger et al. 2008). In essence, home ranges link the movement of animals to the distribution of the resources necessary for survival and reproduction (Börger et al. 2008), which results in the existence of a whole diversity of strategies regarding home range size and exploratory behavior. The present study suggests that the resources available in the home range of the *L. bergylta* individuals are enough to satisfy their metabolic and physiological demands regardless of their individual state (reproduction vs. feeding), with no

need to explore new areas on a seasonal basis. Keeping an invariable home range throughout the year has recognized advantages, like improved feeding efficiency and reduced risk of predation due to increased familiarity and experience with the space used (Eristhee & Oxenford 2001, Ovidio et al. 2002).

Our results showed a seasonal pattern in activity levels, which was related to the prevalence of feeding and reproductive behaviors. Therefore, the life-history strategy is likely to be a key determinant of the variation of the catchability in *L. bergylta*. However, different results should be expected under alternative life-history strategies. For example, capital breeders travelling long distances from feeding to spawning grounds (e.g. cod; Hutchings & Myers 1994) would show an increase in activity in relation to the shift from one state (feeding) to another (spawning), i.e. the migration itself. Contrastingly, income breeders use concurrent energy input to defray the costs of reproduction (Ganias 2013, McBride et al. 2013), and feeding-related behavior would likely be maintained year round. Therefore, no seasonality in the feeding related activity would be expected in these species. The reproductive strategy of other species implies increased movements and activity during the spawning season. This is the case of many species that form resident spawning aggregations, exhibiting daily migrations to spawning sites (Lowerre-Barbieri et al. 2013, 2014). Similar to activity, the home range of other species following alternative life-history strategies may vary seasonally due to, for example, temperature changes, social interactions or reproductive migrations or aggregations (e.g. Bradbury et al. 1995, Weller & Winter 2001, Topping et al. 2006).

Theory predicts a direct relationship between activity levels and catchability. The basis of this prediction is that more active fish have a higher probability to encounter the passive fishing gear and therefore to be trapped in it (Rudstam et al. 1984, Kallayil et al. 2003). In those situations, q is often driven by encounter rates between the fish and the gear (Rudstam et al. 1984, Biro & Post 2008) as much or more than body size, and fish behavior will be the primary determinant of catch per unit effort (Heino & Godo 2002, Biro & Post 2008, Nannini et al. 2011, Olsen et al. 2012). Similarly, catchability in active gears is influenced by fish availability, density variation, temporal changes in distribution at annual, seasonal or diel scales and by changes in fish activity. However, the fish behavior of avoidance of active gears introduces an additional factor that complicates the cause-effect analysis (Handegard et al.

2003). In the case of *L. bergylta*, one would expect that because fish activity showed a seasonal nature, catchability should also display a seasonal pattern, after accounting for variation in abundance (Rudstam et al. 1984). The complete overlap between the sinusoids of fish activity and catchability provided empirical evidence to this prediction. Recently, Alós et al. (2012) demonstrated that fishing with passive gears (e.g. angling, traps or gillnets) consistently selected for high-activity phenotypes but not necessarily the individuals with the larger home ranges, which is also fully consistent with our empirical findings. Our results are in line with previous reports showing the relationship between fish behavior and catchability in both captive and wild fish. For example, Olsen et al. (2012) found that acoustically tagged *Gadus morhua* individuals with a strong diel vertical migration (i.e. more active) had a higher risk of being captured in the fishery compared to fish that stayed in deeper water in the Skagerrak coast in Norway. Similar results were obtained in experimental conditions with *Oncorhynchus mykiss* (Biro & Post 2008). However, none of these works provided empirical evidence of the relationship between environmental cues, physiological state, fish behavior and catchability. In addition, the relationship between behavior and catchability has been demonstrated to affect yield sustainability (Uusi-Heikkilä et al. 2008). Fishing highly active phenotypes may lead to fisheries-induced evolution if behavioral traits are determined, at least in part, genetically (Uusi-Heikkilä et al. 2008). Moreover, through pace of life syndromes correlations (i.e. correlations between behavioral, physiological and life-history traits; Réale et al. 2010), fishing on active fish may reduce the productivity of the resources (Biro & Stamps 2008).

Traditionally, stock assessment models assume constant catchability (Arreguín-Sánchez 1996, Stoner 2004) or that catchability varies with changes in fish abundance, thus requiring a non-linear model of catchability, such as a power curve (Pierce & Tomcko 2003). Our results show that catchability can display a strong seasonal component associated with activity in a sedentary fish, and this should be considered in future stock-assessment models of *L. bergylta* (for which there is not currently a stock assessment) and other species (Wilberg et al. 2009). Ignoring this variability is likely to bias the results and lead to flawed management decisions. In addition, it will impact the correct interpretation of fish abundance indexes (Hancock et al. 2000). Although a number of attempts have been performed to incorporate time-varying catchability into stock assessments (Porch 1999, Mar-

chal et al. 2003, Wilberg & Bence 2006), most models still perform poorly when catchability has a trend over time. Stock assessments and resulting fishery management decisions are highly sensitive to estimates of catchability and often produce unrealistic estimates of catchability (Arreguín-Sánchez 1996, Patterson et al. 2001, Wilberg & Bence 2006). Moreover, seasonal variations in catchability strongly affect performance of scientific surveys and the design of fisheries monitoring (Methot 2009, Thorson et al. 2013), i.e. the sources to estimate stock abundance in stock assessment models. Not considering time-varying catchability may lead to severely biased stock estimates which may produce overfishing and even stock collapse (Walters & Maguire 1996, Wilberg et al. 2009). Therefore, it is important to conduct sensitivity analyses to evaluate the impact that assumptions regarding catchability together with other model parameters can have on stock assessment results (Deroba et al. 2014).

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