



Consequences of trait-selective fisheries on population reproductive potential: An experimental approach

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ABSTRACT

The vulnerability of fish to fishing depends on a range of life-history (e.g. growth; reproduction), behavioural (e.g. boldness) and physiological (e.g. metabolic rates) traits which are usually correlated with reproductive success. Therefore, between-fish differences in catchability may be indirectly affecting the reproductive potential at the population level by removing certain phenotypes. The present study aims to test this hypothesis by assessing the relationship between vulnerability-to-angling and reproductive potential. We first scored the vulnerability-to-angling of a set of *Serranus scriba* adult individuals ($n = 78$), a species targeted by recreational fisheries, using intensive multi-event tests. The fish were then divided into three categories: high, medium and low vulnerability. Fish differing only in their vulnerability degree (i.e. the same average size and culture conditions) were kept in tanks ($n = 6$; two tanks per category). We monitored the tanks throughout a full spawning season to assess differences in seasonal distribution of spawning, total egg production, egg viability and egg quality. Fish with different vulnerability showed no significant differences in egg production (in terms of spawning seasonality and total eggs released) nor on egg viability compared to vulnerable fish. However, low vulnerability fish produced eggs with bigger egg yolk compared to high vulnerability fish but only toward the end of the fishing season. We interpret this difference as part of a portfolio effect in terms of behaviour and reproductive success, i.e., in unexploited populations, low vulnerability fish may contribute little to year class strength in typical years but act as a buffer, if a disturbance affects reproductive success early in the season. Moreover, although our work is based on a captivity experiment, the results are consistent with the hypothesis that harvested populations may compensate for the harvested biomass by investing more energy per fish in reproduction.

1. Introduction

Vulnerability to fishing, i.e., the probability of being caught by a specific fishing gear, defines the phenotype on which fisheries selection acts (Uusi-Heikkilä et al., 2008). Between-individual differences in vulnerability affect the population-level catchability, which is a key parameter for stock assessment and fisheries management (Arreguin-Sánchez, 1996). Vulnerability is, however, a complex feature that results from the combined effects of a range of correlated physiological, behavioural, morphological and life-history traits (Uusi-Heikkilä et al.,

2008). Moreover, vulnerability may depend on physiological state and ecological conditions (e.g. temperature, light, dissolved oxygen) (Lennox et al., 2017). Therefore, quantifying vulnerability of fish to angling is challenging because it requires an integrated understanding of fish behaviour, physiology, morphology, cognition, social context, abiotic environment and fishery specificities (Lennox et al., 2017). Because of this, Cox and Walters, 2002 and Walters and Martell, 2004 conceptualized the idea of vulnerability following the classical foraging arena theory. According to this concept, the fish in a population belong to either a vulnerable or a non-vulnerable pool, but the membership of a

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given fish and the fraction of vulnerable fish are changing at a certain rate. Comprehension of the proportion of vulnerable and non-vulnerable fish is a fundamental issue to understand the dynamics of the population and it should be accounted for when managing exploited species (Ahrens et al., 2012).

Size-dependent vulnerability of fish to fishing is a well-known case in which the existence of a link between vulnerability and reproductive output (e.g., quantity or quality of eggs) will affect population fitness and, thus, population dynamics (Uusi-Heikkilä, 2020). Large-bodied individuals are preferentially captured and removed, and such positively size-biased exploitation leads to juvenescence of the stock. It is well-documented in many species that big, old, fat, fecund females produce a greater number of eggs (Barneche et al., 2018; Beldade et al., 2012; Hixon et al., 2014), thus, a decrease of the number of large, and possibly vulnerable fish, is predicted to reduce the total number of eggs produced at the population level. This vulnerability bias has relevant implications for the sustainability of wild stocks (Jorgensen et al., 2007; Laugen et al., 2014; Palkovacs, 2011). Moreover, it has been suggested that at the same body size, non-vulnerable fish from highly exploited populations could invest more energy into reproduction than vulnerable fish from no-take marine protected areas (Alós et al., 2014). The evolutionary foundation for this hypothesis is the trade-off between investing more energy in growth and experiencing higher mortality risk or investing more energy in reproduction and experiencing a longer lifespan. However, the relative contribution of vulnerable versus non-vulnerable fish to egg production has not yet been studied. According to the pace-of-life syndrome (POLS) hypothesis (Réale et al., 2010), fish that are more active and more vulnerable will also have higher reproductive output, whereas less vulnerable fish, which have lower mortality, might present lower reproductive output. Nevertheless, it might be possible that when non-vulnerable fish are also those that are investing more energy in reproduction, the amount of eggs per biomass unit produced by non-vulnerable fish could at least partially compensate the losses of reproductive output related with harvesting large and vulnerable fish. Given that vulnerability is partially heritable ($h^2 = 0.14$; Dochtermann et al., 2015; Kortet et al., 2014; Philipp et al., 2009), it may be linked to other traits which impact reproductive success such as relative fecundity or egg quality.

Behaviour is one of the mechanisms proposed for linking vulnerability and reproductive output. Recently, empirical evidence linked certain behavioural phenotypes with fish vulnerability (Alós et al., 2012; Diaz Pauli and Sih, 2017). Bold and more explorative fish have been related to the odds of being caught by passive fishing gears, such as angling (Härkönen et al., 2014). Aggressive fish may be also more likely to be fished (Biro and Post, 2008). Those bold, aggressive fish seem to display higher metabolic rates, thus, they must forage more actively to acquire the food needed for fuel those increased metabolic needs, and this increased activity makes them more vulnerable (Alós et al., 2012; Stamps, 2007).

However, in spite of all the above empirical background and its theoretical and applied relevance, direct empirical evidences linking vulnerability to angling and reproductive potential are still scarce. The objective of this study is to experimentally assess the relationship between vulnerability to angling and reproductive potential in terms of quantify egg production and quality in the Painted comber (*Serranus scriba*), a simultaneous hermaphrodite fish species targeted by recreational fisheries.

2. Materials and methods

The *Serranus scriba* was selected as model species because it is a common target species of recreational fisheries and it is widely distributed throughout the Mediterranean Sea (Morales-Nin et al., 2005). The spawning season of this species ranges from May to August (late spring to late summer) in the Balearic Islands (Alonso-Fernández et al., 2011). A total of 78 *S. scriba* individuals were captured along the south coast of

Mallorca (Spain) between 2016 and 2017, using different fishing gears (i.e. hook and a small trawl) in order to mitigate the potential bias of passive fishing gears towards vulnerable fish. *S. scriba* is a simultaneous hermaphrodite fish species and the 50 % of the population reach sexual maturity at 9.3 cm Total Length (Zorica et al., 2006), which is below the length of the sampled fish (Table 1). Once captured, all individuals were transported to the experimental facilities (Laboratory of Marine Research and Aquaculture, LIMIA, in Port d'Andratx, Mallorca, Spain), where they were kept in quarantine in 10,000 L circular tanks, with an open flow seawater system, provided with mechanical filters, UV sterilisation and compressed air supply. The photoperiod was set on a 10:14 h light/dark cycle and water quality was checked daily. Temperature (Mean \pm SD, Min - Max) was 16.53 ± 0.83 , 14.7 – 18.9 °C during the experiment#1 and 21.15 ± 2.92 , 16 – 27 °C during the experiment#2, salinity was 38 ppm and dissolved oxygen was kept close to saturation by aeration through diffusion stones. While the fish remain on quarantine, they were fed *ad-libitum* with shrimp before being distributed in tanks for fish vulnerability experiment (#1) and spawning experiment (#2).

2.1. Experiment#1: scoring vulnerability to angling

A first experiment was carried out from January to February 2018 in order to classify each fish according to its vulnerability to angling. The 78 fish were externally tagged with T-bar tags with a combination of three different colours for a quick visual recognition of each individual. Then, tagged fish were randomly distributed in six circular tanks of 1000 L (13 fish in each tank), which had concrete bricks with openings within them to provide refuge, as well as several plastic strips mimicking seagrass, distributed throughout the tank. The experiment lasted 3 weeks, during which 12 vulnerability tests were performed every week (four tests per day and three days per week). The resting interval between tests within the same day was 10 min. Each vulnerability test consisted on deploying for 10 min a monofilament fishing line with four baited size 7 J-hooks in the centre of the tank with a stationary slip bobber. The barb of the hooks was manipulated to prevent any hooking damage. All the fish in the tank could note the bait during the test, which eliminates any potential experimental noise related with the encounter process (Lennox et al., 2017). The bait used was a piece of shrimp, which is the commonly used bait by recreational anglers targeting *S. scriba* (Alós et al., 2009), and it was bound with Lycra® making it impossible to be detached from the hook. An underwater camera placed on top of the tank was used to record fish behaviour and quantify: i) the number of bites per individual, and ii) the latency time of each individual (i.e., the time to bite the bait for the first time). The fish were randomly re-distributed among tanks every week in order to provide new social relationships and avoid hierarchical dominances, which might affect the measured behavioural parameters.

Regarding the statistical analysis, the objective was to disentangle fish specific effects (i.e., the fish vulnerability score) from any other potentially confounding effect. Accordingly, the counted number of bites of the fish i (13 fish per tank), the week w (3 weeks), the day d (3 days per week), the tank k (6 tanks) and the test t (4 test per day), *Count*.

Table 1

Summary of the mean, standard deviation (SD), minimum and maximum standard length (SL, cm) of *S. scriba* from different experimental tanks and vulnerability groups. Measurement made between the end of experiment 1 and the beginning of experiment 2.

Group	Tank	N	Mean SL (cm)	SD	Min SL	Max SL
High Vulnerable	1	13	14.35	1.41	12.2	16.5
	2	13	14.27	1.05	12.7	15.9
	3	13	13.93	1.26	11.7	15.6
Medium Vulnerable	4	13	13.7	1.35	11.5	15.8
	5	13	14.16	0.99	12.1	15.8
Low Vulnerable	6	12	14.01	1.24	12.3	15.8

$Bite_{i,w,d,k,t}$ (2808 observations) was assumed to be Poisson distributed around a mean value given by (\exp denotes the exponential function, which ensures positiveness):

$$Count.Bite_{i,w,d,k,t} \sim \text{Poisson}(\exp(\text{Intercept} + \text{Week}_w + \text{Day}_d + \text{Tank}_k + \text{Test}_t + \text{Fish}_i)) \quad (1)$$

The time of the first bite, ($F.Bite_{i,w,d,k,t}$ 2808 observations) was assumed to be normally distributed with mean and standard deviation given by:

$$\text{First.Bite}_{i,w,d,k,t} \sim \text{Normal}(\text{Intercept} + \text{Week}_w + \text{Day}_d + \text{Tank}_k + \text{Test}_t + \text{Fish}_i, \text{sd}) \quad (2)$$

Day ($n = 9$) and Test ($n = 216$) was considered fully random effects (i.e., normally distributed values with zero mean and a standard deviation to be estimated; $\sim N(0, \text{sd}_d)$ and $\sim N(0, \text{sd}_t)$ respectively). The other three effects result from combining a fixed part and a random part. In the case of Week ($n = 3$), the fixed part was the week order, with the aim of accounting for any putative learning effect. In the case of Tank ($n = 54$; 6 tanks \times 3 days \times 3 weeks), the fixed part was the tank temperature. Finally, in the case of Fish ($n = 78$ fish), the fixed part was the fish length (Table 1). In the latter case, the random part (i.e., normally distributed values with zero mean and a standard deviation to be estimated) defines the fish-specific vulnerability scores. All the putative explanatory variables (week order, temperature and fish length) were mean-centred to help with convergence.

In addition, the adjusted repeatability of time at the first bite (R) (Nakagawa and Schielzeth, 2010) was estimated for First.Bite . Repeatability is often used to justify the existence of behavioural types (Alós et al., 2017). For normally distributed variables, R is simply the quotient between the between-individual variance (the variance across random intercepts of individuals) and the sum of between-individual variance and residual variance (the variance associated with measurement error and phenotypic variability).

$$R = \text{fish scores variance} / (\text{fish scores variance} + \text{residual variance}) \quad (3)$$

The parameters of the two models (Eqs. 1 and 2) were estimated using a Bayesian approach (Gelman and Shirley, 2011). A Gamma distribution prior (scale = 0.01, rate = 0.01) were considered for the tolerance (1/variance) of all the random effects. A normal distribution prior (mean = 0 and $\text{sd} = 10^5$) was considered for Intercept in eq 1 and 2, and for the slopes of learning, temperature and fish length. Samples from the joint posterior distribution were obtained using JAGS (<http://mcmc-jags.sourceforge.net/> accessed 10 Oct 2019) (Plummer, 2015) and the R2jags package (Su and Yajima, 2015) from the R language and environment for statistical computing version 4.0.2, released 2020-06-22 (R Core Team, 2020). Three Monte Carlo Markov Chains (MCMC) were launched. The first 6000 iterations were discarded and only one out 10 of the remaining iterations were kept in order to prevent autocorrelation. Posteriors were inferred from 240,000 valid iterations after burning and thinning. MCMC convergence was assessed by visual inspection and using $Rhat$, the potential scale reduction factor (Gelman and Rubin, 1992). An R-script and the input data are provided as supplementary material to ensure reproducibility of the results (<https://doi.org/10.17632/xx9j5927ps.1>). Note that observations are right-censored for latency time (i.e., the test last 10 min). Uncertainty for latency time larger than 10 min was managed using the $dinterval$ distribution in JAGS.

2.2. Experiment#2: assessment of reproductive potential

A second experiment was then carried out to assess the reproductive potential of fish regarding the vulnerability scores obtained in experiment#1. To do that, fish were grouped into three categories according with the vulnerability score described above: High Vulnerability (HV), Medium Vulnerability (MV) and Low Vulnerability (LV). Two replicated groups of each category (13 fish per group) were distributed in the same

1000 L tanks described above (Table 1). Between-group differences in mean fish size were tested (ANOVA) and rejected to avoid any confounding effect of fish size on egg production (Table 1).

This second experiment lasted three months (from May to July 2018), during which the released eggs were daily collected from each tank using a net (mesh size 500 μm) attached at the water output (Pastor et al., 2015; Thorsen et al., 2003). The water renewal was in an open circuit, so the temperature in the tanks was close to the sea temperature outside. Fish were fed *ad-libitum* with shrimp every day. The collected eggs were transferred to a beaker and allowed to decant separating the fraction of fertilized (mainly floating) and unfertilized (mainly sinking) eggs. Then, the two layers were separated and the number of eggs in each layer counted in a 10 mL aliquot, in triplicate. Finally, three samples of eggs per tank were photographed, one day every week (30 eggs per sample, tank and day) with a camera-equipped stereomicroscope with the same magnification. We estimated the egg size and the egg yolk size to use them as a proxy of egg quality, although other parameters should not be ruled out when drawing conclusions related to fish spawning success (Reading et al., 2018). ImageJ2 (Rueden et al., 2017) was used to measure those egg parameters. Once the experiment was finished, the animals were sacrificed with a MS-222 overdose (Topic Popovic et al., 2012).

Regarding the statistical analysis, the observational model considered the four fractions of eggs counted in each one of the three replicated 10 mL samples ($i = 1-3$) from the same $\text{day} \times \text{tank}$ combination ($n = 810$; three 10 mL replicates \times 45 days \times 6 tanks). Four variables were recorded for each replicate: (1) the number of viable eggs in the floating fraction, (2) the number of non-viable eggs in the floating fraction, (3) the number of viable eggs in the non-floating fraction and (4) the number non-viable in the non-floating fraction. We separate the fractions (floating, non-floating) because they have a different viability. The actually observed count ($N_{i,\text{fraction}}$) of the four fractions was assumed to be Poisson distributed around the expected value for a given $\text{day} \times \text{tank}$ ($N.\text{hat}_{\text{day} \times \text{tank}, \text{fraction}}$):

$$N_{i,\text{fraction}} \sim \text{Poisson}(N.\text{hat}_{\text{day} \times \text{tank}, \text{fraction}}) \quad (4)$$

The expected counted eggs in 10 mL in each fraction are linked with the expected number of eggs produced per day in a given tank:

$$N.\text{hat}_{\text{day} \times \text{tank}}(\text{Alive} \cap \text{Floating}) = N.\text{total}_{\text{day} \times \text{tank}} * p.\text{float} * p.\text{alive}_{\text{day} \times \text{tank}} / (V_{\text{day} \times \text{tank}} / 10 \text{ mL}) \quad (5)$$

$$N.\text{hat}_{\text{day} \times \text{tank}}(\text{Dead} \cap \text{Floating}) = N.\text{total}_{\text{day} \times \text{tank}} * p.\text{float} * (1 - p.\text{alive}_{\text{day} \times \text{tank}}) / (V_{\text{day} \times \text{tank}} / 10 \text{ mL}) \quad (6)$$

$$N.\text{hat}_{\text{day} \times \text{tank}}(\text{Alive} \cap \text{Non-floating}) = N.\text{total}_{\text{day} \times \text{tank}} * (1 - p.\text{float}) * p.\text{alive}_{\text{day} \times \text{tank}} / (V_{\text{day} \times \text{tank}} / 10 \text{ mL}) \quad (7)$$

$$N.\text{hat}_{\text{day} \times \text{tank}}(\text{Dead} \cap \text{Non-floating}) = N.\text{total}_{\text{day} \times \text{tank}} * (1 - p.\text{float}) * (1 - p.\text{alive}_{\text{day} \times \text{tank}}) / (V_{\text{day} \times \text{tank}} / 10 \text{ mL}) \quad (8)$$

where $N.\text{total}_{\text{day} \times \text{tank}}$ is the expected total number of eggs in a given $\text{day} \times \text{tank}$, $V_{\text{day} \times \text{tank}}$ is the volume of the container where all the eggs accumulated in a given $\text{day} \times \text{tank}$ have been collected, $p.\text{float}$ is the probability that a given egg will float and $p.\text{alive}$ is the probability that a given egg is alive (i.e., fertilized). Note that $p.\text{float}$ and $p.\text{alive}$ are allowed to randomly vary at the $\text{tank} \times \text{day}$ level. Specifically, the (logit-transformed) of $p.\text{alive}$ and $p.\text{float}$ of a given $\text{tank} \times \text{day}$ is assumed to be normally distributed around the $\text{tank} \times \text{day}$ mean value, with a given standard deviation.

The expected total number of eggs in a given $\text{day} \times \text{tank}$ ($N.\text{total}_{\text{day} \times \text{tank}}$) was modelled as a function of temperature because preliminary plots strongly suggest that egg production may show a bell-shaped distribution (Fig. 2). Although it is possible that could be differences in the number of eggs between individuals within the same batch (Fuiman et al., 2005), reproduction needs to be done with all the fish together, making it difficult to obtain a quantity of eggs per individual.

Specifically, the (log-transformed) $N_{\text{total day} \times \text{tank}}$ were modelled as:

$$\log(N_{\text{total day} \times \text{tank}}) = h_{\text{tank}} e^{\frac{(\text{Temp}_{\text{day} \times \text{tank}} - \text{Temp}_{\text{optimal tank}})^2}{2 \text{tol}_{\text{tank}}^2}} \quad (9)$$

where $\text{Temp}_{\text{day} \times \text{tank}}$ is the temperature recorded at a given day and tank, $\text{Temp}_{\text{optimal tank}}$ is the estimated optimal temperature for a given tank (i.e., the temperature at which the number of eggs produced in a day reached the maximum value), tol_{tank} is the temperature tolerance of a given tank (i.e., the spread of the bell shaped distribution of the eggs produced per day) and h_{tank} is the maximum number of eggs produced in a day at the optimal temperature. Note that eq. 9 has been reparametrized according to Oksanen et al. (2001) and Oksanen and Minchin (2002). Note also that a first order autocorrelation term has been added to eq. 9 in order to deal with the potential non-independence of the measures, which were obtained at consecutive days. All those technical details are provided as supplementary material. Finally, differences in $\text{Temp}_{\text{optimal}}$, h and tol between the three vulnerability categories considered (i.e., pooling the two tanks holding fish groups with the same vulnerability score) was assessed *a posteriori* from the tank-level parameters.

The parameters of the integral model above (from Eqs. 4–9) given the observed data were estimated using a Bayesian approach. The first 3000 iterations were discarded and only one out of 10 of the remaining iterations were kept in order to prevent autocorrelation. Posteriors were inferred from 30,000 valid iterations after burning and thinning. MCMC convergence was assessed by visual inspection and using Rhat, the potential scale reduction factor. The input data and an R-script with the (non-informative) priors for each of the estimated parameters and other technical details of the model are provided as supplementary material (Follana-Berná and Palmer, 2021) to ensure reproducibility of the results.

Finally, a conventional (i.e., frequentist) analysis of covariance (ANCOVA) was also completed to assess the differences between vulnerability categories through different months (May, June and July) in the egg yolk diameter, as a proxy of egg quality, with the egg size as covariable. In addition, *Day* was considered a random factor nested in *Month* as random, and *Tank* was considered a random factor. The factor of the interaction between Month and Vulnerability was considered as fixed factors. The *anova* function from the stats package, which is part of R (R Core Team, 2020), was used to returned the results of a linear mixed-effects model. The function used in the linear mixed-effects model was the *lmer* from the lme4 (Bates et al., 2015) and the lmerTest (Kuznetsova et al., 2017) packages.

2.3. Ethical statement

All the procedures with fish were approved by the Ethical Committee of Animal Experimentation (CEE-UIB, Spain; Ref. 60/09/16) and carried out by trained and competent personal, in accordance with the European Directive (2010/63/UE) and Spanish Royal Decree (RD53/2013) to ensure good practices for animal care, health, and welfare.

3. Results

3.1. Experiment#1

The two behavioural variables: i) the number of bites, and ii) the first-bite latency time were used to determine individual fish score of vulnerability to angling. The fish scores obtained showed a gradient through all individuals and allowed to classify them into three vulnerability categories between the 33 quantile and the 66 quantile (low, medium and high vulnerability). The mean number of bites for HV fish was 1.32 ± 0.73 bites, 0.76 ± 0.29 bites for MV fish and 0.46 ± 0.22 bites for LV fish (Fig. 1A). For first-bite latency time (in seconds), the average of each group was 370.14 ± 57.54 s for HV fish, 443.64 ± 31.01

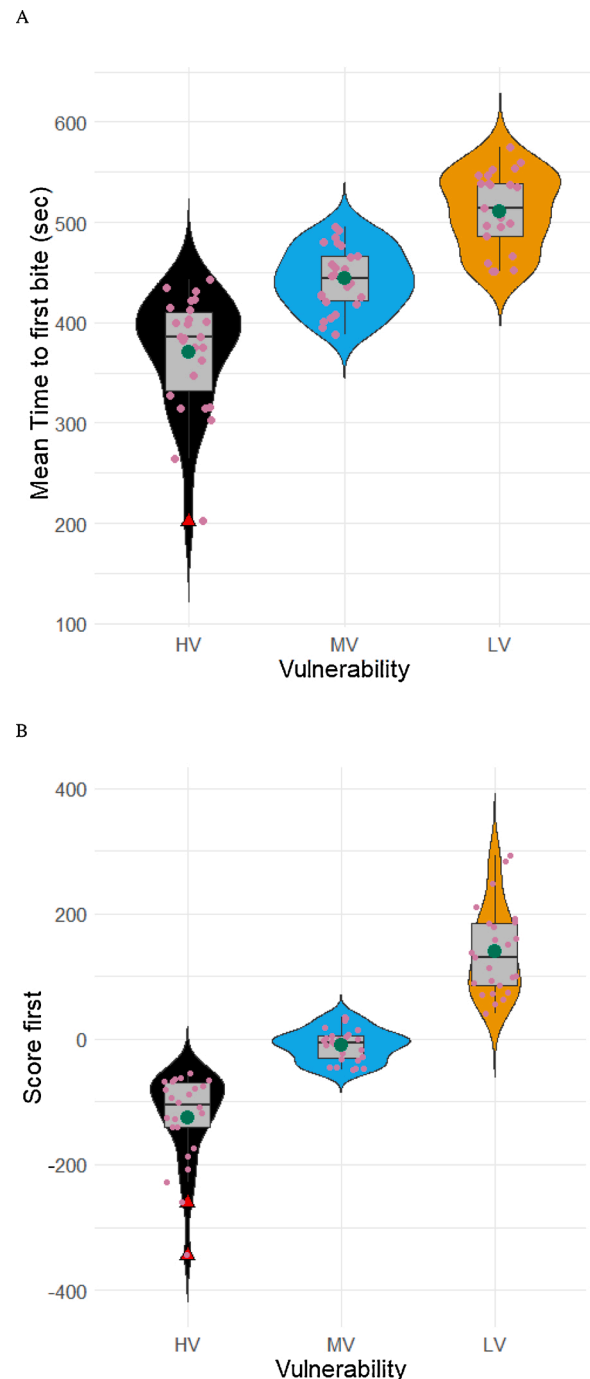


Fig. 1. A) Boxplot of the mean time for first-bite latency for the different vulnerability groups and B) boxplot of the first-bite latency score for the different vulnerability groups (HV-Black: High Vulnerability, MV-Blue: Medium Vulnerability, LV-Yellow: Low Vulnerability). Green dot is the mean. Pink dots are the data of every fish. Red triangles are outliers. Violin shadows represent the distribution of the data. The line in the middle of the box indicates the median; the upper and lower limits of the box represent the interquartile range and whiskers represent values at 1.5 times the interquartile range of the box.

s for MV fish and 511.12 ± 38.17 s for LV fish (Fig. 1B). The number of bites and first-bite latency time were negatively correlated (Pearson 95 % CI [-0.92, -0.81], p -value < 0.001). Accordingly, only first-bite latency time was used for further exploring the relationship between vulnerability and egg production because estimating repeatability is straightforward for normally distributed variables. The adjusted repeatability of the fish level vulnerability for the first-bite latency time

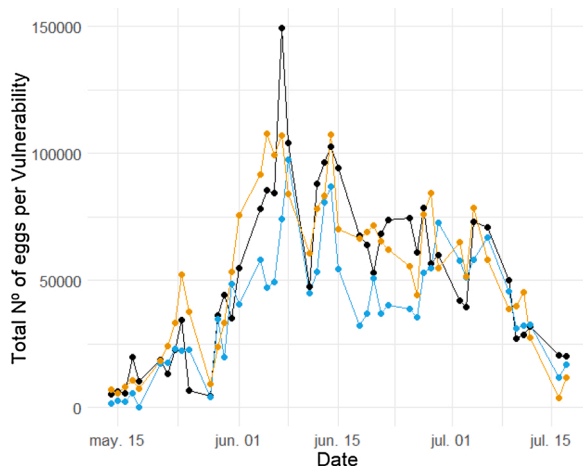


Fig. 2. Time series of observational egg production of vulnerability groups (Total n° of eggs per Vulnerability). HV: High Vulnerable (Black), MV: Medium Vulnerable (Blue) and LV: Low Vulnerable (Yellow).

scores was 0.099 (0.063 – 0.150 95 % Bayesian Credibility Interval, BCI). First-bite latency time was correlated neither with fish standard length before the experiment ($r^2 = 0.0014$; p-value = 0.74), fish standard length after the experiment ($r^2 = 0.0095$; p-value = 0.44), fish age ($r^2 = 0.0138$; p-value = 0.36) nor fish weight ($r^2 = 0.0106$; p-value = 0.42).

3.2. Experiment#2

The spawning period of *S. scriba* ranged from May 14th to July 17th. Thousands of eggs have been successfully produced in all the tanks, strongly suggesting that captivity itself was not a major confounding effect (Fig. 2). Seasonal differences in the spawning patterns seems to be unaffected by vulnerability to fishing (Fig. 2). Note that between-day variability in the same tank and between tank variability for the same treatment were large. Considering the full spawning period, the estimated total number of eggs produced per fish was not significantly different among groups of fish with different vulnerability categories. The total number of eggs per fish were 18079.01–71629.49 (95 % BCI) for HV, 13859.44–56593.42 for MV and 21570.10–85432.07 for LV (Fig. 3). Regarding viability (i.e., fraction of fertilized eggs), the median

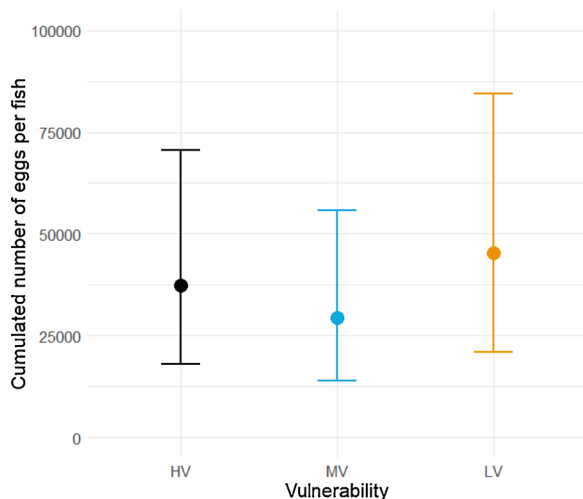


Fig. 3. The cumulated number of eggs per fish (Y-axis) with 95 % Bayesian credible intervals during all the reproductive season from the different vulnerability groups (HV-Black: High Vulnerability, MV-Blue: Medium Vulnerability, LV-Yellow: Low Vulnerability) (X-axis).

survival rate was higher and less variable toward the end of the spawning period, standing between 0.80 – 0.99 (Fig. 4). Since the experiment covered the whole spawning season, it has been possible to explore the temperature-dependence of the spawning pattern. The water temperature in the experimental tanks ranged from 16 to 27 °C. Between tank differences in the three parameters, describing the seasonal pattern of spawning (i.e., *Temp.optimal*, *h* and *tol*) were clearly not relevant. The optimal temperature for egg production of *S. scriba* (i.e. when the maximum number of eggs per day was reached) was 22.3 ± 1.2 °C (mean \pm SE) for HV fish (19.75–24.83 °C 95 % BCI), 22.2 ± 1.2 °C for MV fish (19.89–24.92 °C 95 % BCI) and 22.4 ± 1.2 °C for LV fish (19.61–24.60 °C 95 % BCI). The tolerance (i.e., spread of the bell shaped response of egg production) was smaller than 2 °C for all the fish groups, being 1.7 ± 0.2 °C for HV (1.34–2.19 °C 95 % BCI), 1.6 ± 0.3 °C for MV (1.27–2.20 °C 95 % BCI) and 1.7 ± 0.2 °C for LV (1.23–2.08 °C 95 % BCI). Finally, the number of eggs produced at the optimal temperature was $44,797 \pm 15,234$ eggs (24215.92–77657.42 eggs 95 % BCI) for HV; $55,335 \pm 17,814$ eggs (19515.41–65446.13 eggs 95 % BCI) for MV and $36,732 \pm 12,606$ eggs (29079.85–97192.95 eggs 95 % BCI) for LV.

Concerning the average of the egg yolk size per month, it was 0.097 ± 0.007 mm (mean \pm SE) in May, 0.090 ± 0.007 mm in June and 0.091 ± 0.006 mm in July for LV group. 0.095 ± 0.006 mm in May, 0.089 ± 0.007 mm in June and 0.089 ± 0.007 mm in July for MV. 0.096 ± 0.006 mm in May, 0.088 ± 0.007 mm in June and 0.087 ± 0.007 mm in July for HV (Fig. 5a). The interaction Month and Vulnerability group was significant (p-value < 0.001; Fig. 5b, Table 2), suggesting that egg quality was similar at the beginning of the spawning season, but that eggs from non-vulnerable fish became progressively better toward the end of the spawning season. The ANCOVA residuals were Normal distributed (p-value = 0.1169).

4. Discussion

Differences in vulnerability to fishing are neither related with the total number of eggs produced nor with the seasonal spawning pattern, at least for *S. scriba* in captivity. However, we found that the egg yolk size, which could be considered as a proxy of the viability and egg quality (Reading et al., 2018) although other parameters should not be ruled out when drawing conclusions related to fish spawning success (Brooks et al., 1997; Kjorsvik et al., 1990), was larger in the less vulnerable fish (LV) but only towards the end of the reproductive season. Other life history traits of *S. scriba* have already been empirically proven to be related with vulnerability (Alós et al., 2015), while this is the first experiment exploring the relationship between vulnerability on reproductive potential. Alós et al. (2015) demonstrated that recreational angling intensity was correlated with enhanced gear-avoidance behaviour in *S. scriba*. The strong pressure from angling in many water systems requires management approaches that recognize the potential evolutionary consequences of angling (Cooke et al., 2007). Uusi-Heikkilä et al. (2015) found that fish adapted to selective fishing pressure against larger sizes invested more in reproduction, reached a smaller adult body size, and were less explorative and bold. Additionally, individual differences in vulnerability may result from divergent life-history strategies. Previous studies suggest that recreational angling could reduce the abundance of *S. scriba* (Alós and Arlinghaus, 2013; Alós et al., 2015), favouring non-vulnerable fish and causing a shift in resource investment away from growth and towards reproduction, ultimately resulting in the downsizing of adult body length (Alós et al., 2014). More active, bold or risk-taking individuals might reproduce earlier (i.e. invest more heavily in resource acquisition and enhance reproduction, Campos-Candela et al., 2019) but at a cost of increasing mortality risk (Réale et al., 2010; Dammhahn et al. 2018; Royauté et al. 2018). The consequences that long-term fishing can have on the life history traits of the population have already been proven on fish growth (Biro and Post, 2008; Biro and Sampson, 2015) and reproductive investment and maturation (Alós et al., 2014; Sutter et al., 2012) which may affect population-level

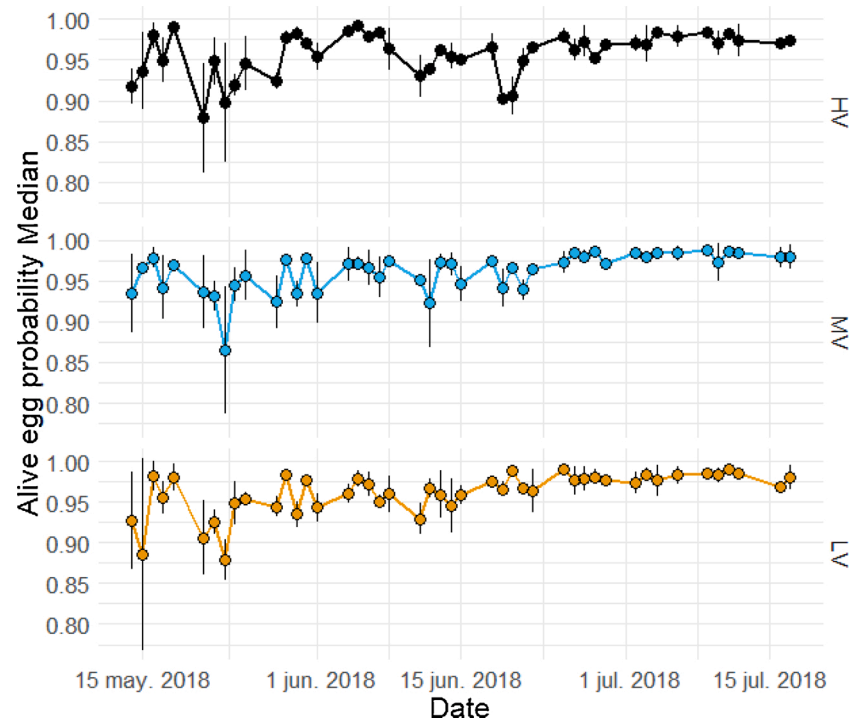


Fig. 4. Time series of survival ratio of all tanks per vulnerability groups. High Vulnerable (HV-Black), Medium Vulnerable (MV-Blue) and Low Vulnerable (LV-Yellow). Dots points are the median of the two vulnerability tanks of the same vulnerability group, the vertical lines are the \pm standard deviation.

variables. However, the results of previous studies have been inconsistent. In common carp, *Cyprinus carpio*, boldness has been found to be linked to angling vulnerability (Klefoth et al., 2017, 2013) and in largemouth bass *Micropterus salmoides* the trait “vulnerability to angling” positively correlates with aggression, intensity of parental care, and reproductive fitness (Cooke et al., 2007; Sutter et al., 2012). Conversely, in eurasian perch *Perca fluviatilis* boldness has not been found to be a driver of vulnerability (Vainikka et al., 2016) and in bluegill *Lepomis macrochirus* it has been negatively linked to angling vulnerability (Wilson et al., 2011). Furthermore, an artificial selection experiment on zebrafish *Danio rerio* found that even after simulated size-selective harvest, metabolic rate remained unchanged (Uusi-Heikkilä et al., 2015). In addition, bold individuals have been shown to take more risks, are more likely to become dominant, are more successful at foraging, and explore novel environments and disperse more than their shy counterparts (for a review see Ariyomo and Watt, 2012). Bolder males may be preferred by females, and aggression is often used to maintain dominance and, in general, dominance status influences reproductive success (Ariyomo and Watt, 2012). However, males that are too bold or too aggressive can reduce their reproductive success after considering their reduced life expectancy (Réale et al., 2009).

Assuming that vulnerability to fishing can be inherited (Philipp et al., 2009), empirical testing of the relationship between behavioural traits related with vulnerability and reproductive potential could help us understand the fate of some populations. The results reported here showed that similar amount of eggs with similar viability and within the same temperature range were produced, irrespective of the vulnerability degree to angling. Fish size can initially also affect vulnerability (Diaz Pauli et al., 2019; Klefoth et al., 2017), but no significant differences of fish mean size were observed between tanks throughout the 5 weeks of the experiment#1, suggesting that behaviour alone can be an important driver of vulnerability to angling despite size.

The present study, however, revealed a direct link between vulnerability and a proxy of egg quality: egg yolk size. The egg yolk size was significantly bigger in LV fish, which may translate into better larval

development (Bobe and Labbé, 2010). It is generally accepted that higher egg yolk reserves lead to larger-at-hatching progeny and higher chance of survival (Garrido et al., 2015; Roney et al., 2018). The vitelline reserves provide an important source of metabolic energy for embryonic and larval development, and therefore, are positively correlated with reproductive success (Bobe and Labbé, 2010). It is assumed that larger amounts of egg yolk allows larvae to feed earlier and grow faster, decreasing the probability of predation (Garrido et al., 2015). Mortality during the early stages is a major cause of the natural variations in the size and recruitment strength of marine fish populations (Garrido et al., 2015). In addition, fish larvae survival probability is closely linked to the larval size at hatching (Maddams and McCormick, 2012). This fact means that larger larvae at hatch have higher chances to survive. It must be noted that all fish in these experiments were reared and kept under the same environmental conditions and the same food availability (fish were feed *ad libitum*).

As expected, the seasonal spawning pattern reported here closely agrees with the seasonal pattern of the gonadosomatic index (GSI; gonad weight/body weight) at the population level (Alonso-Fernández et al., 2011). However, it should be noted that the egg yolk size was maximum at the beginning of the spawning season and continuously decreased across the season (Fig. 5) but the rate of viable eggs displayed the reverse pattern (Fig. 4). This apparently counter-intuitive result does not invalidate the link between larger egg yolk size and better egg quality or between larger egg yolk size and low vulnerable fish. Instead, this is a well-known trend in most fish that spawn in separate batches along a prolonged spawning season (Bagenal, 1971; Roney et al., 2018). This decoupling appears to be gradually corrected in *S. scribe* and toward the peak of the spawning season both, eggs viability is close to 100 % and vulnerability-related differences in egg yolk size became more and more apparent. It is also known that the seasonal reduction in egg size has been supposedly linked to the physiological effects from the maternal component (Trippel, 1998), as batch spawning may place a large physiological demand on spawning fish therefore depleting energy sources over the course of the spawning season (Izquierdo et al., 2001).

The intrinsic properties of the egg itself and the environment in

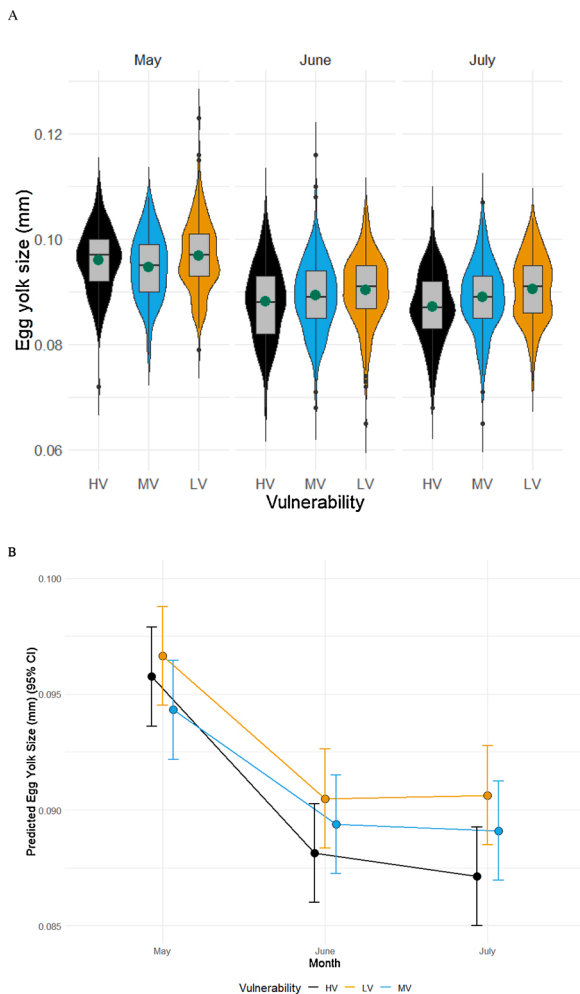


Fig. 5. Observational values of the egg yolk size (mm) of *Serranus scriba* during the whole study period per month (A) and the Predicted Coefficient intervals (95 %) in the different months (B) regarding fish vulnerability groups (HV-Black: High Vulnerability, MV-Blue: Medium Vulnerability, LV-Yellow: Low Vulnerability). Red dot is the mean. Black dots are outliers. Violin shadows represent the distribution of the data. The line in the middle of the box indicates the median; the upper and lower limits of the box represent the interquartile range and whiskers represent values at 1.5 times the interquartile range of the box.

Table 2
Results from the ANCOVA of the egg yolk size (mm) as dependent variables and egg size (mm, S egg) as covariable. Day is nested in Month (random) and Tank (random). Interaction between Month and Vulnerability are fixed effects.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
S egg	1	0.00020	0.00020	5.1399	0.024	*
Month	2	0.00102	0.00051	12.8949	0.002	**
Vulnerability	2	0.00163	0.00081	20.5935	0.019	*
Month*Vulnerability	4	0.00085	0.00021	5.3533	<0.001	***

which the egg is fertilized and subsequently incubated (Brooks et al., 1997) affects egg quality. In addition to the physiological components related to the oocyte development, other components that affect egg quality include the diet of the brood fish and the husbandry conditions (Bobe and Labbé, 2010; Brooks et al., 1997). Assuming a behavioural correlation syndrome (i.e. boldness, aggressiveness and exploration correlate with vulnerability; (Conrad et al., 2011) and being in similar condition of food availability, HV fish might use a larger proportion of energy budget on exploration, feeding competition, territorial defence

or other metabolic process related to this risk-taking behavioural trait. While LV fish individuals may be shy and could balance the energy towards different metabolic process such as egg quality. For instance, Diaz Pauli et al., 2019, showed that in medaka *Oryzias latipes*, size-selection (over ten generations) and resource abundance (over developmental time) led to changes in life history and behaviour. Low food availability led to higher willingness to feed and increased boldness (smaller freezing time) compared to high food availability, although the latter only happened in females. From our results, however, we cannot rule out that LV fish in natural conditions might obtain less food and hence energy than HV fish, and therefore, other processes can also explain the changes in egg quality reported in the present study.

Fishes with the greatest energy reserves typically spawn earlier than fishes at poor condition (Lowerre-Barbieri et al., 2011). The beginning of the spawning season could be a better time for egg survival and thus, it makes sense that HV fish would put their energy into better quality eggs at this time (Fig. 5). Although our result show that LV fish have a good quality in the egg too. But it is the diversity in the interaction between egg quality and reproductive timing which provides resilience to the population (i.e., a natural buffer). Presumably, in most years the greatest reproductive success occurs early in the season. However, weather conditions could occasionally change this dynamic and in those years, LV fish would have an advantage in reproductive success at the end of the spawning season because they have better egg quality at that time. But during most years, they may contribute relatively little to year class strength, i.e., the portfolio effect (Lowerre-Barbieri et al., 2017). Thus, although selecting HV fish did not affect total egg production it could have really significant effects on population productivity if the late spawning season is the temporal window which leads to the best offspring survival in an average year.

On the other hand, egg yolk size and egg size directly could affect buoyancy of the eggs and larvae (Ospina-Álvarez et al., 2012a; Petereit et al., 2014; Sundby, 1997). This is a critical life history feature that determines the vertical position of the early life stages in the water column and consequently their exposure to oceanographic processes that influence their transport and dispersal by ocean currents (Castro et al., 2019; Parada et al., 2003; Sundby and Kristiansen, 2015). Egg buoyancy and larval behaviour have been shown to be crucial dynamic parameters in biophysical transport and larval connectivity between spawning and nursery habitats (Blanco et al., 2019; Ospina-Álvarez et al., 2018, 2013, 2012b). The ontogenetic variability in the lipid drop/egg size ratio of LV fish highlights the necessity of including behavioural traits of spawners and physiological parameters of their progeny when estimating larval and population connectivity and reproductive success (Lowerre-Barbieri et al., 2017). This biological information is particularly important for obtaining a more realistic representation of connectivity patterns, which should guide an effective management based on spatial planning (Ospina-Álvarez et al., 2020).

In summary, any behaviourally selective fishing will enhance the survival probability of low vulnerability phenotypes by increasing the average levels of shyness as an evolutionary response (Alós et al., 2014, 2015). Accordingly, non-vulnerable individuals might act as offspring reservoirs in fish populations under artificial selection, as in the case of angling. When vulnerability is heritable, the outcome would be an evolutionary response. However, further research is needed to investigate the potential evolutionary changes on larval survival and development, as well as other changes of life-history trait of *S. scriba* related with recreational fishing. Fish behaviour plays a key role in determining and modulating the impact of fishing on wild populations (Pine et al., 2009), and the incorporation of the behavioural dimension on egg production and larval development should, therefore, improve the conservation and management measures of recreational fishing activities on coastal fish populations.

Authors' statement

Guillermo Follana-Berná, Miquel Palmer, Andrea Campos-Candela, Josep Alós and Pablo Arechavala-Lopez: Conceptualization, Methodology. Guillermo Follana-Berná: Investigation. Guillermo Follana-Berná and Miquel Palmer: Formal analysis. Guillermo Follana-Berná: Writing - Original Draft. Guillermo Follana-Berná, Miquel Palmer, Andrea Campos-Candela, Josep Alós, Andrés Ospina-Alvarez, Amalia Grau, Susan Lowerre-Barbieri and Pablo Arechavala-Lopez: Supervision, Writing - Review & Editing. Guillermo Follana-Berná: Data Curation.

Declaration of Competing Interest

The authors report no declarations of interest.

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