Selective exploitation of spatially structured coastal fish populations by recreational anglers may lead to evolutionary downsizing of adults

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ABSTRACT: When gene flow is limited and harvesting is intensive, fishing may alter life histories and favour trait combinations that collectively reduce adult body size. However, empirical evidence of downsizing of adults in small-bodied coastal fish is still scarce, in part due to the lack of knowledge about the selective nature of certain fishing gears, such as recreational angling, and the difficulties in estimating the dispersion of pelagic early-life stages. Using the small-bodied sedentary coastal marine fish *Serranus scriba* as a model, we first empirically show that recreational angling selects for life-history traits (i.e. increased reproductive investment) that promote downsizing of adults. Second, using Lagrangian particle dispersion modelling, we show how local hydrodynamics generates patterns of limited connectivity and the emergence of meta-population structure. Finally, the life histories presently observed in isolated populations of *S. scriba* that experienced differential fishing pressure matched expectations of fishing-induced downsizing of adult body size. Body size is an important trait in aquatic food webs, and evolutionary downsizing might have unforeseen consequences. From a precautionary perspective, maintaining the meta-population structure and the full range of genotypes inherent in them is important, even for small-bodied, geographically restricted fish species that are mainly harvested by recreational anglers.

KEY WORDS: Body size · Function-valued approach · Life-history traits · Population connectivity · Recreational fishing · Selective fisheries

INTRODUCTION

Exploitation of wild-living animals by humans is often intensive and never random with respect to traits carried by the animal (Allendorf & Hard 2009). In fact, selective exploitation of species, gender, phenotypes and genotypes is common around the world (Heino &

Godo 2002, Jørgensen et al. 2007, Allendorf et al. 2008). Elevated and/or non-random harvesting can generate selection responses of certain traits, and result in harvest-induced adaptive changes of life-history traits, such as maturation schedule, reproductive investment and growth rate (Jørgensen et al. 2007, Heino et al. 2013, Laugen et al. 2014). Fisheries-

induced selection should select for fast life histories (Heino et al. 2013) characterised by small size and age at maturation coupled with high reproductive invest-ment, which collectively reduce the individual's adult body size (Law 2000, Jørgensen et al. 2007). Any change in adult fish body size can have negative con-sequences for the productivity and utility of exploited systems (Jørgensen & Fiksen 2009, Audzijonyte et al. 2013b, Jørgensen & Holt 2013). Consequently, knowl-edge about the selection differentials on life-history traits exerted by fisheries is important for sustainable fisheries management (Arlinghaus et al. 2009).

The potential for fisheries-induced downsizing of body size has been mainly discussed in the context of commercial fisheries, where positive size selection is well documented (Laugen et al. 2014). More complex exploitation patterns with respect to traits selected by fishing are conceivable for passively operated fishing gears (where the odds of capturing a fish depends on a fish's decision to attack and/or ingest baited hooks), such as recreational angling (Uusi-Heikkilä et al. 2008). In many recreational harvesting situations, such as hook-and-line angling, selection of a range of behavioural, physiological and life-history correlated traits is conceivable (Cooke et al. 2007, Uusi-Heikkilä et al. 2008, Philipp et al. 2009, Redpath et al. 2009, 2010, Wilson et al. 2011, Sutter et al. 2012). The re-sulting complexity of selection pressures on a range of traits that are correlated with the overarching trait 'vulnerability to fishing' suggests that the selection differentials caused by recreational angling may not necessarily show the expected sign. In fact, while negative selection differentials on body size were re-ported in some recreationally exploited salmonids (Saura et al. 2010, Kendall & Quinn 2011), the positive correlation between physiological traits, including metabolic rate, metabolic scope, anaerobic capacity or biochemical response to exercise, aggression and vulnerability to fishing may render slow-growing fish more vulnerable to angling gear (Redpath et al. 2009). Therefore, the resulting impact of recreational angling on life histories cannot be easily foreseen (Johnston et al. 2013), and more stock-specific analy-ses that represent local fishing conditions and pat-terns are needed (Heino et al. 2013, Laugen et al. 2014). Limited work on fisheries-induced selection pressures on recreationally exploited fish stocks in marine environments exists (Olsen & Moland 2011).

Besides a detailed knowledge of the selective nature of fishing gear on life-history traits, in open systems, there is a need to consider the dispersal ability of fish if one wants to understand whether the specific life histories observed in the wild are the results of exploitation. Marine environments have been traditionally assumed to operate as systems with high levels of gene flow due the pelagic nature of many early-life stages in a range of species (Roberts 1997). Indeed, gene flow in open marine systems has been identified as a possible mechanism that mitigates fisheries-induced selection pressures from an evolutionary perspective (Olsen et al. 2004, Kuparinen & Merilä 2007, Dunlop et al. 2009, Pelc et al. 2010). However, coastal currents may create bar-riers to dispersal (Cowen et al. 2006). Recent studies that combined genetics and oceanography have sug-gested that marine fish populations are not as open as expected (Palumbi & Warner 2003, Teacher et al. 2013). Even at spatial scales of a few kilometres, meta-populations with limited gene flow can emerge in the marine environment (e.g. Jones et al. 2005, Carreras-Carbonell et al. 2007, Galarza et al. 2009, Teacher et al. 2013). Indeed, specific oceanic fronts and local hydrodynamic conditions can generate small-scale patterns of isolation within sub-popula-tions in many coastal species, which will increase the vulnerability of local populations to human impacts such as fishing (Galarza et al. 2009, Kough et al. 2013). However, studies matching the selective na-ture of fishing and the population's connectivity to explain phenotypic life-history variation in the wild are still scarce (Kough et al. 2013).

Capitalising on this idea of matching fishing selec-tion and the structure of the population, we adopted a multidisciplinary approach to provide empirical evi-dence in relation to whether (1) recreational angling is selective for individual life-history traits, (2) local hydrodynamics plays a role in generating sub-popu-lations exposed to a high level of self-recruitment and limited dispersal and (3) matching the selective nature of recreational angling and the meta-popula-tion structure can jointly explain the lower adult body size in heavily exploited marine coastal fish compared to those in protected areas. We used the simultaneous hermaphrodite serranid *Serranus scriba* in the Medi-terranean Sea as a model. *S. scriba* is a highly seden-tary species whose adult dispersions are restricted to few square kilometres (March et al. 2010). The spe-cies is heavily exploited by the local recreational an-gling fishery (e.g. Morales-Nin et al. 2005, Alós & Arlinghaus 2013). The early-life stages of *S. scriba* are pelagic and exposed to dispersion following the hydrodynamic conditions of the Mediterranean. Our study was based on a comprehensive analysis of the phenotypic variation of the individual life-history traits in nearby areas at small geographical scales subjected to varying historic fishing pressure com-

bined with the results from a high-resolution numerical model that allowed estimation of the connectivity of the studied meta-populations. We discuss our results in the context of evolving fish stocks and derive implications for the development of sustainable coastal fisheries.

MATERIALS AND METHODS

Three lines of evidence were addressed in our attempt to analyse whether selective fishing might contribute to phenotypic variation in the wild. (1) We assessed whether the particular gear under investigation induced selection differentials in reproductive investment and adult body size. (2) We studied evidence of restricted connectivity among local populations. (3) We assessed whether phenotype variations among sub-populations that experienced different selection pressures due to fishing were adequately explained by both processes. We compiled all 3 lines of evidence for *Serranus scriba*.

Selective effects of recreational angling on life-history traits

We compared the life history of individuals sampled with an active (experimental beam trawl) and a passive (hook-and-line) sampling method, collected jointly at the same locality and time. We assumed that the experimental beam trawl would capture a greater fraction of the variation in life history present in the fish assemblage than recreational angling. We selected an experimental area of 1.1 km² corresponding to the average home range of *S. scriba* (March et al. 2010; see Fig. 1). During May at the peak of the spawning season (Alós et al. 2013), *S. scriba* were sampled using both methods at the same temporal and spatial scale.

The experimental beam trawl was designed for scientific assessment of fish assemblages inhabiting *Posidonia oceanica* seagrass (see e.g. Moranta et al. 2006, Deudero et al. 2008). The trawl was 3 m long and 1 m high. The beam trawl had a net body of 8 m (1.2 cm square mesh) and a 2 m long cod end (0.6 cm square mesh). The gear was towed over the seagrass for 20 min over a distance of ~900 m. We conducted 3 different fishing hauls using the experimental beam trawl to obtain a sufficient sample size (n = 50, mean [± SD] fish size was 141.8 ± 26.1 mm, and mean age was 3.6 ± 1.6 yr). We also conducted a number of experimental angling sessions in the experimental

area to obtain a corresponding hook-and-line sample (n = 165, fish size = 144.8 ± 26.6 mm; and age = 3.59 ± 1.6 yr). The experimental angling sessions were conducted following protocols described by Alós et al. (2009). All of the individuals were measured (total length in mm) and weighed (total weight in g), and their sagittal otoliths were dissected. Additionally, the gonads of a sub-sample of the fish captured using each sampling method (experimental beam trawl: n = 23, fish size = 138.6 ± 32.9 mm, and hook-and-line: n = 45, fish size = 146.24 ± 21.8 mm) were used to directly assess the fishes' reproductive investment (batch fecundity) following the method described by Alós et al. (2013). By comparing the life-history traits estimated from individuals sampled by beam trawl and angling, the direction of selection by angling was inferred assuming that the beam trawl captured a more random sample of the population.

Connectivity of *Serranus scriba* meta-populations that experience differential harvesting pressure

We explored the possible isolation of some populations of *Serranus scriba* by analysing the dispersal of early life stages, because dispersal in adult *S. scriba* is negligible (March et al. 2010). Based on these results, we then selected reproductively isolated sub-populations exposed to contrasting contemporary harvesting pressure.

To estimate the degree of sub-population connectivity, we selected 25 areas (see Fig. 1) potentially inhabited by adults of *Serranus scriba* (any seagrass or rocky bottoms with <30 m depth) and estimated the self-recruitment and population connectivity following the procedures of Basterretxea et al. (2012). Briefly, the Lagrangian trajectories (Watson et al. 2011) of weekly releases of passive tracers (virtual eggs) were simulated over a 10 yr period (2000 to 2009) in the peak reproductive season (11 wk from April to June). We used a high-resolution (200 m) 3-dimensional density-resolving model of the hydrodynamics of the southern Mallorca Island waters, based on the previously validated Princeton Ocean Model (Basterretxea et al. 2012). The real and historical records of flow fields produced by surface wind forcing were obtained from the 12-hourly wind maps from a data-base of 10 yr (Basterretxea et al. 2012).

At the end of the 10 yr simulation, a total of 2 125 750 virtual eggs and larvae had been tracked up to the end of the pelagic larval duration (PLD), corresponding to the moment of settlement to the seagrass (for *Serranus scriba*, estimated as 28 d since
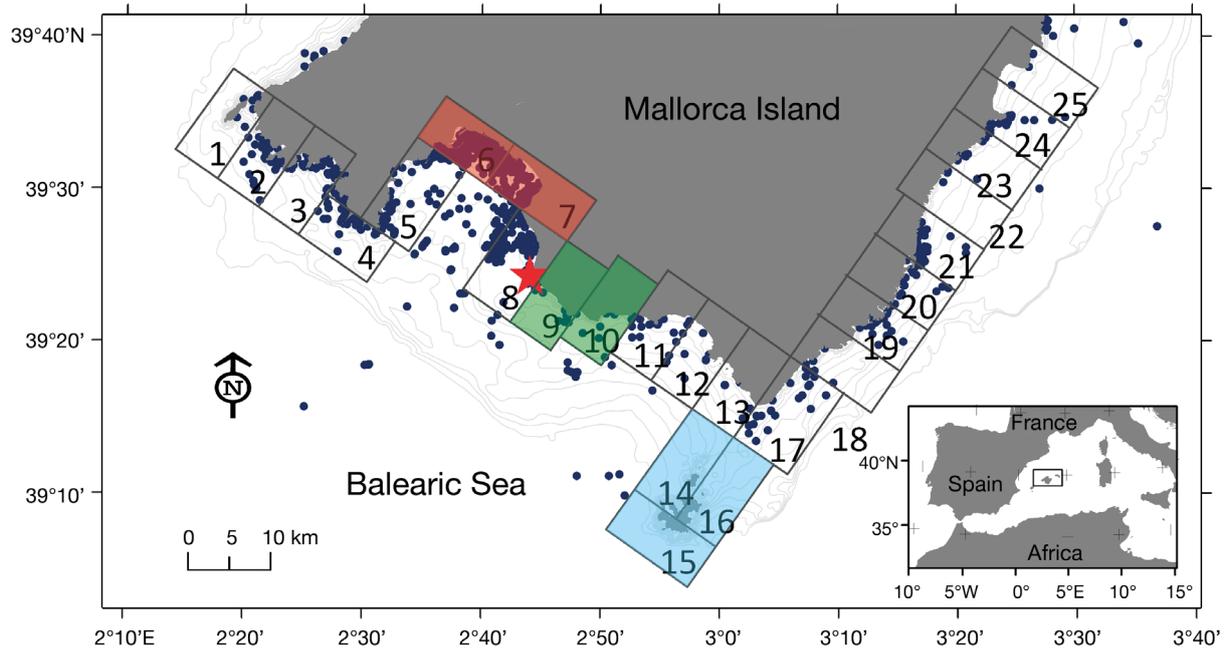
Fig. 1. Mallorca Island in the Balearic Sea (NW Mediterranean) and the location of the 25 sites (delimited by boxes) where virtual eggs were released. Sites 6 and 7 represent the inner region of Palma Bay (in red), Sites 9 and 10 represent the open population (in green), and Sites 14, 15 and 16 correspond to the National Park of Cabrera (in blue). The experiment of harvesting selection (see 'Materials and methods') was performed in the location marked by a red star. Each blue point corresponds to a recreational fishing boat censed in the framework of the research project CONFLICT. Note the large fishing effort concentrated on the inner area of Palma Bay

hatch; Macpherson & Raventos 2006). The virtual eggs were homogeneously distributed in each area of the top (10 m) layer (see Basterretxea et al. 2012 for further model details). A reflective boundary condition was used to prevent the particles from moving onto land. We assumed individual larvae to have been recruited to a particular area if they were found in the inner-shore habitat (defined by each site) at the end of the PLD. We determined the degree of self-recruitment (mean and SD) defined as the number of particles remaining in area j at the end of the prescribed PLD divided by the numbers of particles initially released in area j in each releasing period (11 wk) (Basterretxea et al. 2012).

The probability that a particle was transported from one area to another by the end of the PLD was considered a measure of direct connectivity. Direct-connectivity estimates provide a good indication of the relationship between self-recruitment and dispersal (Basterretxea et al. 2012). However, heritable components of phenotypic variation can also be exchanged through indirect transport involving several generations (Casabianca et al. 2012). We therefore also assessed the indirect connectivity (IC) between paired populations, calculated as follows:

$$IC = \sum_{n=1}^{N} DC^n \qquad (1)$$

where N is the number of hatching cycles, DC identifies the direct routes, and DC^n includes all of the routes requiring $n − 1$ steps (or n direct routes). It is important to note that IC conveys a temporal term that provides information about the velocity of the exchange. In the case of phenotypic variation, this definition may be relevant because longer routes of exchange, involving a higher number of generations, may imply loss of the heritable signal (Casabianca et al. 2012).

The results of this simulation experiment showed that the population connectivity of *Serranus scriba* was dictated by the coastal morphology at the spatial scale we studied (Fig. 2). Two main areas, the inner part of Palma Bay (IPB) and the National Park of Cabrera (NPC), were markedly different from the others, showing the highest degrees of self-recruitment (Fig. 2). In comparison to a control population, which we named open population (OP) (characterized by the average of all other sub-populations in terms of dispersal properties), the final position of the virtual eggs released suggested a notoriously high degree of retention within IPB and NPC (Fig. 3). The correspon-
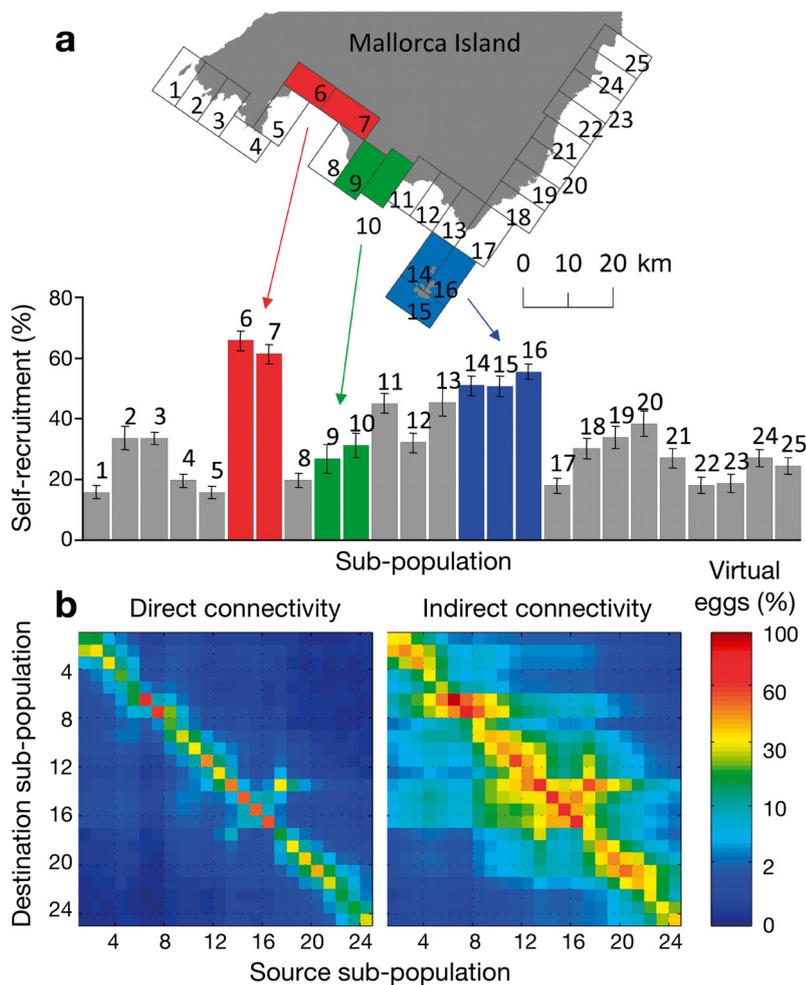
Fig. 2. (a) Local self-recruitment (10 year mean ± SD) of the 25 populations where virtual eggs were released. Red, green and blue: highest values observed in the inner part of Palma Bay, the open population and the National Park of Cabrera, respectively. (b) 2-paired matrix of direct and indirect connectivity among the 25 sites studied. The scale bar represents the percentage of virtual eggs that moved from one site to another (note that the scale is exponential) and the general limited connectivity among sites

area [MPA]) in 1991 (Francour et al. 2001). Since recreational fisheries were abandoned in NPC, top-predator species and potential predators of small individuals of *Serranus scriba* have notably increased in abundance (e.g. *Epinephelus marginatus*; Reñones et al. 1999). In contrast, the IPB hosts the most important recreational angling fishery on Mallorca Island (Cabanellas-Reboredo et al. 2012), and consequently there is substantial recreational fishing effort in this area (see Fig. 1 for the spatial distribution of fishing effort around Mallorca Island). Therefore, we hypothesized that the life-history traits of the actual populations in IPB and NPC should respond to the selective nature imposed by angling or natural mortality and that the life history of *S. scriba* in OP should be intermediate to that in IPB and NPC.

Life history of fish in exploited and unexploited sites

To test the hypothesis that life history differs in exploited and unexploited sites, we compared the actual status of the populations in terms of average individual life-history strategies in the 3 areas by collecting adult individuals of *Serranus scriba* from the IPB (n = 201), OP (n = 215) and NPC (n = 353). The fish sampling was conducted with identical gears (conventional hook-and-line; Alós et al. 2009) at areas with similar habitat characteristics (seagrass meadows of *Posidonia oceanica*) and depths. Samples were processed as described before. In addition, the gonads from sub-sampled individuals from May and June (n = 53 from the IPB, n = 41 from the OP and n = 79 from the NPC) were used to directly measure reproductive investment. Moreover, in all 3 sites, we assessed the relative abundance of fish (using catch per unit effort as an index) and enumerated the size and age of fish vulnerable to conventional hook-and-line gear. Although the relationship between catch rate and abundance is sometimes problematic (Walters & Martell 2004), catch rate data can serve its purpose in comparative studies when effort is highly standardised and the capture method is replicable, as

ding direct and indirect (calculated for 50 yr) connectivities between these 2 population (IPB and NPC) areas were low (Fig. 4), indicating low potential gene flow. These 2 areas also showed a low degree of direct connectivity to the OP (Fig. 4). Therefore, while the populations in the OP were considered to have gene flow, IPC and NPC were considered to be more isolated from each other and from the OP.

Apart from the limited connectivity of NPC or IPB to other areas, these sub-populations were also unique because they were the only sites exposed to the minimum and maximum harvesting selection pressure. These features rendered NPC and IPB unique casestudy candidates to test our hypothesis. The NPC was declared a sanctuary (a no-take marine protected

Fig. 3. The spatial plots of fixed kernel probability distributions (kernel density value gradient estimated in a grid of 250 × 250 m) of the positions at the end of the pelagic larval duration of the virtual eggs released in each of the selected main areas: the inner part of Palma Bay (IPB), the open population (OP) and the National Park of Cabrera (NPC)

in our study. We performed experimental fishing sessions (IPB: n = 54, OP: n = 24, and NPC: n = 64) using the standardised recreational angling gear described by Alós et al. (2009), visiting each sub-population on randomly selected days during a 1 yr period.

Fig. 4. Directional flow diagram showing the paired direct and indirect connectivity (black arrows) calculated among the 3 sub-populations studied (each number and the thickness of each arrow can be interpreted as the percentage of eggs released in a specific sub-population that recruited in another): the inner part of Palma Bay (IPB), the open population (OP) and the National Park of Cabrera (NPC). Indirect connectivity values are the maximum values of connectivity over a 50 yr period. The grey arrows show the connectivity attributed to other sub-populations. The 360° black arrows indicate the self-recruitment values for each specific sub-population

Estimation of individual life-history traits of *Serranus scriba*

A function-valued approach was chosen to infer key individual life-history traits in which parameters (traits) estimated from individual growth curves were used as data characterising each individual fish (Stinchcombe & Kirkpatrick 2012). Back-calculation of length-at-age using growth marks contained in otoliths can offer a reliable method to obtain repeated measures of length-at-age over the lifespan of the same individual whenever there is a strong relationship between fish and otolith size (Pilling et al. 2002, Swain et al. 2007, Alós et al. 2010, Mollet et al. 2010, Brunel et al. 2013). We fitted the individual length-at-age points extracted from the otoliths of *S. scriba* following the protocol by Alós et al. (2010) to the bi-phasic growth model proposed by Lester et al. (2004). This approach allowed us to obtain individual measures of the annual reproduction investment (g), maximum theoretical size (L_∞), age of initiation of maturation (T) and immature growth rate (h) independently of the fish size at sampling (Shuter et al. 2005, Arlinghaus et al. 2009, Matsumura et al. 2011). The model assumes linear growth in the juvenile phase and a trade-off between the energy allocation to somatic growth and reproduction in the adult ages (Lester et al. 2004). The model developed by Lester et al. (2004) is a special case of a more general version developed by Quince et al. (2008a,b) and is valid for a length-weight relationship with an exponent $b = 3$, which is the case for *S. scriba* (Alonso-Fernández et al. 2011).

The somatic growth rate before the age of the onset of maturation (T, years) in the model by Lester et al. (2004) is given as follows:

$$L_t = h(t - t_1) + \varepsilon \quad \text{when } t \leq T \qquad (2)$$

where L_t is the length at age t (mm), h is the immature growth (mm yr^{-1}), t_1 is the theoretical age at size 0 mm, and ε is the Gaussian error.

When the individual starts investing in reproduction at age T, the somatic growth is represented by the von Bertalanffy growth equation with parameters that provide explicit information on the energy allocated to reproduction (g, yr^{-1}) as follows:

$$L_t = L_\infty(1 - e^{-k(t-t_0)}) + \varepsilon \ \ \text{when } t \geq T \qquad (3)$$

where $L_\infty = 3h/g$.

These 2 equations provide a biologically meaningful interpretation of the von Bertalanffy growth parameters (Lester et al. 2004). Accordingly, the growth factor k is proportional to the reproductive investment g and reflects the relative investment averaged over the entire reproductive cycle, and L_∞ is the ratio of net production to reproductive investment ($L_\infty = 3h/g$), which is representative of the adult body growth (Lester et al. 2004). The growth model was fitted using a hierarchical Bayesian approach for each individual. Two different models were fitted (between fishing methods and between populations).

The model was implemented and run using the runjags library of the R package (www.r-project.org), which opens JAGS (http://mcmc-jags.sourceforge.net). It was fitted for individuals of age ≥5 at capture, which substantially improves the accuracy of the method (Alós et al. 2010, Brunel et al. 2013). Moreover, due the over-dispersed representation of older ages in the unexploited NPC site in the second model, 50 individuals were randomly selected. Using this approach, the ages and the number of observations per individual included in the analysis were not different among samples in the fitting of the first (χ^2 test, p = 0.46) and second model (χ^2 test, p = 0.1). Therefore, any significant variation in life-history traits among the gears or sites was independent of the fish size at sampling and the number of samples (ages). A hierarchical structure for population and individuals of minimal priors was used (see Supplement 1, www.int-res.com/articles/suppl/m503p219_supp.pdf). Three Monte Carlo Markov chains (MCMC) were run, and the convergence was assessed using a Gelman-Rubin diagnostic (Plummer et al. 2006). The feasibility of the Bayesian framework adopted here was assessed through a simulation analysis (see Supplement 2).

We estimated the direction of selection of recreational angling by comparing the distributions of the individual Bayesian means of each life-history trait for the 2 fish sampling methods (beam trawl and hook-and-line). Subsequently, inter-population comparisons of the average life-history traits were conducted by comparing the Bayesian population means of each life-history trait using Bayesian credibility intervals (BCI) (2.5 and 97.5%). Unlike the frequentist p-value, the Bayesian posterior distributions are interpreted correctly as a belief that there is a given probability that the parameter of interest lies within the interval (Ellison 2004). To make robust conclusions regarding the between-populations differences, we considered differences when the BCI did not overlap at all. L_∞ and h were expressed in mm of otolith, but in some cases, the scale was translated to total length using the regression model provided by Alós et al. (2010) to facilitate interpretation.

Between-gear and between-population differences in the direct measures of reproduction investment (batch fecundity controlled for fish size) and population differences in the relative abundance, age and size of the vulnerable fish sampled by experimental angling were analysed using general linear mixed effects models (GLMM). The models were fitted following a forward step-by-step procedure until maximum explanatory power was reached (Akaike's information criterion) (Zuur et al. 2009). The p-values for each parameter were estimated through MCMC simulations using the library *languageR* of the R package.

To help identify whether actual life-history traits can be adequately explained by the direction of recreational harvesting and the population's connectivity, we also included ancillary environmental data. A 10 yr record of satellite (MODIS-Aqua)-derived monthly averages of sea surface temperature (SST) and chlorophyll *a* as a measure of productivity was obtained for each of the 3 sub-populations included in the analyses and compared among them. In both of the cases (temperature and productivity), chronograms were used to visually inspect variation among sites.

RESULTS

Selection pressures on life history caused by recreational angling

The average g of the fish vulnerable to hook-and-line fishing gear was smaller than that of those captured in the experimental trawl (Table 1). Moreover, the mean of the maximum size (L_∞) was significantly different between the 2 gears, with larger values found in the hook-and-line individuals compared to fish vulnerable to the beam trawl (Table 1). While the results of the immature growth rate (h) and onset of maturation (T) suggested on average an older age of maturation and smaller immature growth of the hook-and-line individuals compared to the fish vulnerable to trawl, the BCI overlapped notably, sug-

Table 1. Bayesian mean (±SD) and Bayesian credibility intervals (BCI; 2.5, 50 and 97.5 %) of the life-history traits, annual reproduction investment (g), individual maximum theoretical size (L_∞ of otolith and fish total length, in parentheses), age of onset of maturation (T) and immature growth rate (h) of otoliths and fish (in parentheses) estimated for the sampling methods used (experimental beam trawl and hook-and-line) and the 3 analysed sub-populations (inner Palma Bay, open populations and the National Park of Cabrera)

| | g (yr^{-1}) | | | | L_∞ (mm) | | | | T (yr) | | | | h (mm yr^{-1}) | | | |
	Mean ± SD	2.5%	BCI Med.	97.5%	Mean ± SD	2.5%	BCI Med.	97.5%	Mean ± SD	2.5%	BCI Med.	97.5%	Mean ± SD	2.5%	BCI Med.	97.5%
Between-methods																
Experimental beam trawl	0.88 ± 0.12	0.75	0.86	1.11	3.50 (222.8) ± 0.11	3.28	3.5	3.7	1.33 ± 0.08	1.17	1.33	1.45	1.03 (80.3) ± 0.11	0.9	1.01	1.24
Hook-and-line	0.74 ± 0.06	0.68	0.73	0.81	3.84 (242.4) ± 0.07	3.72	3.84	3.95	1.43 ± 0.05	1.35	1.43	1.49	0.94 (75.1) ± 0.05	0.89	0.93	1.01
Between-populations																
Inner Palma Bay	0.75 ± 0.04	0.67	0.75	0.83	3.59 (228) ± 0.07	3.45	3.6	3.74	1.5 ± 0.05	1.4	1.51	1.61	0.89 (72.2) ± 0.04	0.81	0.89	0.98
Open population	0.7 ± 0.04	0.63	0.7	0.78	3.85 (243) ± 0.07	3.7	3.85	3.99	1.48 ± 0.05	1.38	1.47	1.57	0.89 (72.2) ± 0.04	0.82	0.89	0.98
National Park of Cabrera	0.61 ± 0.03	0.55	0.61	0.67	3.88 (244.7) ± 0.06	3.75	3.87	4	1.55 ± 0.05	1.46	1.55	1.65	0.79 (66.5) ± 0.03	0.72	0.79	0.85

gesting a lower potential for angling-induced selection differentials on these traits (Table 1). A box-plot of the individual values of the life-history traits estimated for the 2 fishing gears revealed directional fishing-induced selection favouring fish with higher reproductive investment and smaller terminal length under conditions of intensive recreational harvesting (Fig. 5). Therefore, the results of our experimental approach demonstrated fishing-induced selection pressures favouring downsizing of adult body length.

The direct measures of reproduction investment (batch fecundity) were in line with those obtained for the indirect measures of g inferred from the growth curves. Accordingly, there were significant differences between the fish caught using a beam trawl and via hook-and-line (GLMM, p < 0.05; Table 2): individuals sampled using hook-and-line invested less in reproduction than the trawl-captured fish (Table 2). The relationship between the batch fecundity and g estimated from the growth curve was positive and highly significant (GLM, p < 0.01).

Sub-population alteration of life history in response to recreational fishing

The actual wild populations of *Serranus scriba* mirrored the selective nature of the expected source of mortality (fishing-induced or natural predator-induced): while a life history characterized by small body adult size was observed in the exploited population (IPB), the opposite was found in the marine protected area (NPC). In the open control area (OP), both life-history strategies were observed. There were non-overlapping posterior distributions of reproductive investment g between the IPB and the NPC (Table 1). Thus, we accepted the hypothesis of higher reproductive investment in the exploited site IPB relative to the unexploited site NPC (Table 1, Fig. 6). By contrast, the posterior distribution of the OP population had intermediate values that notably overlapped with the distributions of the other 2 populations (Table 1). We found differences for L_∞ between the Bayesian means of IPB and NPC, indicating a lower final size of the fish living in the exploited site IPB (Table 1, Fig. 6). In the case of T and h, the posterior distributions of the 3 populations overlapped, indicating the implausibility that the cause was an adaptive response (Table 1, Fig. 6).

The life-history strategy associated with small (IPB) or large (NPC) adult body size was also confirmed through the direct measure of reproductive investment (batch fecundity). Accordingly, the individuals

Table 2. Results of the 5 GLMM fitted to test (1) the relation-ship between the batch fecundity (number of eggs per fish) between (*i*) the sampling methods and (*ii*) sub-populations (IPB: inner Palma Bay, OP: open population) and (2) the differ-ences between the (*iii*) relative abundance (no. of fish collected in 30 min by angler), (*iv*) average fish size (mm) and (*v*) average ages (years) in the sub-populations. The full model for the reproductive investment included fish size and month as fixed factors. In the case of the relative abundance, fish size and age of vulnerable fish, the full model included depth (m), angler, bait and month as fixed factors. In all of the models, fishing session within-day was included as a random factor. The table shows the Monte Carlo Markov chains (MCMC) mean of the parameter, the highest 95% credibility intervals (HDP) and the significance of the parameter. In all of the cases, a $\log_{10}(x + 1)$ transformation was applied

Parameter	MCMC mean	Lower	Upper	p-value
Batch fecundity (between methods)				
(*Intercept*)	5.83	5.0	6.63	<0.001
Fish size (mm)	0.02	0.01	0.02	<0.001
Method (hook-and-line)	−1.31	−1.93	−0.68	0.022
Batch fecundity (between populations)				
(*Intercept*)	5.21	4.67	5.75	<0.001
Fish size	0.02	0.02	0.02	<0.001
Population (IPB)	0.74	0.42	1.08	0.011
Population (OP)	−0.08	−0.38	0.22	0.87
Month (May)	−1.04	−1.3	−0.77	<0.001
Fish abundance (between populations)				
(*Intercept*)	1.35	0.86	1.87	<0.001
Population (IPB)	−0.64	−1	−0.27	0.003
Population (OP)	−0.3	−0.77	0.16	0.2
Depth (m)	−0.04	−0.06	−0.01	0.018
Month (Jan)	0.43	0.03	0.81	0.082
Month (Feb)	0.12	−0.26	0.53	0.588
Month (Mar)	0.16	−0.3	0.61	0.57
Month (May)	0.31	−0.12	0.75	0.17
Month (Jun)	0.52	−0.02	1.03	0.076
Month (Jul)	1.16	0.49	1.84	0.002
Month (Aug)	0.99	0.53	1.43	<0.001
Month (Oct)	0.75	0	1.57	0.073
Month (Nov)	0.91	0.15	1.69	0.031
Fish size (between populations)				
(*Intercept*)	4.83	4.73	4.93	<0.001
Population (IPB)	−0.17	−0.24	−0.1	<0.001
Population (OP)	−0.1	−0.17	−0.03	0.006
Bait (Shrimp)	0.08	0.04	0.13	0.003
Depth (m)	0.01	0	0.02	0.019
Fish age (between-populations)				
(*Intercept*)	1.33	1.1	1.54	<0.001
Population (IPB)	−0.49	−0.62	−0.36	<0.001
Population (OP)	−0.46	−0.62	−0.29	<0.001
Bait (shrimp)	0.14	0.04	0.24	0.016
Depth (m)	0.03	0.01	0.04	0.004

Fig. 5. Box-plot of the individual life-history traits (annual re-production investment (*g*), individual maximum theoretical size (*L∞*), age of onset of maturation (*T*) and immature growth rate (*h*) estimated for the individuals sampled using the ex-perimental beam trawl (BT) and hook-and-line (HL) meth-ods. Horizontal bars: median; box: 25 and 75th percentiles of the data; whiskers: non-outlier range; diamonds: outliers
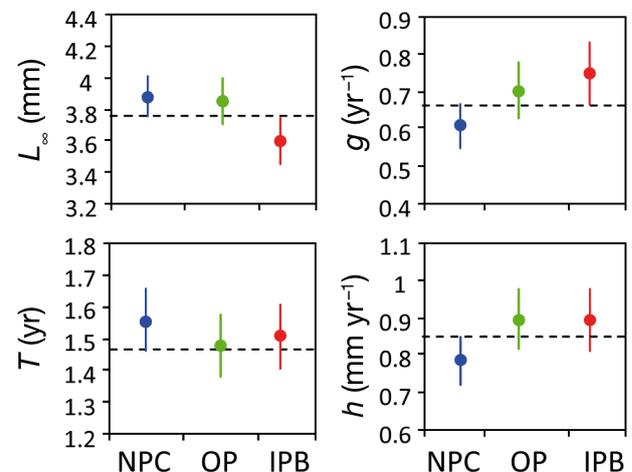
Fig. 6. Bayesian means (colored dots) and credibility inter-vals (2.5 and 97.5%, colored vertical bars) of the posterior distribution of the population means estimated for each life-history trait to assess the differences among sub-populations: the inner part of Palma Bay (IPB) in red, the open population (OP) in green and the National Park of Cabrera (NPC) in blue

sampled in the IPB had a significantly higher size-corrected batch fecundity than those sampled in the NPC (GLMM, p < 0.05; Table 2). In terms of abun-dance and average size and age, the population of IPB was characterised by a significantly lower abun-

dance (as inferred based on angling catch rate), and the fish were on average smaller and younger (Table 2).

In terms of environmental co-variates, the temper-ature oscillated in the same way on a daily and sea-sonal basis in the IPB and NPC sites, suggesting no differences in temperature regimes (Fig. 7). This finding was to be expected due to the close proximity between the 2 areas. By contrast, chlorophyll *a* con-
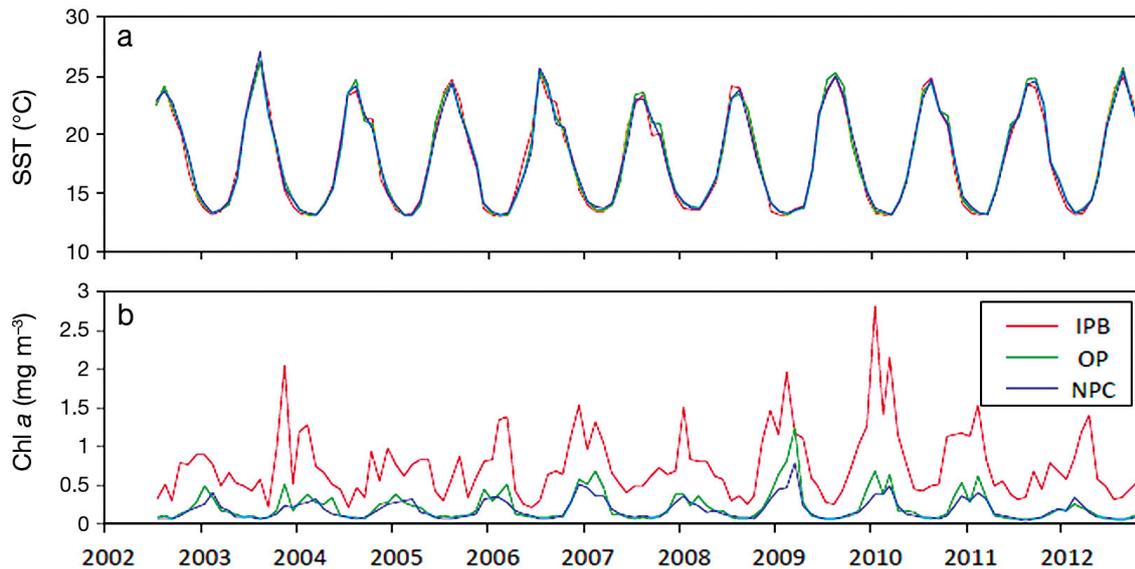
Fig. 7. Chronograms of 10 yr of the sea surface temperature (SST) and concentration of chlorophyll *a* in the inner part of Palma Bay (IPB, in red), the open population (OP, in green) and the National Park of Cabrera (NPC, in blue)

centrations estimated from the sea-colour images available for the IPB and NPC showed a clear seasonal periodicity in both cases, and the IPB had higher values, suggesting that the IPB was a more productive site than the NPC (Fig. 7). Therefore, one would have expected larger bodied adults in the IPB sites due to elevated resources, but the opposite was found in our study.

DISCUSSION

We have shown that recreational angling operates non-randomly on *Serranus scriba*, preferentially capturing individuals with low reproductive investment and high adult body size. Therefore, one would expect a selective response toward increased average reproductive investment and a decline in terminal body length in exploited stocks, which agreed with empirical observations in the highly exploited IPB site compared to the marine protected area. Considering the limited dispersal of adult *S. scriba* (March et al. 2010), the limited connectivity of early life-stages demonstrated through the particle modelling in our study and the selective nature of intensive recreational angling, we can explain the phenotypic variation observed in different sites in the wild. Based on our data, we propose that trait-selective and intensive recreational angling exploiting meta-populations of *S. scriba* constitute a potential mechanism that contributes to the decline of adult body length in heavily exploited coastal populations. The

decline of the adult body size can have negative implications for the productivity and biomass of fish stocks (Jørgensen et al. 2007, Audzijonyte et al. 2013b). Both selective fishing and meta-population structure are, therefore, important to consider when managing coastal populations that are exploited by recreational anglers.

We demonstrated that recreational angling leads to adaptive changes in adult body size by selectively targeting fish with low reproductive investment. These findings are in agreement with theoretical models and empirical data that found that size-selective recreational fishing leads to the evolution of high reproductive investment and small maximum body length (Arlinghaus et al. 2009, Saura et al. 2010, Kendall & Quinn 2011). Such effects have been well recognized in size-selective commercial fisheries (Jørgensen et al. 2007, Audzijonyte et al. 2013b), and they can have negative implications for the utility that stocks provide to society (Eikeset et al. 2013, Laugen et al. 2014). We propose that recreational angling leads to lowered body size of adult stages similar to effects previously reported in size-selective commercial fisheries.

A particularly novel methodological aspect of our work was related to the fitting of individual growth curves, which resulted in the derivation of individual-level life-history traits that were largely independent of the individual's size at sampling. Deriving life-history traits other than growth rate, e.g. reproductive investment, from an individual growth trajectory has only rarely been used in the literature

on fisheries-induced evolution (Mollet et al. 2010, Brunel et al. 2013). Our methodological approach should be useful for more long-lived species because the back-constructed individual growth curve can more easily be estimated for such species than for the short-lived species we studied.

We have focused our work on life-history traits, but our approach cannot answer whether fishing directly selects life history or whether there is indirect selection through a correlated response to selection on other traits. Vulnerability to fishing gear is a complex process where correlated life-history, and behavioural and physiological traits constitute the 'vulnerability phenotype' (Uusi-Heikkilä et al. 2008). Fish behaviour plays a major, yet underappreciated, role in the selection process in recreational angling. For example, bold and aggressive fish are, possibly independent of body size, more prone to attack and are more likely to ingest angling baits than shy and less aggressive fish (e.g. Klefoth et al. 2012, 2013, Sutter et al. 2012). Using an individual-based model calibrated to the exploratory behaviour of *Serranus scriba*, we have demonstrated negative selection differentials on exploration (Alós et al. 2012). Specific behavioural types are correlated with life-history productivity (Biro & Stamps 2008). We propose that recreational angling-induced selection directly acts on feeding and activity-related behavioural traits, which are correlated with life-history traits in *S. scriba*, in turn leading to a selection response in the correlated life history through selection on behaviour. This selective process should drive exploited populations of *S. scriba* to become less bold, less aggressive and less explorative in addition to evolving a smaller adult body size, as implicated in our study.

In direct contrast to the direction of recreational fishing-induced selection, natural selection should drive meta-populations of *Serranus scriba* in the opposite direction by favouring large investments in rapid growth to outgrow gape-size-limited predators. That is, in environments where the abundance of natural predators of *S. scriba* is high, smaller individuals will experience a greater likelihood of death, in turn yielding selection for large body size and fast growth (see Edeline et al. 2007 for an example in northern pike *Esox lucius*). The optimal life-history strategy under predation risk in a natural environment should, therefore, imply low reproductive investment and large body sizes (Reznick 1982, Hutchings 1993, Edeline et al. 2007, Olsen & Moland 2011) to maximize life-time fitness (Roff 1984, Charnov 2005). The wild populations we studied directly confirmed to these expectations. On one hand, *S.*

scriba inhabiting the highly exploited sites had life histories characterized by large reproductive investment (estimated both directly and indirectly through batch fecundity and the life-history parameter *g*) and small maximum adult body size. On the other hand, the individuals sampled in the no-take area were dominated by phenotypes with a greater capability of achieving large size by investing less energy into reproduction. These between-population results were supported by the 'average' results observed in the open population studied. We can therefore explain the phenotypic variation of the populations of *S. scriba* by the nature of the natural and fisheries-induced selective process acting on the life histories. Note that our individual methodological approach allows us to explain the decline of the adult body size in the exploited population as stemming from selection acting on life-history traits rather than as a result of demographic truncation and gear-dependent size-selectivity.

One important aspect of any comparative study such as the one performed here is to address any non-fishing-related environmental drivers that might also explain the among-site variation in life history (Dunlop et al. 2005, Kendall & Quinn 2011). In fact, all of the differences observed in the life history in our sub-populations could be related to unaccounted environmental characteristics (McDermid et al. 2010). While we cannot discount that the phenotypic change may be entirely environmentally related, the bulk of the evidence presented here makes this explanation unlikely. First, we could discard the hypothesis of substantial variation in temperature among our sites. The only environmental driver that varied between the high- and no-take sites was the greater productivity of the exploited system, as inferred from chlorophyll data. Greater resource availabilities can plastically increase annual reproduction investments due to greater resource intake (e.g. Craig & Kipling 1983). However, one would then also expect faster growth rates of both immature and mature individuals in the more productive high-exploitation system. Moreover, the reduced density of fish due to exploitation should also elevate growth due to relaxed competition (Lorenzen & Enberg 2002). In fact, we found fewer fish in the protected site, as revealed by hook and line catch rate data. Even if these data are biased due to lower vulnerability of fish to capture in the exploited site (Klefoth et al. 2013), the higher productivity should still result in faster growth. As a result, the maximum adult body size should correspondingly increase in the exploited sites if only plastic responses were at play (McDermid et al. 2010, Wright et al.

2011). However, we observed directly opposing patterns. First, the immature growth rates (*h*) did not differ statistically among the sites, and second, the adult body size was significantly smaller in the high-exploitation sites, although the environmental plasticity hypothesis should have predicted large adult body size. There is no other obvious environmental factor that may explain the life-history difference, rendering fisheries-induced adaptive change a parsimonious mechanism of life-history differentiation.

Providing conclusive cause-and-effect evidence for evolutionary changes in the wild induced by harvesting is currently not possible (Enberg et al. 2012, Audzijonyte et al. 2013a). In fact, whether adaptive changes in life histories are evolutionary or merely indicative of phenotypic plasticity is still under debate for most of the studied commercial populations (Browman et al. 2008, Jørgensen et al. 2008). A range of approaches has been put forward to study fisheries-induced evolution. Theoretical modelling of fisheries-induced evolution (e.g. Arlinghaus et al. 2009, Dunlop et al. 2009) has shown that recreational fishing exploitation can be strong enough to cause selection differentials and for fisheries-induced evolution to be plausible. Naturally, inference of models to the wild is limited, and models will also never conclusively answer whether evolution has truly happened in nature (Audzijonyte et al. 2013a). Many observational studies using time series of phenotypic data from the wild have been conducted to test evidence for fisheries-induced evolution (Audzijonyte et al. 2013a). However, such long time series are very scarce in species with low importance for commercial fisheries such as *Serranus scriba*. There have been a few observational studies that have used molecular techniques suggesting that genetic change has taken place in response to fishing (Ãrnason et al. 2009, Jakobsdóttir et al. 2011, Pukk et al. 2013), but any genetic information for *S. scriba* is still missing. A final approach to studying fisheries-induced evolution is observing experimental evolution under controlled conditions (e.g. Conover & Munch 2002, Conover & Baumann 2009, Philipp et al. 2009). The strength of these studies is that they can provide cause-and-effect evidence and demonstrate that phenotypic change has a genetic basis, but inference of the observations to the wild is limited.

Comparative field studies such as ours may provide a useful compromise to study whether fishing differentially targets certain phenotypes and whether populations with common ancestry and low current gene flow differ in their average phenotype in directions expected from theory and in line with selection differentials estimated in the wild (e.g. Drake et al. 1997, Bevacqua et al. 2012). Therefore, based on our study, one should consider the plausibility for fishery-induced genetic change in exploited populations of *Serranus scriba*. We demonstrated selective harvesting in relation to underlying productivity-related life-history traits, which usually have at least a modest heritability (Law 2000). We also provided evidence for limited population connectivity, which likely leads to limited gene flow in *S. scriba*. Often, the large effective population size of marine fish has been proposed to constitute barriers to fisheries-induced evolution (Cuveliers et al. 2011). We have shown, however, that meta-populations of the small coastal species *S. scriba* may develop reproductively isolated sub-populations on small spatial scales, which are characterised by high levels of local self-recruitment and low direct and indirect connectivity with each other. These findings are in line with recent literature indicating that local hydrodynamics and life history may also result in fine meta-population structures with limited gene flow in many marine areas (Mora & Sale 2002, Carreras-Carbonell et al. 2007, Galarza et al. 2009). Although we cannot conclusively differentiate between the possibilities of plastic adaptive change or evolutionary adaptation in life history, our study justifies the plausible hypothesis that fisheries-induced genetic change might happen in spatially structured coastal species targeted by recreational angling on very small geographical scales. This occurs because whenever there is no contemporary natural gene flow among sub-populations, differential selection pressures should generate sub-populations that adapt their life histories to the local selective pressures (Reznick et al. 1990).

A potentially fruitful avenue of research for disentangling genetic changes from environmental responses to explain the origin of the decline of body size in *Serranus scriba* would be to compare the life-history traits of the offspring of the different populations reared under identical environmental conditions (Conover & Baumann 2009). Until such research becomes available, our study proposes a new paradigm of the potential for widespread fisheries-induced evolution of small-bodied coastal fishes at small scales. Due the potential negative effects of fisheries-induced evolution, which may negatively affect productivity, recovery and catch per unit effort of the stock (Sutter et al. 2012, Audzijonyte et al. 2013b), managers may adjust their management polices to prevent or decrease the selective impacts of harvesting for successful fish-stock management (Walsh et al. 2006).

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