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Fishery-induced change in the morphology of coastal fish with implications for management

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S'autoritza la Universitat a incloure el meu treball en el Repositori Institucional per a la seva consulta en accés obert i difusió en línia, amb finalitats exclusivament acadèmiques i d'investigació

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1. Resum

La pesca selecciona unes formes corporals determinades dels peixos, afavorint la captura de peixos amb la boca més gran (més habilitat per enviar-se un ham) i amb un cos més fusiforme i hidrodinàmic (més probabilitat de trobar-se amb un pescador). Hem estudiat dues poblacions extremes de *Serranus scriba* amb diferents pressions pesqueres: el Parc Nacional de Cabrera (NPC) sense pressió pesquera i la badia de Palma, amb una forta pressió pesquera. Els resultats dels anàlisis mostren que els individus de la població de la badia de Palma tenen la boca més petita degut a que els individus amb la boca gran s'han anat extraient durant els darrers anys. No s'han trobat diferències significatives entre la mida del cos, per la qual cosa seria necessari fer futurs estudis per obtenir algun resultat. A més, hem estudiat l'origen d'aquests canvis físics, i pot ser genètic o ambiental. Per estudiar l'origen, hem criat una descendència dels individus capturats de les dues localitats per poder comprovar possibles similituds amb els adults, però no es varen trobar diferències significatives en quant a la mida de la boca i del cos entre les dues poblacions de larves. Aquestes larves varen morir al tercer dia, per la qual cosa seria interessant obtenir individus juvenils per estudiar el desenvolupament fisiològic en aquestes etapes de creixement. Aquest estudi ofereix una eina per determinar l'origen d'un individu aleatori de *S. scriba* analitzant la seva forma del cos, podent ser extrapolat a altres espècies fent prèviament el mostreig pertinent a localitats amb diferents pressions pesqueres i l'anàlisi de les dades obtingudes.

2. Abstract

Fishing select particular body fish, favouring catch fish with a big mouth (more ability to swallow a hook) and a more fusiform body with better hydrodynamic (more likely to meet with a fisherman). We have studied two extreme locations of *Serranus scriba* with different fishing pressure: National Park of Cabrera (NPC), with no fishing pressure and the Palma bay, with a very strong fishing pressure. The results of the analysis show that the population of the Palma bay has the smallest mouth compared with NPC because big mouthed individuals have been removed last years. No significant differences were seen between body heights, so further testing would be necessary to get some conclusive. We also studied the origin of these physiological changes, and they may be genetic or environmental. To study the origin, we obtained larvae from captured individuals of both locations to discuss possible physiological similarities with adults, but no differences in mouth and body sizes were found between larvae of two locations. These larvae died on the third day, so it would be interesting to get youth individuals to study the physiological development in these growth stages. This study provides a tool to determine the origin of a random *S. scriba* individual analysing their body shape, and this can be extrapolated to other species doing previously the sampling in different fishing pressure localities and doing the data analysis.

3. Introduction

Fishing is one of the most important sources of energy worldwide and consequently wild fish has been harvested through hooking and netting for ages (see the case of the oldest hook found ever in O'Connor *et al.*, 2011). The actual consequence of the historical intensive exploitation above the sustainable yields is that today many stocks are exploited under unsustainable yields and most of them show signs of overexploitation (Pauly *et al.*, 2003; Worm *et al.*, 2009). This has generated important social and economical conflict (Hilborn and Walters, 1992). For example, the collapse of the Northern Cod generated fish populations with early ages of maturation and smaller sizes (yields) which affected negatively the important industry associated to the harvest and distribution of this important marine resource (Olsen *et al.*, 2004). However, the assessment and management of fisheries is not trivial and demands sophisticated social and ecological approaches which, in many cases, it generates conflicts among stakeholders.

One key of the aspect of the assessment and management of fisheries is understanding the selective consequences of fishing mortality in the population dynamics of fish stocks (Kuparinen and Merilä, 2007). Fishing directly exercises a pressure on the fish populations that inhabit coastal waters by direct extraction of biomass. These changes do not only affect the population dynamics structure of a given stock, but also to the entire ecosystem (Pauly *et al.*, 1998). However, fishing can generate indirect consequences on the fish stocks because harvesting is almost never random (Heino and Godø, 2002). That is, fishing gear are usually designed to catch specific sizes, sex or other traits which generates differential selection in the wild populations which can enhance the direct consequences of the biomass extraction with also implications for recovering that population (Fisheries-induced evolution) (Allendorf and Hard, 2009). Therefore, understanding the selective process of fishing gear and their later consequences in the population is a key aspect for successful management of fish stocks.

Positive-size selection due to the properties of the commercial fishing gear is by far the most studied trait that is subjected to induce selection of wild stocks (Laugen *et al.*, 2012). During the last decade it has been theoretically and empirically evidenced that size-selective fishing may generate selection differential in heritable life-history traits (age of maturation, growth and

reproduction) that collectively reduce the adult body size (Jørgensen *et al.*, 2007). The size-independent selection properties of the fishing gear, for example, behaviour or morphology, are less studied and understood (Uusi-Heikkilä *et al.*, 2008). However, size-independent selection of behavioural and morphological traits is common in many passive fishing situations such as recreational fisheries (Sutter *et al.*, 2012). There is growing literature that shows how fishing is selective for shy and low exploratory fish (Biro and Post, 2008). For example, hook and line fishing mainly captures fish with larger swimming speed that explores more habitats (Alós *et al.*, 2012). Thus, there is evidence that behaviours can generate differential selection of fish population independently of the fish body size.

The relationship between morphological traits and fishing selection (within a given species) is much less studied and understood, but the physical interaction between the fishing gear, the fish and the well known relationship between morphology and behaviour should eventually generates selection differential favouring certain morphologies. In fact, Alós *et al.* (2014b) have just demonstrated how recreational fishing selects for the size independent small mouth fish and deeper body shapes in a marine costal fishery. That findings agreed with previous studies that demonstrates how commercial fishing selects for certain body shape configurations (Slender fish and fishing nets,(Heino and Godø, 2002)) because the direct fishing interaction across the fishing nets and body morphology (Hamon *et al.*, 2000). Moreover, Alós *et al.* (2014b) explains that shallow and elongated bodies are more vulnerable because these body configurations are adopted by fish that has more steady swimming and larger swimming speed and, therefore, has a larger spatial coverage and a higher probability to encounter a fisher (Alós *et al.*, 2012). Therefore, recreational fishing should generate a selection on body shape which generates changes in the whole of the exploited population as fishing mortality is not a random process for body shape. Still, no works tested this prediction in natural populations.

The objective of this study is to provide empirical evidence that populations exposed to angling pressure present a different configuration on body shape in accordance to those predictions made by Alós *et al.* (2014b) (i.e. smaller mouth areas and deeper and elongated bodies). Distinguishing if these changes are generated by the fishing or by environment is not easy (e.g. for the natural

predation). There is substantial literature demonstrating how chemical cues from predators or congeneric individuals exposed to predation can induce changes in the morphology (Domenici *et al.*, 2008; Frommen *et al.*, 2011; Hulthén *et al.*, 2014). In fact, although the changes expected by natural selection on body shape are the same in terms of size-independent body shape (recreational fishing induces and natural predators selects for deeper bodies), for the mouth size natural selection should drives the population in the opposite direction (favouring larger mouth) (Alós *et al.*, 2014b). Therefore, the real image of the population in terms of body shapes exposed to fishing and natural mortality is difficult to foreseen. In this study, we studied the size-independent body shape of different population of the serranid *Serranus scriba* exposed to a different level of historical angling pressure and natural predators (from the most important fishery to a sanctuary area; see the studied areas in Alós *et al.* (2014a)) to test the hypothesis of: *i*) The largest fishing pressure, the smallest mouth size and *ii*) the largest predator mortality, the largest mouth size. If we find consistency in our results we are able to get a direct metric explaining the fishing consequences of fish populations due to analysis of morphology, and this do not requires killing samples (e.g. study of growth using otoliths) or large expansive investment to ensure behaviour in the field (e.g. acoustic telemetry). Moreover, to demonstrate if the image of the population is caused by a plastic response or comes from genetic changes of the population under identical environmental conditions, we need to test for consistency in body shape differences in the offspring following the findings found by Marcil *et al.* (2006). The final objective of this work is understanding the differences of body shape to identify fish stocks. That is, usually body shape is used to identify and classify fish stocks. However, exist a very limited number of studies with the causes of this changes. Here we specifically test such a causes and deeper inside our understanding of how eco-morphology can help us into the development of sustainable fisheries.

4. Materials and methods

4.1 Study-case species: *Serranus scriba*

Serranus scriba (Linnaeus, 1758) is small specie that belongs to the family Serranidae, distributed in temperate coastal areas of the Mediterranean, Black Sea and the Atlantic coast to Mauritania (Bauchot, 1987). *S. scriba* usually inhabits seagrass (*Posidonia oceanica* and *Cymodocea nodosa*) and rocky bottoms, being common in lower than 20 meters depths (Fasola *et al.* 1997). *S. scriba* feed on small fish and benthic invertebrates, and is one of the main contributors to the total biomass of fish that occupy these habitats (Deudero *et al.*, 2008; Pinnegar *et al.*, 2000). It is a simultaneous hermaphrodite with external fertilization and the early life stages (eggs and larvae) are pelagic. Its reproductive potential (number of eggs that can lay a female in a year) is highly variable and the spawning season has a peak in the months of May and June. The life span is relatively short and sexual maturity is reached during the first or second year (Alós *et al.*, 2009).

S. scriba has a little importance to the commercial fishery, but it is one of the most exploited species (both in terms of abundance and yield) for recreational fishing in the north-western Mediterranean sea (Morales-Nin *et al.*, 2005). In fact, there is growing evidence that the depletion of biomass by recreational angling can alter the wild populations of *S. scriba*. Cardona *et al.* (2007) reported a negative relationship among the relative abundance, biomass and average size of *S. scriba* and the recreational fishing intensity. Alós *et al.* (2013) and Seytre *et al.* (2013) have reported similar result, and exploitation across a gradient from marine protected areas (MPAs) to open access areas resulted in lower intensities of *S. scriba* in the exploited areas than the protected ones. Alós *et al.* (2014) have recently reported that the exploitation of *S. scriba* by recreational angling may induce strong effect on the life-history of this specie with a result of a downsizing of adults with implications for the fisheries sustainability. The high vulnerability to recreational angling has been attributed to the bold behaviour of this specie (Alós *et al.*, 2014a), the large mouth area with respect of the body size (Karpouzi and Stergiou, 2003) and its strong site fidelity (March *et al.*, 2010).

In terms of morphology, its body shape is long and tall (see Figure 1) with a pointed outline. The head is big and the mouth is wide with extensible jaws. The teeth are small and pointed. It has three spikes at the operculum and at the

preoperculum, with the top side jagged. The dorsal and anal fins are yellow with blue, pink and red spots, while the pectoral has blue transversal stripes. The pelvic fins are brown. The body presents a multitude of colors from yellow to red. It has between five and seven vertical stripes which can be divided. These bands are gray or violet. The head has a pink and orange tone with lines that remember the characters of pictographic writing. Adults have a blue ventral stain.

4.2 Study site I: the National Park of Cabrera (NPC)

The NPC was declared a sanctuary (a no-take marine protected area or MPA) in 1991 (Francour *et al.*, 2001). Since recreational fisheries were abandoned in NPC, *S. scriba* top-predator species and potential predators of small individuals have notably increased in abundance (e.g. *Epinephelus marginatus* (Reñones *et al.*, 1999)). NPC comprises the archipelago of the same name and its maritime environment, defined by the entire land, sea and underwater area within the following geographical positions:

39° 13'30" N, 2° 58' E
39° 13'30" N, 3° E
39° 6'30" N, 3° E
39° 6'30" N, 2° 53' 30"E
39° 10' N, 2° 53' 30"E

4.3 Study site II: Palma bay location

The Palma bay is situated on the southwest of the island of Mallorca. In contrast, the Palma bay 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. Therefore, we hypothesized that the life-history traits of the actual populations in Palma bay and NPC should respond to the selective nature imposed by angling or natural mortality, and the life history of *S. scriba* in OP should be intermediate to that in Palma bay and NPC. Palma bay is bounded on the west by *Cape Cala Figuera* (39°27'25.0" N, 2°31'19.6" E), and on the east by *Cape Blanc* (39°21'45.6" N, 2°47'15.1" E).

4.4 Sampling of adult individuals

On May 17, 2012 were collected by experimental angling 68 individuals from NPC and 45 individuals from Palma bay. The fish were transported in oxygenated pounds to the *Laboratori d'Investigacions Marines i Aqüicultura* (Limia, Andratx). We proceeded to dial (with an external identification mark) and kept them under natural light tanks with a continuous supply of filtered seawater by ultraviolet rays. Then, measures of total length and total weight were taken.

4.5 Offspring: rearing fish under controlled conditions

In order to separate the effect of the environment in the hypothetical changes on body shape observed in adult individuals, we reared the sampled adult fish in captivity to obtain the offspring of both populations (Conover and Baumann, 2009). Previous studies show how *S. scribe* do not spawn under lab conditions, likely due to the combination of captivity-induced stress and the lack of an appropriate natural spawning environment (Alós *et al.*, 2013). Therefore, spawning was induced through administration of synthetic agonists of gonadotropin-releasing hormone (GnRH α), which has been successfully used in other species of the Serranidae family, such as *Ephinephelus marginatus* (Marino *et al.*, 2003). GnRH α stimulates the pituitary synthesis and the releasing of LH, and induces ovarian steroidogenesis and oocyte maturation (Mylonas and Zohar, 2000; Zohar and Mylonas, 2001). Individuals were slightly anesthetised with MS222, and a dose of GnRH α (mean and s.d. of 0.0018 ± 0.0009 ml per g of fish) was inserted in the peritoneal cavity using a hypodermic needle. The fish were allowed to spawn undisturbed in the tank, which was examined every hour for the presence of eggs. After spawning, the tanks were checked for the presence of fertilised eggs (floating eggs in an intermediate position). Adult individuals were removed from the holding tank, and the water flow and aeration were reduced to prevent damage to the eggs. The temperature and salinity remained constant throughout the experiment and the offspring of both populations was obtained. We finally obtained and analysed 22 larvae from NPC and 20 larvae from the Palma bay.

4.6 Measuring body shape

The basis of our approach was to compare the geometric body shape of individuals sampled in both populations (NPC and Palma bay) in the two ontogenic groups (larvae and adults). We processed a subsample to confine the analysis to a narrow size range. Although the mean size did not differ from the original sample, limiting the body shape analysis to fish within the same narrow size interval controlled for possible allometric effects of size on body shape ensures that our results were size-independent.

Adult fish with different condition due to variation in food resource intake are likely to have different body proportions influencing the body shape analysis (Einen *et al.*, 1998). To account for systematic variation in fish condition of fish sampled with both methods (Huse *et al.*, 2000), we calculated the relative condition index (RCI) of adults and it was used as co-variate in the data analysis. RCI was calculated as the ratio between the observed weight and the predicted weight from an independently estimated length-weight relationship for both species of the area (Morey *et al.*, 2003) following the protocol by Morgan (2004). The RCI was preferred because is independent of body size (Morgan, 2004). Narrowing body size and controlling body condition were done to remove any potential confounding effect on body shape and obtaining a cleaner relationship of body shape and the origin of the sample (population or ontogeny stage).

4.7 Data analysis

The body shape of each individual was analysed using a landmark-based method (Rohlf and Marcus, 1993) and we performed two independent analysis (one per ontogenic stage). To that end, we selected 18 homologous landmarks in adults and 17 homologous landmarks in larvae (Figure 1). The coordinates of these landmarks for each individual were acquired from a dorsal (left side) image of the fish using the tpsDig2 software (Rohlf, 2004). The selected homologous landmarks of individual adults were: *i*) tip of the upper jaw, *ii*) anterior of the middle axis eye, *iii*) posterior of the middle axis eye, *iv*) first hard ratio insertion of the dorsal fin, *v*) last hard ratio insertion of the dorsal fin, *vi*) last ratio insertion of the dorsal fin, *vii*) dorsal junction between the tail and body, *viii*) central junction between the tail

and body; *ix*) ventral junction between the tail and body, *x*) posterior insertion of anal fin, *xi*) anterior insertion of anal fin, *xii*) anterior insertion of pelvic fin, *xiii*) posterior corner of the upper jaw, *xiv*) corner of the pre-operculum, *xv*) ventral insertion of the pectoral fin, *xvi*) middle insertion of the pectoral fin, *xvii*) dorsal insertion of the pectoral fin and *xviii*) upper corner of the operculum (see Figure 1).

The selected homologous landmarks in larvae were: *i*) tip of the upper jaw, *ii*) junction between upper jaw and cranium, *iii*) anterior of the middle axis eye, *iv*) centre of the middle axis eye, *v*) posterior of the middle axis eye, *vi*) junction between central transversal gap with dorsal side, *vii*) upper posterior black spot, *viii*) tail tip, *ix*) lower posterior black spot, *x*) black spot junction between posterior yolk sac tip and ventral side, *xi*) posterior yolk sac tip, *xii*) anterior yolk sac tip, *xiii*) posterior corner of the upper jaw, *xiv*) tip of the lower jaw, *xv*) tip under the eye, *xvi*) junction between central transversal gap with ventral side and *xvii*) centre of the central transversal gap (see Figure 1).

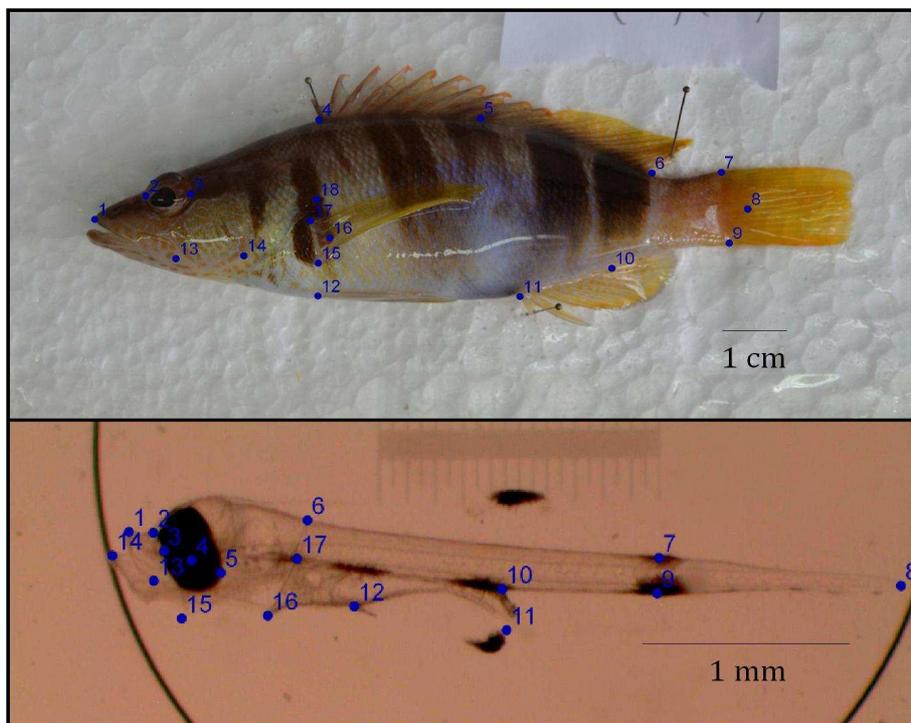


Figure 1 Landmarks (n =18 in adults and larvae n = 17) acquired to describe the body shape of the *S. scriba* in the populations studied: the NPC and Palma bay.

The raw coordinates were superimposed using General Procrustes Superimposition (GPA) as implemented in the function *procGPA* from the *shapes* library (Dryden, 2012) of the R package (R Development Core Team, 2011). The superimposed coordinates were used as shape descriptors for further analyses. Although adult fish were carefully placed under the camera in a standardized way, they suffered from some dorso-ventral bending. The shape differences associated with this bending would not represent true shape differences among gears (called arching effect, (Valentin *et al.*, 2008) that might obscure any shape patterns. We removed the arching effect by projecting the shape descriptors onto a vector (Burnaby's orthogonal projection, figure 2) that modelled the shape changes associated with bending following the method provided by Valentin *et al.* (2008).

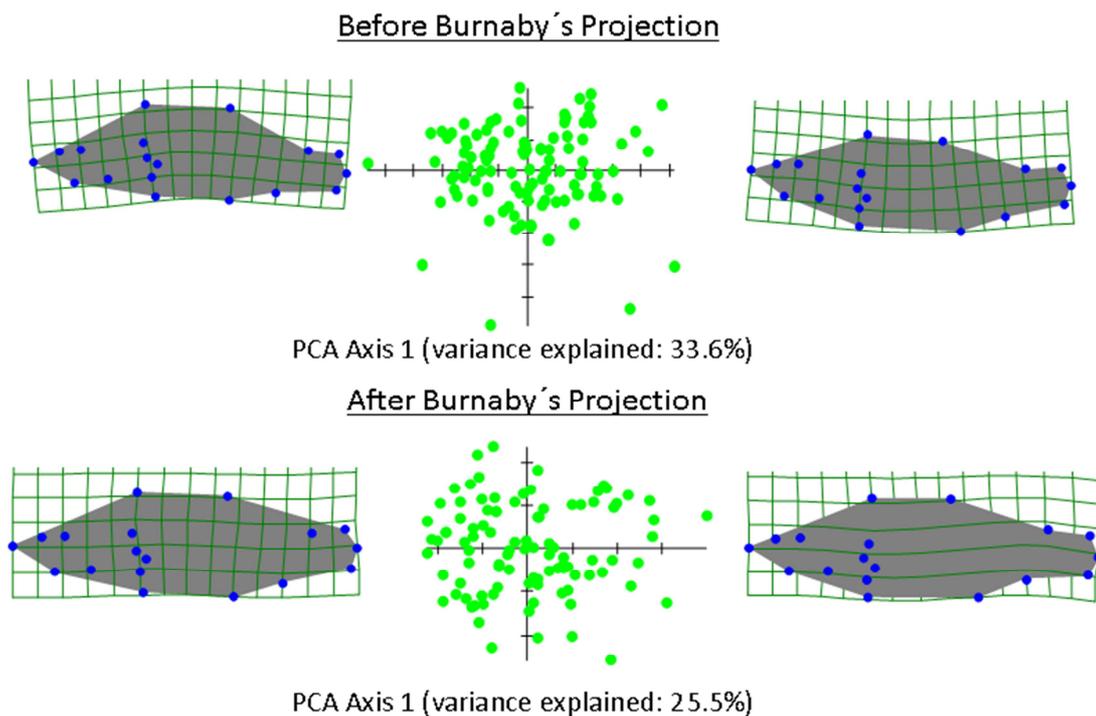


Figure 2 Principal Component Analysis (PCA) of the body shape descriptors before and after removing the arching effect on the adults of *S. scriba* (Burnaby's projection method). The plot shows the bi-plot (the first two components of the PCA) as well as the variance explained by the first component. The configuration and deformation grids of the extremes (positive and negative) of the first axis is also shown. Note how before the Burnaby's projection, an arching effect was evident.

Then, arching-free shape descriptors were analysed by conventional multivariate linear modelling. The response matrix (arching-free body shape) was constructed by the shape descriptors (columns) of each fish (rows). The explanatory variables were fish size and fish condition in the case of adults and study site (NPC and Palma Bay). The multivariate analysis was completed using the function *rda* as implemented in the *vegan* library (Oksanen, 2005) of the *R* package. After removing (backward elimination) non-significant variables or interactions, the partial effects of the variables of interest were tested using a permutation approach. Finally, a Linear Discriminant Analysis (LDA) was completed with the multivariate residuals after removing the effects of size, condition and study site. The reliability of the differences between sampling methods inferred from LDA was checked via leave-one-out cross validation.

5. Results

5.1 Adult and larvae sample sizes, fish sizes and condition

To test the hypothesis of body shape differences in *S. scriba* between populations, we selected a sub-sample from the whole individuals sampled to avoid differences on fish sizes and condition (in the case of adults) (see M&M). In adults, the final sample for morphometric analysis included a total of 103 individuals (NPC = 59 individuals and Palma bay = 44 individuals), while for larvae the final samples included a total of 35 individuals (NPC = 19 individuals and Palma bay = 16 individuals). Figures 3 and 4 show the distribution of fish sizes and adult condition of the used sample for the analysis. Adult and larvae fish sizes (as total length in mm) and the adult conditions were measured and significant differences between means were tested using ANOVA and the residuals of the model were tested for normality (Table 2). In all cases there were no significant differences, and all samples were not different in terms of fish size (Table 1).

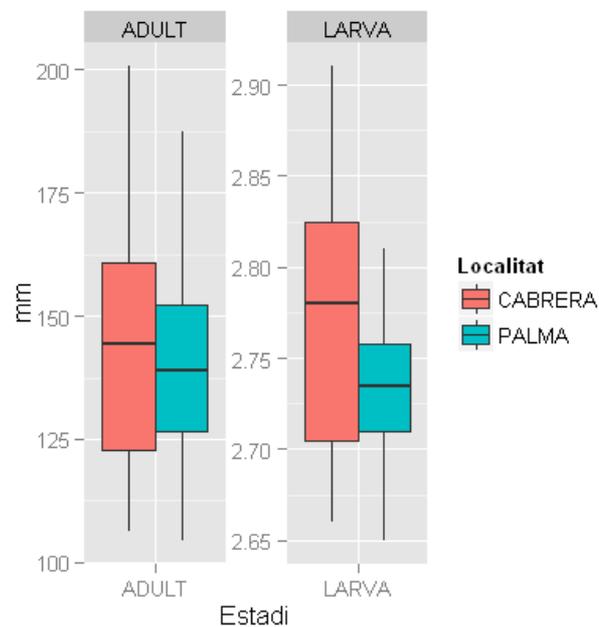


Figure 3 Box-plots showing the adult and larvae sizes (in mm) in both populations: the NPC and Palma bay.

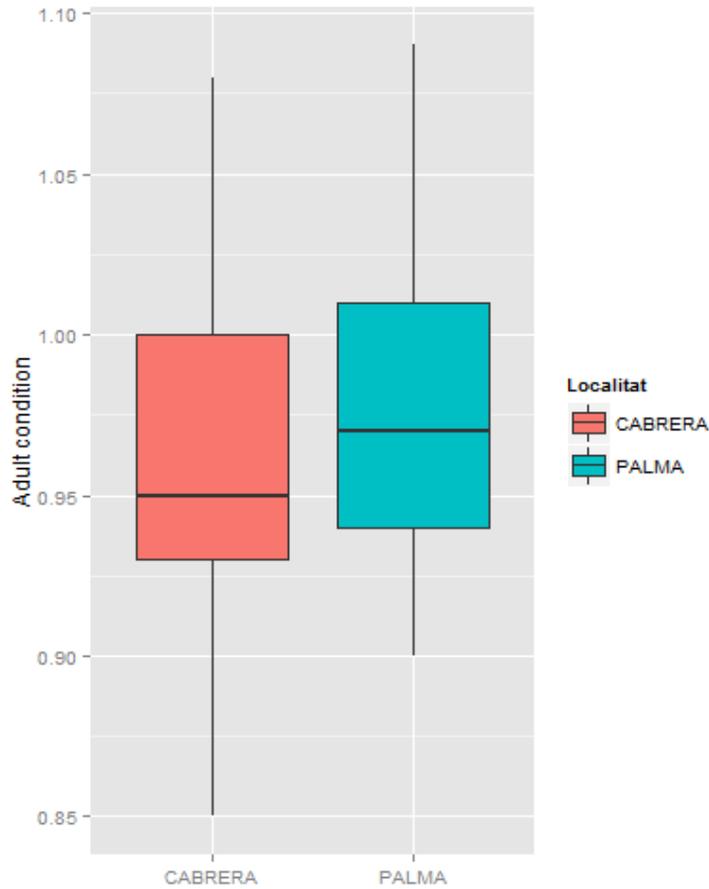


Figure 4 Box-plots showing the adult condition (as relative condition) of the adults in both populations: the NPC and Palma bay.

Table 1 Results of the generalized linear model (GLM) to test the absence of differences for size and condition (in the case of the larvae) between the samples obtained in NPC and in Palma bay. The table shows the estimate and their standard error (s.e.), the t-value and their probability. Note how the effect of interest was not significant in all cases (p-values > 0.05). All models were tested for normality.

	Estimate	s.e	t-value	Pr(> t)	Pr(> t)
<i>Fish size adults</i>					
(Intercept)	4.96	0.02	249.24	<2e-16	***
Site (Palma Bay)	-0.02	0.03	-0.70	0.48	
<i>Fish condition adults</i>					
(Intercept)	0.96	0.01	148.95	<2e-16	***
Site (Palma Bay)	0.02	0.01	1.70	0.09	
<i>Fish size Larvae</i>					
(Intercept)	2.77	0.01	200.69	<2e-16	***
Site (Palma Bay)	-0.04	0.02	-1.91	0.07	

5.2 Adult body shape and between-population differences

The Principal Component Analysis (PCA) of the body shape descriptors for the adults of *S. scriba* showed the variability of our sample and suggested a separation between the individuals of the populations (as many individuals of the exploited population deviated from the average mean, Figure 5). These differences were confirmed by the redundancy analysis (RDA) and not only population, but also the variance attributed to the adult fish size and condition was significant (Table 2). A total of a 60% of the variance explained was attributed to the effect of the population, 27% to the effect of the fish size and a remaining 13% to the effect of the condition (Table 2). The Linear Discriminate Analysis (LDA) performed with the size- and condition-independent scores showed high degree of classification of the samples (knife leave one cross validation) and the 91.5% and the 79.5% of the individuals were successfully classified as individuals from the population of NPC and Palma Bay respectively. These high power of classification of our individual's suggested that populations were very different in terms of body shape. Figure 6 shows the projection of one individual of average size and condition inhabiting the exploited and unexploited population. Results suggested a clear decrease in the size of the head (including a strong change in the mouth size, landmarks 1 and 13) where in exploited populations individuals were characterized by small mouth areas (Figure 6). Other differences were also mainly attributed to the landmark 5 (point of change between hard and soft radius in the dorsal fin). No changes in the body depth were evident (Figure 6).

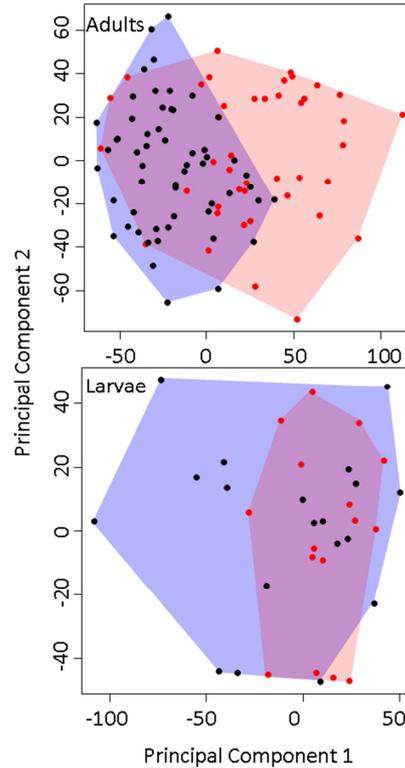


Figure 5 Principal Component Analysis (PCA) of the body shape descriptors for the adults (upper panel) and larvae (lower panel) to preliminarily explore the patterns of variability on the morphology. Each individual is shown as a dot and categorized by population (the NPC in blue and Palma bay in red).

Table 2 Results of the redundancy multivariate analysis performed to test differences in the geometry of the body shape and the explanatory variables considered here for each of the ontogenic stages (adult and larvae). The table show the variance attributed to each of the variables considered, the F-statistic and their probability (p-value) after 999 free permutation tests. Significant (*), highly significant (**) and very highly significant (***).

	Variance	F-value	Pr(>F)	
<i>Adults</i>				
Population	635.00	12.91	<0.001	***
Fish size	290.50	5.91	<0.001	***
Fish condition	141.00	2.87	0.008	**
Residual	4869.30			
<i>Larvae</i>				
Fish size	309.80	2.53	0.014	*
Population	285.10	2.33	0.017	*
Residual	3912.40			

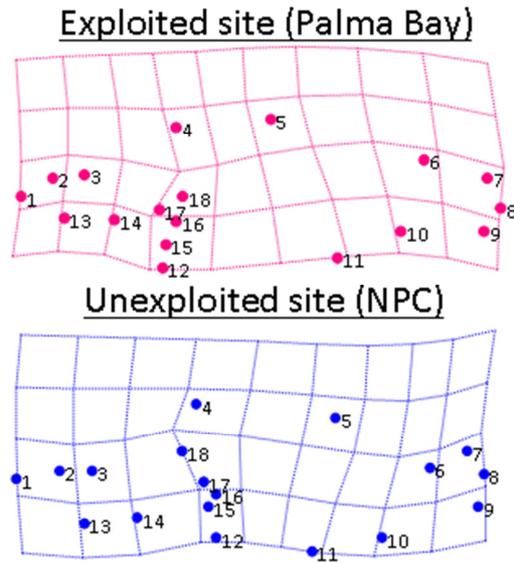


Figure 6 Configurations and deformations grids (from the average) of the extremes (positive and negative) of the first axis corresponding to the population effect in the adults of *S. scriba*. The red configuration shows the average individual with average size and condition of *S. scriba* in the exploited population (Palma bay) and the blue configuration from unexploited population (NPC). A 10x magnification is applied to better visualize the highly significant effect of the population on the body shape.

5.3 Larvae body shape and between-population differences

The PCA of the body shape descriptors for the larvae of *S. scriba* showed the variability of our sample and suggested some separation between the individuals of the populations (although variance was much larger than adults, see axis 1 in Figure 5). These differences were confirmed by the redundancy analysis (RDA) but results were no as evident as for the adults (Table 2). A total of the 57% of the variance explained was attributed to the effect of the population, while the effect of size accounted for the 47% of the variance explained and in both cases the variance was significant (Table 2). The LDA was much less powerful and only 47% and 50% of the individuals were successfully classified as individuals from the population of NPC and Palma bay respectively. Figure 7 shows the projection of one average sized individual of inhabiting the exploited and unexploited population. Considering the main drivers of the difference of body shape observed in the adults, differences in the mouth of larvae (landmarks 1 to 13) were consistent and individual inhabiting exploited areas has also smaller mouths (Figure 6). The landmark 10 in larvae (equivalent to the landmark 5 in adults) also showed a strong change between populations. Landmark 14 also exerted a strong

influence on the differences on the population (this landmark was the anterior point of the lower jaw). Also no changes in the body depth were evident (Figure 6).

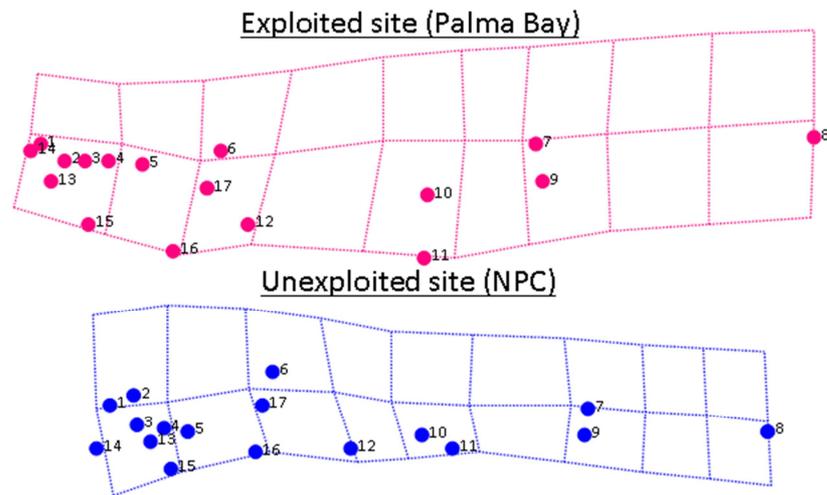


Figure 7 Configurations and deformations grids (from the average) of the extremes (positive and negative) of the first axis corresponding to the population effect in larvae. The red configuration shows the average individual with average size and condition of *S. scriba* in the exploited population (Palma bay) and the blue configuration from unexploited population (NPC). A 10x magnification is applied to better visualize the highly significant effect of the population on the body shape.

6. Discussion

A recent theoretical work suggested that recreational angling generates a selection differentials independently of the body size for certain body shape traits due to two different mechanisms: the physical interaction of the hooks (selecting against large-mouth individuals) and the co-variation between behavioural and morphological traits (e.g. body depth and swimming performance). The work performed here supports this theoretical prediction. We found a consistent pattern of morphological divergence between the unexploited and exploited populations mainly characterized by the presence of adult individuals with small mouth sizes in the exploited ones (while controlling for the body size or/and condition). Therefore, our initial working-hypothesis has received substantial empirical evidence. Morphological divergence was consistent in the offspring reared in captivity under identical conditions, and we also found significant differences on

the body shape of the unexploited and exploited population. Due to the limit age of the offspring that were available for the morphometric analysis (only 3 days after hatching larvae) and the large unexplained variability, we have to be cautioned interpreting this last finding. However and overall, our work suggests that recreational angling can induce changes in the body shape configuration that can be used for monitoring the ecological and evolutionary consequences of recreational fishing in the wild populations.

We found a clear size- and condition-independent pattern of morphological divergence in the exploited and unexploited population characterized by small mouth sizes and a difference in the landmark that determines the change between hard and soft radius of the dorsal fin (landmark 5 in adults). The strength of these differences was evidenced by the high power of classification of individuals to one or the other population (LDA results). There is substantial evidence that recreational angling may select against the larger individuals by the physical interaction of the body and the fishing gear (Lewin *et al.*, 2006; Cerdà *et al.*, 2010), causing both ecological and evolutionary implications for the exploited populations (Matsumura *et al.*, 2011). Fishing can also select for morphological traits independently of the body size as studied here. For example, Hamon *et al.* (2000) demonstrated how deeper bodied sockeye salmon, *Oncorhynchus nerka*, had a larger probability of being entangled in the fishing nets; the resulting fisheries-induced selection pressure acted in the opposite direction of sexual selection and predation-based natural selection pressures (Kendall and Quinn, 2013; Alós *et al.*, 2014a). In recreational angling, the fishing gear (hooks) interact with the mouth and it has been recently predicted that those individuals (at the same size) with larger mouth sizes are prevalently removed from the population (Alós *et al.*, 2014b). This fact agrees with the finding obtained here as the exploited population is characterized by individuals with small mouth areas (those survivals) and can be directly the image of the selective exploitation against the vulnerable morphotypes (those with larger mouth areas). It is interesting to note that the PCA describing the variance of the different body shape configurations studied here shows a full overlap of the individuals of the unexploited population (NPC) with the individuals of the exploited one (Palma bay), while most of individuals of the exploited population do not overlap with the unexploited ones.

This means that most of the morphological configurations present in Palma Bay are not present in the NPC (where most of the individuals are characterized by large mouth areas). This suggests that new body shape configurations could be generated by the effect of fishing in the exploited population due to the selective nature of angling on the body shape and the historical exploitation rates.

However, not only the mouth area, but also the point of change between hard and soft radius of the dorsal fin (landmark 5 in adults) changed between populations. Individuals inhabiting the unexploited population have a larger section of the dorsal fin with hard radius. It is very difficult to interpret this finding, however, it is well known that the hard radius of the dorsal fin play an important role on the enhancement of the escape behaviour from predators (Webb, 1984; Langerhans and DeWitt, 2004). Since the no-take MPA of the NPC was born, the number of predators of *S. scriba* has increased notably (e.g. larger groupers, (Reñones *et al.*, 1999)), which could eventually being favoured (through natural selection) changes in the dorsal fin of *S. scriba* in response to this higher predation risk. This is only a speculation and needs further work to be validated. However, this increased natural predation risk observed in the NPC could be the reason to the absence of differences in the body depth between populations. The selective properties of the selective exploitation by angling predicts deeper bodies (Alós *et al.*, 2014b). However, the final image of the exploited population is difficult to foreseen in the wild as the natural selection imposed by the natural predators acts in the same direction (i.e. both natural predators and angling predict deeper bodies due to the relationship between body depth and behaviour (Brönmark and Miner, 1992; Chivers *et al.*, 2007; Domenici *et al.*, 2008; Alós *et al.*, 2014b)). We found no evidence for a change in the body depth, but we compared two populations that are in the extremes of angling and predation risk. Therefore, the lack of differences does not necessary imply that recreational fishing does not play a role in the body depth of the individual (as in the NPC individuals can also be enhance to be deeper due to the presence of predators). The consideration of another population exposed to small levels of predation risk as well as angling pressure should eventually solve the question. However, as predation risk and angling pressure are usually negatively correlated in species targeted by angling (recreational fishing reverently captures predatory fish species (Donaldson *et al.*,

2011)), while MPA favour the presence of large predatory species. In all cases, our work provides for the first time strong evidence that the morphological divergence induced the selective properties of the adult fish on morphological traits.

One should discuss what the expected negative consequences of this morphological divergence are for exploited wild stocks. The mouth size or the relative mouth size (Karpouzi and Stergiou, 2003), are the morphological traits key for many life-history functions. For example, the mouth morphology has an important role facilitating the exploitation of foraging niches, which in some species has been strongly involved in sympatric speciation (Wainwright, 1988). Population characterized by individuals who respond to the selective nature of recreational fishing may strongly alter the predator-prey relationships in natural environment. Larger mouth gapes benefit individuals that are specialized to prey on large-bodied prey items, like *S. scriba* (Karpouzi and Stergiou, 2003), and fishing selection on mouth size may affect negatively the foraging success and energy intake of surviving individuals. This should negatively affect the productivity (the biomass) of the individual and the overall productivity (yield) of the population. In fact, reduced population yield is one of the most important negative consequences of the exploitation of natural wild fish stock (Pauly *et al.*, 1998). Decreased yields not only has consequences at different scales of the food web (Audzijonyte *et al.*, 2013), but also for the economical and social consequences for human (Eikeset *et al.*, 2013). Therefore, the fishery-induced changes in the mouth morphology of the exploited populations observed here could eventually generate a number of indirect negative consequences for the whole of the fishery. In the opposite site, fish with larger mouth sizes (as those observed in the NPC) are expected to increase the productivity of the individual as well as the overall population yield. This finding agrees with the recent empirical evidence on the populations of *S. scriba* in the Mediterranean sea (Alós *et al.*, 2014a). The awareness of the impact of recreational fishing in the Mediterranean sea is growing (Font and Lloret, 2014), therefore our contribution provides a hidden indirect consequence of recreational fishing on the wild populations never described.

The morphological divergence observed here could be the result of environmental plasticity or attributed to genetic changes. The study fisheries-induced evolution or genetic changes in wild stocks has gained interest during the last two decades due to the negative consequences, not only for wild stocks and associated ecosystem, but also due to their negative social and ecological consequences (Law, 2000; Heino and Godø, 2002; Jørgensen *et al.*, 2007; Law, 2007; Dunlop *et al.*, 2009). The historical selective nature of fishing should eventually induce changes in the genetic architecture of the exploited species by selectively removing certain vulnerable phenotypes and associated genotypes (Allendorf *et al.*, 2008). Genetic changes due fishing on morphological traits should be particularly favoured due to the larger heritability of those traits compared to the behavioural and life-history ones (Mousseau and Roff, 1987). This suggests the idea that our morphological divergence can be attributed to the genotypic selection of vulnerable body shape by recreational fishing. However, if the changes in exploited stocks are caused by phenotypic plasticity or are caused by genetic changes is still under debate (Jørgensen *et al.*, 2008), mainly due to the absence of a robust cause-and-effect methodology to disentangle those effect imposed by the environment from those by fishing. Conover and Baumann (2009) proposed that a possible solution is rearing under identical environmental conditions the individuals exposed to different degree of historical exploitation. In the work performed here, we reared the adult fish in captivity and we obtained a weak consistent pattern on the morphological divergence in the offspring in the same line with the adult populations (especially regarding the mouth area). However, these results have to consider with many caution as the limitations of our approach that are discussed below.

Particularly the major limitation of this study is the young nature of our offspring. Ideally, the hypothesis of heritability on the morphological divergence in fully-developed life stages (i.e. juveniles) should be tested. In a similar approach than those performed here, Marcil *et al.* (2006) used 60 days post-hatch juveniles to extract robust conclusion to detect countergradients of environmental and genetic morphological divergence in the Atlantic cod, *Gadus morhua*. Although we found some differences between populations, our 3-day after hatching may be not enough developed to obtain a clear body shape of the further juvenile individual,

and maybe are not representative of the true heritability of the adult body shape. In fact, the large variability observed in our larvae sample (for example, represented by the level of aggregation of the samples or the magnitude of the axis 1 in the PCA) may notably difficult the interpretation of the body shape variability and may hide the real patterns of variability. Because that reason, we recommend using older life stages of development of fish for this purpose for testing morphological divergence in adults and offspring and take care with the interpretation of the results present here. However, obtaining older offspring is extremely challenging in *S. scriba*. In fact, this is the second published case of viable offspring in this simultaneous hermaphrodite. As *S. scriba* has no interest neither for commercial fisheries nor aquaculture companies, there is no a standardized protocol to get viable offspring. This species has a particular mating behaviour and they need an induction for spawning (Alós *et al.*, 2013). The next step for further work should be improve this rearing protocols and test if our differences are consistent in older development stages to deep inside our understating on how recreational angling can induce ecological and evolutionary changes in the wild fish populations.

Besides the major limitation of the absence of a population with low levels of angling and predation risk and low representativeness of our offspring results, our work allows for drawing two important key messages. First, we found evidence for the hypothesis tested in this study and we observed that the exploited population by recreational angling responded to the selective nature of the exploitation by reducing the size of the mouth, independently of the body size or condition. Understanding the later consequences of selective fisheries as well as identifying traits under selection are key aspect for proper management and assessment of any fishery (Kuparinen and Merilä, 2007). Therefore, we provide evidence for the first time that recreational fishing can induce changes in the average body shape of the population with implication for management, as new configurations could reduce population yield. In this sense, the study of the body shape using geometric morphometry could be a useful index for detecting and management exploited stocks. Second, our findings suggest that the fishery-induced changed in the morphology could be generated by heritable morphological variance. However, our work only provide a weak evidence for this

changes and improved approaches should be developed involving older development fish stages as mentioned. Consistent selection on body shape could induce relatively fast genetic changes in exploited populations. Therefore, disentangle if the morphological divergence observed here comes from environmental plasticity or from genetic changes should be the most important research question in the nearest future. Genetic changes favouring maladaptive traits (as the reduction in the mouth size) should eventually limit the potential for recovery the initial situation (Walsh *et al.*, 2006). Then, we hope our contribution to be your better later consequence understanding of the fisheries-induced evolution.

7. Conclusions

1. In this study we provide empirical evidences that populations exposed to different degree of historical angling pressure can show difference in the morphological traits (body shape configuration) while controlling for the individual body size and condition.
2. Our results show a significant difference in the size of the mouth of adult individuals, with the largest ones in the unexploited population (NPC) and the smaller ones in the exploited populations (Palma bay) as recently predicted (Alós *et al.*, 2014b). Individuals with smaller mouths can induce changes in the ecosystem as affect the foraging and the feeding rate of *S. scriba*.
3. No differences in the adult body depth were found. High natural predation risks are expected to increase the body of the individuals in many species (Brönmark and Miner, 1992; Chivers *et al.*, 2007; Domenici *et al.*, 2008). In a similar way, recreational fishing can generate populations of individuals with deeper bodies (Alós *et al.*, 2014b) . Therefore, our results suggest that recreational fishing exercises a similar role than natural predators in shaping the individuals in terms of body depth.
4. We have found a weak pattern of consistency in the body shape across ontogenic stages suggesting the heritability of the body shape configurations. This pattern has to be considered with caution due to two

major reasons: *i*) large variability and *ii*) differences could appear in older stages of development (i.e. juveniles, (Marcil *et al.*, 2006)). We need further work to fully disentangle the reason of the lack of differences.

5. Our relationship between population and body shape allow us to obtain an easy-to-take metric for monitoring wild population of *S. scriba* exposed to fishing for sustainable development of the fishery. Moreover, our contribution is one of the first that copy with the reason for differences in morphology across exploited stocks (separation of stocks may be the result of difference sin fishing intensities).

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