Caudal region regeneration in a natural population of the morid fish *Physiculus cyanostrophus* in the tropical eastern Atlantic ocean.

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ABSTRACT

The present study describes a remarkable caudal regeneration capacity of *Physiculus cyanostrophus*, a bentho-pelagic fish from the twilight zone. This trait reveals the ability of this particular morid to survive attacks that would be lethal in other species. In teleosts, the most widespread sublethal predation is confined to scale-eating and fin-nipping by specialized predators. In *P. cyanosytrophus* the larger sized individuals the greatest amount of tissue loss occurred in the caudal region (maximum 28 vertebrae, corresponding to 45% lost body length). The amount of regenerated tissue was independent of body losses and ranged between 5 and 19% of total length for the entire range of sizes. The frequency of regenerated individuals in the population increases with ontogeny (16.8–67.5%). Tissue losses represent a significant allocation of costs in terms of growth and offspring production. Nevertheless, regeneration capability decreases mortality in the large breeding females of a population, maximizing maternal fitness.

1. Introduction

In marine ecosystems, fishes are subject to injuries due to aggressive behaviour, predation and diseases (Winemiller, 1990; Ziskowski et al., 2008; Sinclair et al., 2011). From a trophic viewpoint, some predators in aquatic ecosystems have specialized in sublethal attack mechanisms (Farmer and Beamish, 1973; Papastamatiou et al., 2010).

Among fishes (as prey), the most widespread sublethal predation, in both fresh and marine waters, is due to specialized scale-eating (lepidophagous) and fin-nipping predators (e.g., Sazima, 1983; Winemiller, 1990; Nakae and Sasaki, 2002). Additionally, in marine ecosystems, some prey species have developed mechanisms to revert potential lethal attacks into sublethal injuries. This sublethal predation in marine ecosystems occurs among prey species with regenerative abilities and autotomy (Bely and Nyberg, 2010), such as, crustaceans, polychaetes and echinoderms. In animals, sublethal predation is the predominant mechanism of tissue loss (Bely and Nyberg, 2010). Nevertheless, it is widely accepted that sublethal predation may influence prey dynamics. The degree and consequences of these predatory effects depend on the amount of lost biomass or the loss of function resulting from sublethal attacks (Maginnis, 2006).

Research studies on regeneration, based on the ability of fish to regenerate lost tissues, has largely focused on zebrafish and electric fishes (Unguez, 2013). However, in nature, evidence of tissue regeneration is quite rare. From an ecological perspective, the population-level consequences of the regeneration of body parts are poorly understood in fishes (Maginnis, 2006; Unguez, 2013). Studies that incorporate the costs associated with the regeneration process into understanding population dynamics are necessary.

The genus *Physiculus* Kaup, 1858 currently comprises 41 valid species (see Gonzalez et al., 2018) exhibiting the highest degree of diversity within the family Moridae (Paulin, 1989). The *Physiculus* species are mainly known from a taxonomic perspective, but few data are available concerning their ecology and population structure. The *Physiculus* species are distributed in all tropical, subtropical, and warm-temperate seas of the world at depths of 100–600 m (Paulin, 1989). Some *Physiculus* species has the ability to regenerate the caudal fin. This newly regenerated fin develops a replacement skeletal structure known as the "pseudo-hypural plate" (Brüss, 1986; Paulin and Matallanas, 1990). Sublethal injuries (or regenerated caudal fin) frequently occur in Macrouridae and other Moridae genera to such an extent that total length has been replaced by preanal fin length in taxonomic and ecological studies (Atkinson, 1991). Within benthopelagic species belonging to these groups (e.g., grenadiers, rattail fishes and deep-sea cods), a high percentage of individuals with sublethal injuries or regenerated caudal fins have been found (e.g., Paulin and Matallanas, 1990; Massutí et al., 1995; Andrews et al., 1999). Nevertheless, sublethal predation in the deep-sea has not yet been explored, probably

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because ecological knowledge of these species is lacking and because most sublethal injuries are often attributed to the trawl net effect (Massutí et al., 1995). Regeneration of caudal fins has been described in macrourids and morids (Brüss, 1986; Atkinson, 1991) and tail loss occurs frequently in deep-sea gadiformes e.g *Bathysaurus mollis* specialises in biting tails off marcrourids and hence avoids parasitic infections (Campbell et al., 1980). Our study describes and evaluates the importance of caudal region regeneration in *Physiculus cyanostrophus*, including consequences in their population dynamics, growth and fitness.

2. Materials and methods

2.1. Biological data collection

Seven expeditions were undertaken to investigate the marine epi- and benthic macrofauna of the Cape Verde archipelago. Sampling was carried out off the islands of Boa Vista, Santiago, including the Bancona Bank, São Vicente, Santa Luzia, Sal, and São Nicolau in order to search for new living resources, between 2010 and 2012 and 2017, at depths of 66 m and 458 m. Expeditions were conducted in the spring (April and March), summer (June and July), autumn (November) and winter (January and February). In all cruises bottom traps and semi-floating traps (operated around 2.4 m above the seafloor) (see González et al., 2014 for trap design) were used as sampling system.

2.2. Morphology measures

Each fish was sampled (n = 917) following standard measurements for family Moridae (Paulin, 1989; Trunov 1989). The total length (TL), head length (HL) and regenerated total length (regTL) were measured to the nearest 0.01 mm. The theoretical total length (tTL) was obtained from the linear regression between HL and TL from the non-regenerated (NR) specimens to estimate the corresponding TL of regenerated individuals (R). Body lost length was estimated as the difference between tTL and the length after injury. Other measurements are explained in Fig. S1. Gutted mass and gonad mass were recorded to the nearest 0.001 g. Sex determination was assessed according to macroscopic differences in gonads. Otoliths (n = 767) were extracted, and otolith mass was recorded to the nearest 0.0001 g. Based on current ontogenetic data (maturity and fecundity), three ontogenetic groups were defined for both sexes: juveniles (females TL < 210 mm; males TL < 190 mm), young-adults (females 210 mm > TL < 300 mm; males 190 mm > TL < 240 mm) and old-adults (females TL > 300 mm; males TL > 240 mm). The specimens (n = 120) were prepared with their fins fully extended and were then photographed with a digital camera for further image analysis to obtain fin surface estimates (mm^2). Similarly, specimens with a "pseudo-hypural plate", considered regenerated individuals (R), were photographed (n = 73) to estimate their regenerated fin surface (body area from the beginning of the length regenerated to the end of the body, including fin surface; mm^2). Vertebral counts on a subsample of specimens (n = 30) were obtained from radiographs by means of an X-ray machine and were then processed with eFilm Lite™ software. The percentage of body lost length was calculated along with the number of lost vertebrae (Fig. S4).

2.3. Growth

Otolith mass versus TL and tTL of R (n = 215) and NR (n = 562) females within the same size range were compared. Otolith sections from R (n = 72) and NR (n = 159) females were prepared according to protocols described by McCurdy et al. (2002). Age was estimated twice, with two researchers reading the otolith sections according to Wright et al. (2002). Observed length-at-age was described by the *von Bertalanffy growth model* using a non-linear least square procedure of a *Gauss-Newton algorithm* for R and NR females.

2.4. Fecundity outputs

The ovaries (n = 764) were fixed and preserved in 4% buffered formaldehyde and were subsequently processed for histological analyses to verify the macroscopic maturity stage using H&E staining, following standard procedures for fish biology studies. Following the terminology of Brown-Peterson et al. (2011), spawning capable fish were selected from R (n = 42) and NR (n = 58), covering the entire range of sizes (Murua et al., 2003), to estimate the total fecundity (TF) and batch fecundity (BF) (Hunter et al., 1985). TF and BF were estimated using gravimetric methods (Murua et al., 2003). Each subsample was weighted to the nearest 0.0001 g and was then filtered via 100 μm mesh to exclude previtellogenic oocytes for the estimation of TF. The mesh size was estimated by calculating the diameter of previtellogenic oocytes with image analysis (Thorsen and Kjesbu, 2001) from early-developed subphase ovaries, following the methods of Brown-Peterson et al. (2011).

2.5. Data analysis

Differences in the HL–TL relationship between the sexes were evaluated by an *F-test*, and differences between *b* values and the expected value from isometric growth (b = 1) were evaluated by a *t-test* (Sachs, 1982).

Differences in mean TL and TM between sexes were analysed using *Student's t-test*. The *Kolmogorov–Smirnov non-parametric Z-test* was used to analyse differences in TL and TM distributions between groups male-female and R-NR (each sex).

The regeneration-ratio (R:NR) and the sex-ratio (male:female) were estimated for the whole population and for each of the three ontogenetic groups. A *Pearson Chi-square test* was conducted to test the null hypothesis of equality of frequencies between R and NR and by sexes (H_0 = 1:1 ratio) with a significance level of $\alpha = 0.05$ (Sachs, 1982; Sokal and Rohlf, 2012).

The bias and precision of annuli counts in otoliths were compared between readers, using paired *t-tests* (Campana, 2001). Estimates of ageing precision were determined using the coefficient of variation (Chang, 1982). The multivariate *Hotelling's T^2-test* was used to compare growth parameters between R and NR females (Bernard, 1981).

Otolith mass, TF and BF for R and NR females were represented as a function of tTL and TL, respectively. Potential regressions for different groups were statistically compared with slope homogeneity and covariance of linearized potential regression applying an *F-test* (Sachs, 1982). These tests evaluated the null hypothesis of equality of two regressions estimated by sexes with a significance level of $\alpha = 0.05$. The same procedure was conducted to compare TF and BF within R and NR against age.

3. Results

3.1. Regeneration pattern

A total of 917 individuals classified into two groups were sampled: non-regenerated (NR, n = 659) and regenerated (R, n = 258). R individuals had fewer vertebrae than NR individuals as a consequence of sublethal attacks, causing body loss in the caudal region. Most R individuals had a thicker caudal peduncle, produced by the regeneration process. By means of X-ray, the absence of a caudal skeleton, as well as the transformation of the last present vertebra after injury into a "pseudo-hypural plate" for insertion of new C-rays, was observed (Fig. 1).

3.2. Prevalence of tail regeneration in a natural population

The NR females reached a mean size and a mean mass larger than males (TL, $t = 8.86$ $p < 0.05$; TM, $t = 7.92$, $p < 0.05$) (Table S1). R
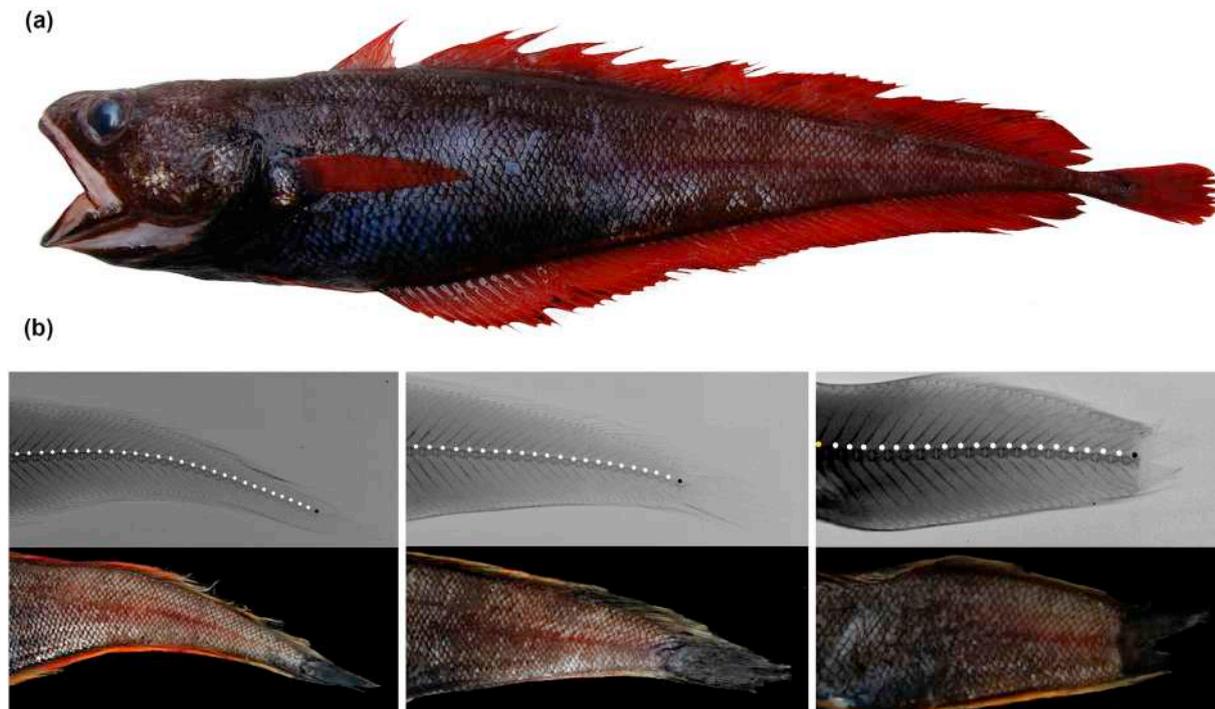
Fig. 1. (a) *Physiculus cyanostrophus* with intact and regenerated tails. (b) Radiographs of three regenerated individuals (R) within 10 and 35% of body losses in total length (blTL). Examples of a regenerated caudal region "pseudo-hypural plate" with regenerated new c-rays.
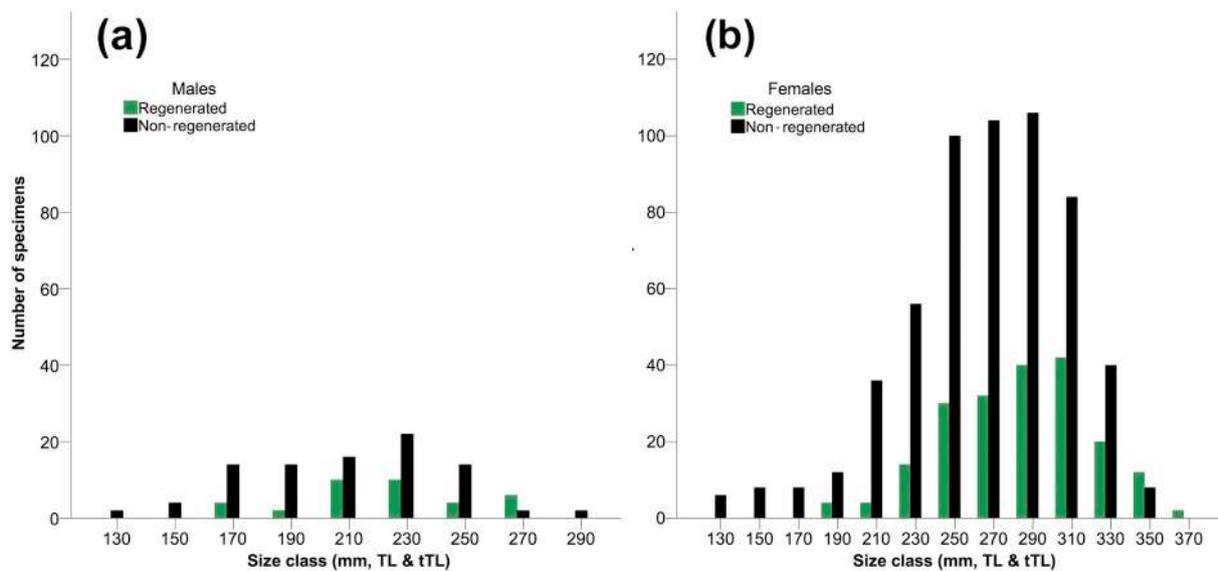
Fig. 2. Size distribution of males (a) and females (b) population of *Physiculus cyanostrophus*. Bars correspond to individuals for each size class of 10 mm TL. Green bars are regenerated individuals (R), and black bars non-regenerated ones (NR). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

females presented a mean size and mean mass greater than R males (tTL, $t = 6.62$ $p < 0.05$; TM, $t = 6.36$, $p < 0.05$). The TL and TM distributions of NR and R also differed significantly between females and males (Fig. S4b; TL, $Z = 3.93$ $p < 0.05$; TM, $Z = 3.72$, $p < 0.05$). The distribution of tTL and TM of R individuals also differed significantly between females and males (tTL, $Z = 2.61$, $p < 0.05$; TM, $Z = 2.62$, $p < 0.05$). For R females, the mean size was larger than NR ($t = 3.30$, $p < 0.05$). Conversely, a similar mean size between R and NR males was found ($t = 0.799$, $p > 0.05$) (Fig. 2a). The size distribution of R and NR groups was different, with NR females being present in the small classes, but the R group was absent in these classes ($Z = 1.47$, $p < 0.05$). Male size distributions were similar in both

groups ($Z = 0.80$, $p > 0.05$) (Fig. 2b).

NR females were more abundant than NR males (1:6.3, $\chi^2 = 348.17$, $p < 0.05$). Size classes less than or equal to 180–200 mm TL showed similar numbers of NR males and NR females (1:1, $\chi^2 = 0.923$, $p > 0.05$). However, NR females were more abundant in size classes larger than 200 mm TL ($\chi^2 > 7.14$, $p < 0.05$), mainly over 300 mm TL, where only females were observed. R Females were also more abundant than R males (1:5.14, $\chi^2 = 117.35$, $p < 0.05$). With size classes, R females and R males followed the same pattern as that observed for NR individuals. Female regeneration-ratio (R:NR) was 1:2.6 ($\chi^2 = 79.02$, $p < 0.05$). Statistical differences were found among ontogenetic groups, where dominance of NR females
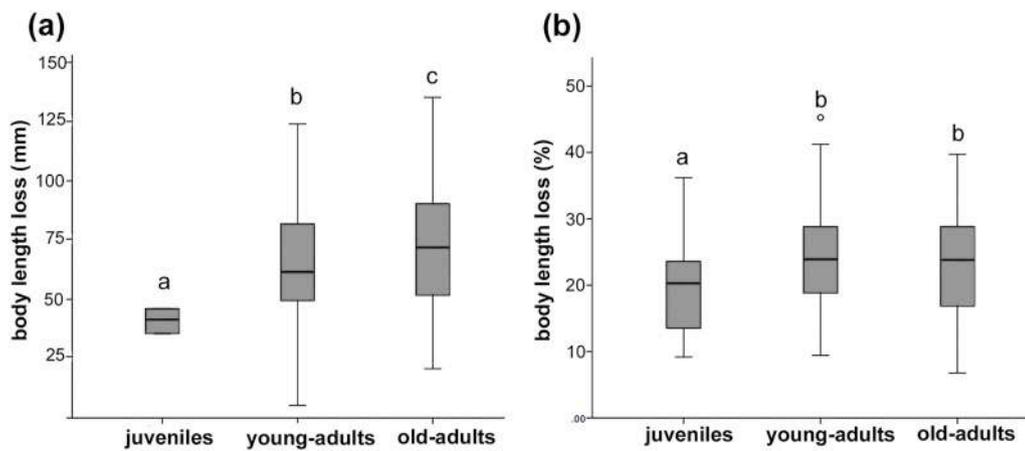
(a)

(b)

Fig. 3. Box-plot showing ranges of body lost length (a) and in % of theoretical total length (tTL) (b) for juveniles, young-adults and old-adults in regenerated individuals of *Physiculus cyanostrophus*. Different letters above bars denote statistically significant differences (p < 0.05) between ontogenetic groups. The line within each box is the median value, box ends represent the inner and outer quartiles, and whiskers are the inner and outer tenths.
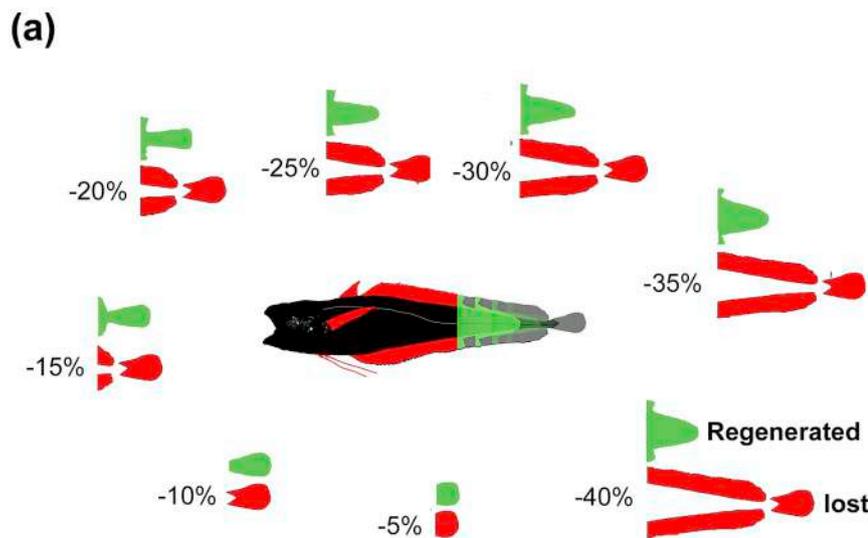
(a)

Fig. 4. (a) Schematic representation of *Physiculus cyanostrophus* lost fin surface (red) and regenerated fin surface (green) for each % in total body lost length. (b) Net balance in fin surface for each % of body lost length of *P. cyanostrophus*. The green line denotes regenerated fin surface, the red line represents lost fin surface, and the grey line represents the balance between both measurements. Net balance means values for each interval of body lost length have been indicated. Net balance was completely offset up to losses of 15% of the total length. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

(b)
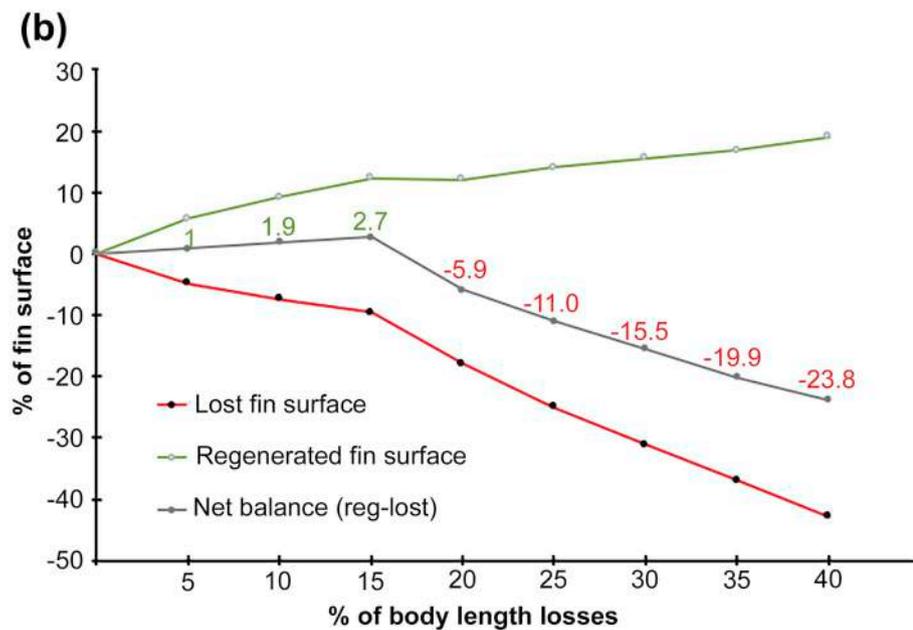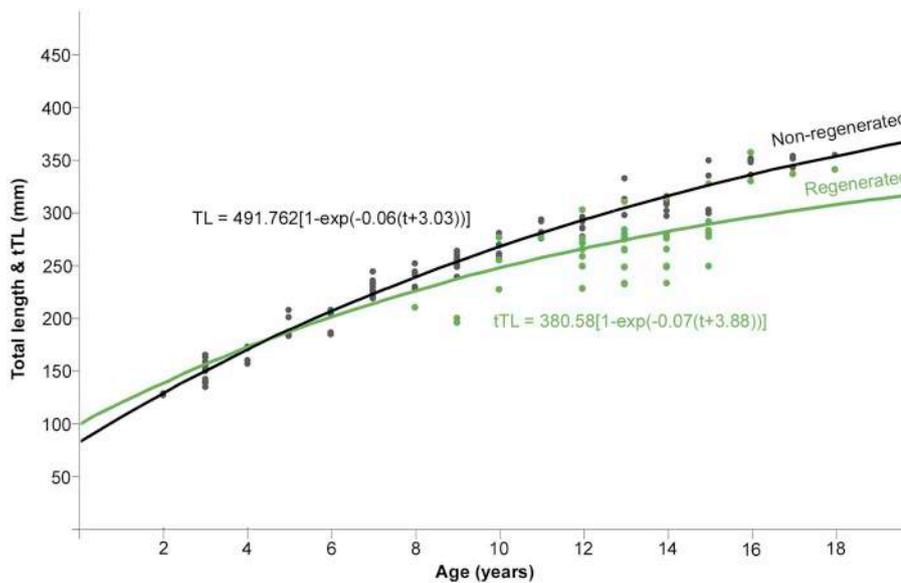
Fig. 5. Length-at-age data for regenerated (R) and non-regenerated (NR) females of *Physiculus cyanostrophus* with fitted von Bertalanffy growth curves: $LT = L_\infty [1 - \exp(-k(t - t_0))]$, where LT is the length of fish at age t, L_∞ is the estimated asymptotic length, k is a constant that determines the rate at which TL approaches L_∞, and t_0 is the hypothetical age at zero length. Age-range for regenerated individuals was 8–18. No individuals younger than 2 years were located in the studied population. Percentage agreement between otolith readings of Reader 1 and Reader 2 (83.6–86.2%) was similar. Moreover, the exact match of the average readings between both readers was high (85.3%) with a quite low variability of IAPE ($t = 1.654$ $p < 0.001$) and CV indices (3.9% and 3.4%, respectively).

decreased from juveniles (1:5.6, $\chi^2 = 16.03$, $p < 0.05$) and young-adults (1:3.1, $\chi^2 = 65.05$ $p < 0.05$) to old-adults (1:1.6, $\chi^2 = 5.84$ $p < 0.05$). Moreover, NR males were more abundant than R males in the ratio 1:2.1 ($\chi^2 = 11.57$, $p < 0.05$). This ratio was similar through the ontogeny of males (1:2.6, 1:2.1 and 1:1.8; $\chi^2 = 0.297$, $p > 0.05$).

3.2.1. Tail loss

Estimations of tTL based on the HL–TL relationship of NR individuals yielded significant differences between sexes ($F = 29.1403$, $p < 0.05$), being isometric in females and males ($t > 7.69$, $p < 0.05$). The body lost length increased with ontogeny ($F > 18.154$, $p < 0.05$): being 43.21 ± 18.37 mm (mean ± s.d) for juveniles, 61.90 ± 25.29 mm for young-adults and 77.33 ± 28.36 mm for old-adults, with the last group exhibiting the highest losses (Fig. 3a). Young-adults showed the widest range of body lost length (0–45%), (Fig. 3b). A *post hoc test* showed differences in body lost length between young-adults and old-adults ($p < 0.05$). Indeed, these groups showed differences within juveniles ($p < 0.05$). The relationship between tTL and the number of vertebrae in regenerated specimens is shown in Figs. S2 and S3. The highest vertebrae loss was 28, corresponding with a specimen of 45% body lost length. We also measured the net balance between lost fin surface and regenerated fin surface, and our results indicate that they were completely offset until losses reached 15% of tTL (Fig. 4).

The regenerated length (regL) is independent of body lost length and of total length regenerated in % of theoretical total length (tTL). Values of regL showed a mean increase of 13 ± 3.31 mm (mean ± standard deviation, in %) and ranged between 5 and 19% of tTL for the entire range of sizes (Fig. S4).

3.3. Growth

Statistical differences between NR and R females were found in the otolith mass–TL power function relationship ($F = 180.58$, $p < 0.05$). Indeed, mean otolith mass of R females (80.187 ± 18.47 mg) was heavier than that of NR females (70.90 ± 20.15 mg) ($t = 3.696$, $p < 0.05$) for the same size range distribution.

Based on the annual growth, ring counts of 173 (75%) readable female otoliths ranged from 2 to 18 years (age). Fish younger than 2 years were absent in the study sample. The youngest R individual was 8 years. The *von Bertalanffy growth curves* for observed TL and tTL at age of R and NR females are shown in Fig. 5. *Hotelling's T^2-test* showed significant differences in the growth parameters between R and NR

females ($T^2 = 106.930$, $p < 0.05$). Differences in growth between both groups increased with longevity. NR and R individuals at 9 years exhibit differences of 18 mm in TL (NR, 252 mm TL; R, 234 mm tTL), and this value increased in individuals aged 17 years: 44 mm in TL (NR, 345 mm TL; R, 301 mm tTL).

3.4. Total fecundity, offspring and maternal fitness

The fecundity outputs by ontogeny are summarized in Table 1. There were no significant differences between mean values of TF and BF between the NR and R groups ($t > 0.840$, $p > 0.05$). Throughout ontogeny, mean fecundity outputs between NR and R groups showed no significant differences within young-adults. Nevertheless, R old-adults showed lower BF than NR old-adults ($t = 2,180$, $p < 0.05$) (Table 1). TF and BF plotted against TL and tTL for NR and R, respectively, showed significant differences between groups (Fig. 6a) ($F > 5.03$, $p < 0.05$), wherein the slope of TF plotted against size was lower in R females than NR females. This difference was greater when TF and BF data were plotted and compared against the ages of the individuals (Fig. 6b) ($F > 180.30$, $p < 0.05$).

4. Discussion

Our study describes a remarkable capacity to withstand sublethal tail loss in *Physiculus cyanostrophus* a fish species not listed in previous reviews of sublethal tissue loss in freshwater or marine ecosystems (Maginnis, 2006; Unguez, 2013).

4.1. Regenerated individuals in natural populations

Regenerated individuals represent a large fraction of the population (27.0%). This is a high prevalence of tail loss in a marine species far exceeding the 3.1–15.5% observed in the winter flounder in which the cause is bacterial fin-rot disease (Ziskowski et al., 2008). However, the distribution of regenerated individuals and its importance change within the natural population. Thus, the frequency of R individuals increases throughout ontogeny (16.8–67.5%), whereas females dominate the long-lived fraction of the population. This phenomenon may be because the species studied shows a marked sexual dimorphism, where R or NR females are bigger and more abundant than R or NR males; a common strategy in deep-water species to avoid intraspecific competition for resources (Shine, 1989; Fairbairn, 1997). An important consequence of ontogenetic niche shifts is that a population can

Table 1
Mean values (± standard deviation) and range (minimum-maximum) of total fecundity (TF) and batch fecundity (BF) for non-regenerated (NR) and regenerated (R) individuals of *Physiculus cyanostrophus* in young-adults and old-adults ontogenetic groups. *Significant differences ($p < 0.05$) between bold values.

| | young-adults (200 < TL < 300 mm TL) | | | | | | | | old-adults (TL > 300 mm TL) | | | | | | | |
| | Non-regenerated (n = 31) | | | | Regenerated (n = 27) | | | | Non-regenerated (n = 20) | | | | Regenerated (n = 25) | | | |
	Min	Max.	Mean	SD	Min	Max.	Mean	SD	Min	Max.	Mean	SD	Min	Max.	Mean	SD
TF	12,545.19	69,902.06	35,558.39	2993.72	23,700.58	46,756.23	31,143.98	1400.24	33,056.43	137,322.37	65,999.81	5821.83	8320.83	117,309.64	53,907.20	6623.64
BF	2212.05	29,766.23	10,018.10	1080.44	4651.03	14,930.94	9140.64	783.87	8488.68	44,959.84	**18,254.08***	1705.28	1632.03	27,698.11	**12,473.30***	1758.57

potentially be divided into ecologically distinct stages (Olson, 1996). Concerning the subject of ontogeny, early stages and juveniles of our studied species exhibit a pelagic behaviour, in contrast with adults, which are benthopelagic (Okamoto et al., 2007), as has been described in closely related groups, such as macrourids (Bergstad and Gordon, 1994). These differences in ontogenetic niches could explain the absence of regenerated juvenile specimens, because predation is more likely to be lethal.

4.2. Body losses in caudal region

The ability to withstand body losses varies with size and is higher in large individuals, which can survive losses of up to 28 vertebrae, equivalent to 45% of total length. However, the capacity to regenerate the caudal zone in our studied species is limited. The balance between body lost length in a sublethal attack and the length of the newly regenerated caudal region shows a limit of maximum recovery of 19% in tTL versus a maximum of 45% of the body lost length. This limited regeneration of the caudal zone could be an adaptive mechanism, as an imperfect or limited regeneration could represent an optimal investment into the regeneration process for the injured animal (see Bely and Nyberg, 2010). This result is in line with those of studies on caudal fin regeneration in fishes (e.g., Fu et al., 2013).

4.3. Tissue loss allocation cost in growth

Our results describe a smaller somatic growth in regenerated females than NR females. This statement was achieved through two approaches. On the one hand, a close relationship between otolith mass and age exists (e.g., Boehlert, 1985; Pawson, 1990; Worthington et al., 1995; Cardinale et al., 2000). Taking into account that otolith mass continues to increase throughout the life of an individual, even if somatic growth is small or null (e.g., Fowler and Doherty, 1992; Ashworth et al., 2016), a different context can be considered when comparing regenerated and non-regenerated individuals. We found that predation does not affect the increments in otolith mass with age. Nevertheless, injuries change the growth rate, resulting in the R individuals showing a lower phenotypic growth compared to non-regenerated individuals. On the other hand, estimates of age based on the number of growth increments also reveal differences between R and NR individuals. Our results showed that the youngest R individual was 8 years old. The magnitude and effects of the body loss on growth have a different degree of influence according to the percentage of body lost and the elapsed time from the injury. This can be seen in the disribution of age data. Therefore, the size of R individuals compared to NR individuals depends on the time since the injury, and on the percentage of body loss. When a natural population is studied, the period in which the sublethal attack occurred on individuals is unknown. Therefore, our results indicate that regeneration implies a reduction in long-term growth. The benefit of structure replacement in their lifetime will depend on the age of the animal at injury and its expected longevity (Vitt and Cooper, 1986). The slow growth and long age (18 years) observed in our species compensates for the energy allocation during the regeneration process, since in the long term, it benefits from producing offspring during many seasons.

4.4. Tissue loss effects in offspring and maternal fitness

In nature, two well-differentiated strategies can be developed by a species depending on whether natural selection maximizes the maternal or offspring fitness. Species in which evolution has prioritized offspring fitness tends to produce a single, very large offspring (Bernardo, 1996). In contrast, species wherein selection favours maternal fitness tend to have a greater number of offspring with low fitness. The ability of mothers to produce lower quality offspring (selfish maternal effect) does not imply a worsening of maternal fitness, but quite the opposite
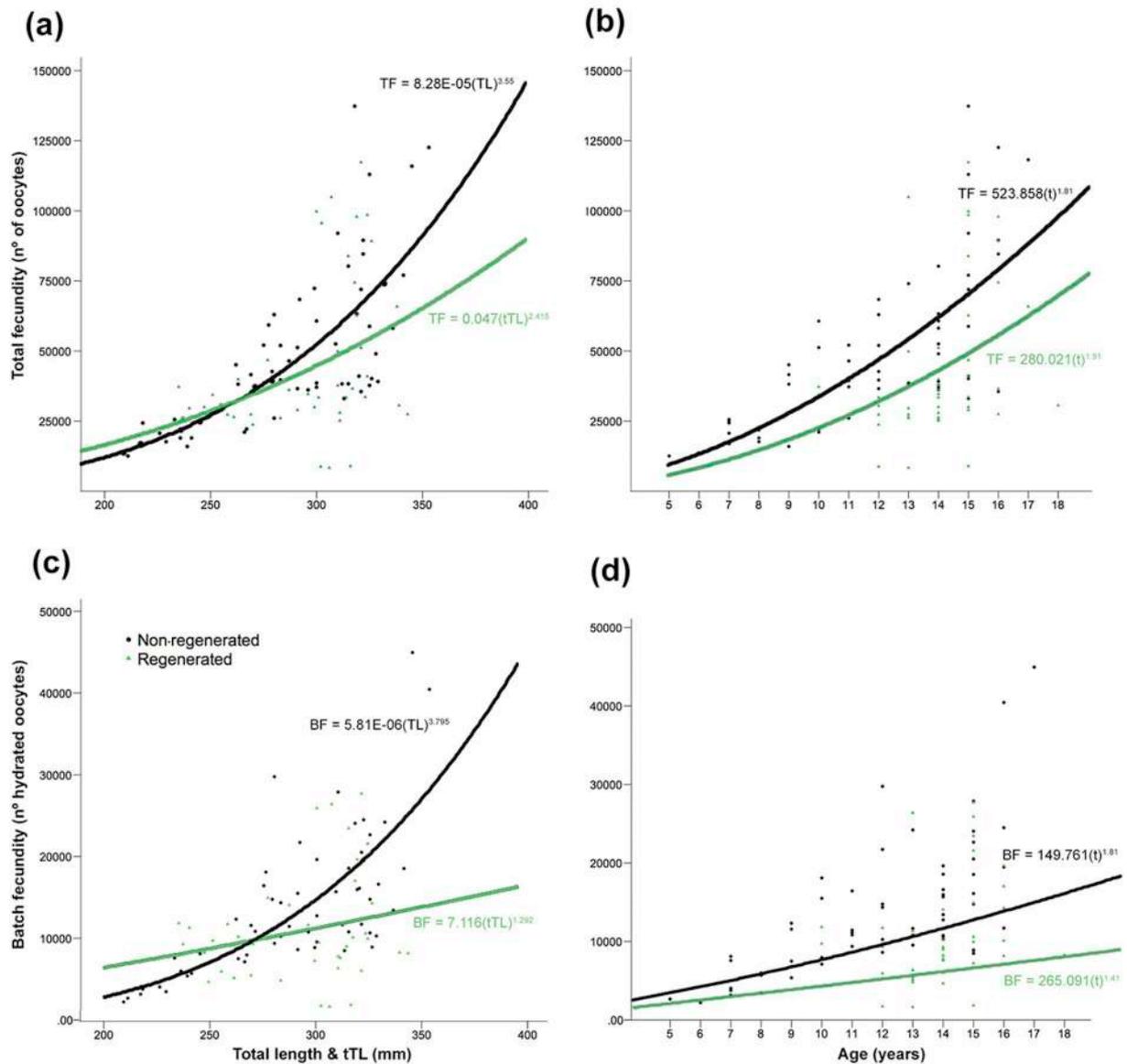
Fig. 6. Power function relationship of total (TF; a and b) and batch fecundity (BF; c and d) between length (a and c) and age (b and d) of *Physiculus cyanostrophus*. Black circles are non-regenerated (NR) individuals, whereas the green triangles are regenerated (R) individuals. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

(Marshall and Uller, 2007). Our studied species is a batch spawner. This reproductive strategy maximizes maternal fitness and produces numerous smaller offspring (batches). Our comparative results on fecundity outputs between R and NR groups showed no significant differences in mean values. However, across the ontogeny, the R older-adults showed low offspring fitness. Indeed, the slope of the relationship between fecundity or offspring and size for the whole population showed lower values in R individuals. If we add growth as a factor in offspring fitness, these differences become greater. Since there are regenerated individuals with less growth than individuals without regeneration allocations (NR), the ability to regenerate the lost caudal area allows the population to maintain a large number of mothers that contribute significantly to the next generation. It is important to bear in mind that, in this population group (old-adults), a higher frequency of regenerated specimens was found (67.5%). Some authors argued that the contribution of larger females to self-recruitment is significantly greater than the expected on the basis of the relationship between body size and fecundity, indicating that female size has an important maternal effect on traits in their offspring (see Beldade et al., 2012).

Survivorship of R individuals in the population of our studied species, even at the expense of a decrease in offspring, generates a relevant contribution to maternal fitness at the population level. Following Einum and Fleming (2000), selection acts to maximize maternal fitness. Mothers tend to make smaller, more numerous offspring, effectively sacrificing individual offspring fitness for maternal fitness.

4.5. Loss of the tail

While it is true that sublethal predation implies an important allocation cost in different groups of metazoans (Alvarado, 2000), it should be noted that the most widespread sublethal predation in teleosts is reduced to scale-eating and fin-nipping specialized predators (e.g., Sazima, 1983; Winemiller, 1990). In this scenario, sublethal predation in fishes has been usually considered as an opportunistic mechanism to keep prey abundant as a rapidly renewable resource for specialized predators (Northcote et al., 1986; Nico and Taphorn, 1988). Our study suggests a well developed capacity of *Physiculus cyanostrophus* to survive following a predator attack. However, the putative predator has

not been identified. The loss of the tail and regrowth with a pseudo-hypural plate suggests the tail loss was traumatic event rather than disease as in the winter flounder (Ziskowski et al., 2008).

Competing interest

The authors declare no competing interests.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.dsr.2019.06.008.

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