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Life-history strategies of a conspicuous reef fish, the Canary damsel *Similiparma lurida* (Pomacentridae) in the northeastern Atlantic

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Summary: *Similiparma lurida* is a common fish inhabiting shallow-water rocky bottoms of the northeastern Atlantic oceanic archipelagos, and the coasts from Portugal to Senegal. This study was conceptualized to integrate information relative to key population traits of *S. lurida*, including length and age structure, growth, reproduction and length at maturity, with a description of abundance patterns on shallow reefs, including temporality of recruitment and habitat preferences by juveniles, sub-adults and adults. We then hypothesized that seasonal cycles of spawning and recruitment were synchronized. This species reaches a total length (TL) of up to 15.7 cm and an age of 18 years. Males grow faster and longer (K=0.28 years^{-1}, L_∞=14.487 cm TL) than females (K=0.23 years^{-1}, L_∞=13.461 cm TL), which affects the overall ratio of males to females (1:0.26). The size at which 50% of sexual maturity is reached was 10.344 cm TL for males and 8.471 cm TL for females. Fish increase growth during the spawning season, which occurs from November to March, including a maximum in February. After two months of this peak, juveniles reached maximum abundances (April) in high relief reef areas. Adults, however, show a preference towards rocky bottoms covered with algae interspersed with sand patches, suggesting ontogenetic changes in microhabitat preferences when juveniles turn into adults.

Keywords: Pomacentridae; *Similiparma lurida*; life history; recruitment; coastal fish; spatial distribution; northeastern Atlantic.

Estrategias de vida de un relevante pez de arrecife, la fula negra *Similiparma lurida* (Pomacentridae) en el Noroeste Atlántico

Resumen: *Similiparma lurida* es un pez común que habita en aguas poco profundas de fondos rocosos someros de los archipiélagos oceánicos del Atlántico Norte, y las costas desde Portugal a Senegal. Este estudio se conceptualizó para integrar información relativa a atributos poblacionales clave de *S. lurida*, incluyendo: estructura de tallas y edad, crecimiento, reproducción y talla de primera madurez con la descripción de los patrones de abundancia en arrecifes poco profundos, incluyendo la temporalidad en el reclutamiento y preferencias de hábitat por juveniles, sub-adultos y adultos. Esta especie alcanza hasta 15.7 cm de longitud total (LT) y 18 años de edad. Los machos crecen más rápido y son más largos (K=0.28 years^{-1}, L_∞=14.487 cm LT) que las hembras (K=0.23 years^{-1}, L_∞=13.461 cm LT), lo que afecta a la sex ratio de machos y hembras (1:0.26). El tamaño en el que se alcanza el 50% de la madurez sexual fue 10.344 cm (LT) para los machos y 8.471 cm (LT) para las hembras. El crecimiento es mayor durante la temporada de desove, que ocurre de noviembre a marzo, incluyendo un máximo reproductivo en febrero. Dos meses después de este pico (abril), los juveniles alcanzaron abundancias máximas en zonas de arrecifes de gran relieve. Los adultos, sin embargo, muestran una preferencia hacia los fondos rocosos cubiertos de algas intercaladas con parches de arena, lo que sugiere cambios ontogenéticos en las preferencias de micro-hábitat cuando los juveniles se desarrollan en adultos.

Palabras clave: Pomacentridae; *Similiparma lurida*; historia de vida; reclutamiento; peces costeros; distribución espacial; Atlántico Nororiental.

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INTRODUCTION

A crucial goal in fish population ecology is to describe the temporality of key life-story traits, such as growth, reproduction (spawning) and subsequent recruitment in the benthic system. This information is essential for proper management of fish species subjected to human exploitation (Caldow and Wellington 2003, Morgan 2008, Smallwood et al. 2013).

The pomacentrids (damselfishes) are a diverse fish family, including ca. 29 genera and 396 species distributed throughout tropical to temperate oceans of the world (Robertson 1998, Nelson 2006, Eschmeyer 2015). They are among the first fishes described by Linnaeus, back in the 18th century, and they have subsequently received the attention of other well-known fish taxonomists and naturalists (Bleeker 1877, Cuvier and Valenciennes 1830). In terms of the number of species, this family is the third-largest fish group in coral-reef ecosystems, after Gobiidae (>1500 species) and Labridae (>600 species) (Wainwright and Bellwood 2002), although they often reach larger abundances on reefs (Frédérich et al. 2009).

Most damselfishes are territorial and show aggressive behaviour when defending their territories (Randall et al. 1997, Randall 2005, Gordon et al. 2015); this behaviour has led to a plethora of studies that have used them as model organisms to test a range of ecological and behavioural questions (Frédérich et al. 2009). Pomacentrids deposit elliptical eggs, which have a tuft of adhesive filaments, on the substratum (Hutchinson 2006). During the incubation time, males, but in some cases females, guard eggs until they hatch, frequently attacking intruders (Allen et al. 2006). This parental care may range from hiding eggs to guarding their offspring in elaborately prepared structures for up to several months (Balshine and Sloman 2011). Moreover, damselfishes change their colour patterns according to their reproductive patterns (Souza et al. 2011). The bridal colour (Bakker and Mundwiler 1994), size (Schmale 1981, Côté and Hunte 1989) and courtship behaviour are phenotypic characteristics of males to improve their reproductive success (Knapp and Kovach 1991). Because patterns of sexual development differ among pomacentrids, attempts to assess gonadal development require data of the different phases of the fish life cycle and at different times of the year (Sadovy de Mitcheson and Liu 2008). Recruitment of pomacentrids is widespread on onshore reefs, but juveniles may prefer alternative microhabitats to adults; ontogenetic shifts in habitat preferences can influence the spatial distribution of adult and juvenile damselfishes (Lirman 1994).

The diversity of damselfishes drops rapidly with increasing latitude (Kingsford 1999). This pattern can be observed in the oceanic archipelagos of the northeastern Atlantic, including the Azores, Madeira, Canaries and Cabo Verde. In the Azores, two species cohabit, *Similiparma lurida* (Cuvier, 1830) and *Chromis limbata* (Valenciennes, 1833) (Santos et al. 1997, Leite et al. 2009, Afonso et al. 2013, Froese and Pauly 2015). Both species also occur in Madeira, in addition to *Abudefduf saxatilis* (Linnaeus, 1758) and *Chromis chromis* (Linnaeus, 1758) (Freitas and Araújo 2006, Wirtz et al. 2008, Froese and Pauly 2015). In the Canary Islands, *Stegastes imbricatus* Jenyns, 1840 also occasionally appears in addition to the species mentioned before (Brito et al. 2002; Froese and Pauly 2015). Finally, in Cabo Verde Islands, five species are abundant, *A. saxatilis*, *Abudefduf taurus* (Müller and Troschel, 1848), *Chromis lubbocki* Edwards, 1986, *Similiparma hermani* (Steindachner, 1887), and *S. imbricatus*; and seven species are occasional, *Abudefduf hoefleri* (Steindachner, 1881), *C. chromis*, *Chromis cyanea* (Poey, 1860), *Chromis multilineata* (Guichenot, 1853), *Microspathodon chrysurus* (Cuvier, 1830), *S. lurida*, and *Stegastes leucostictus* (Müller and Troschel, 1848) (Wirtz et al. 2013, Freitas 2014, Hanel and John 2014).

Damselfishes are excellent species as biological indicators, since they are small-sized, abundant, non-migratory and easily recognizable in the field and they are not usually a fishing target (Linton and Warner 2003). In the Canary Islands, *S. lurida*, before known as *Abudefduf luridus* (Cooper et al. 2014), is a common fish inhabiting shallow-water rocky bottoms, especially vegetated reefs (Brito et al. 2002, Tuya et al. 2004), being abundantly captured by the artisanal fisheries fleet through traps deployed at <50 m depth (García-Mederos et al. 2015). Knowledge on this species in the Macaronesian area is limited to its ethology and spawning seasonality in the Azores Islands (Mapstone and Wood 1975, Afonso and Santos 2005). In this study, the main goal was to provide biological and ecological information on the population structure of *S. lurida* on rocky reefs at Gran Canary Island (Canary Islands, northeastern Atlantic). First, we assessed the reproductive ecology and inferred growth patterns. This approach provides important information from a fisheries perspective, i.e. spawning seasons and first maturity sizes. Second, we analysed the spatial and temporal patterns of abundance, describing annual recruitment patterns and therefore connecting the timing between reproduction and subsequent recruitment. Additionally, we sought to determine whether variation in abundance patterns of adults, sub-adults and juveniles varied at small spatial scales in relation to habitat composition and complexity. Overall, integration of this information provided insight into the life history of this species.

MATERIALS AND METHODS

Study area

This study was performed in Gran Canaria Island (Fig. 1), which is located at the centre of the Canarian Archipelago, with ca. 45 km diameter and a maximum elevation of 1950 m above sea level (Carracedo et al. 2002). Sediments and rocky reefs mainly compose the nearshore bottoms, with a high variability in the distribution and complexity of these habitats, which can be colonized by a range of canopy-forming species (Tuya and Haroun 2006, Tuya et al. 2014).

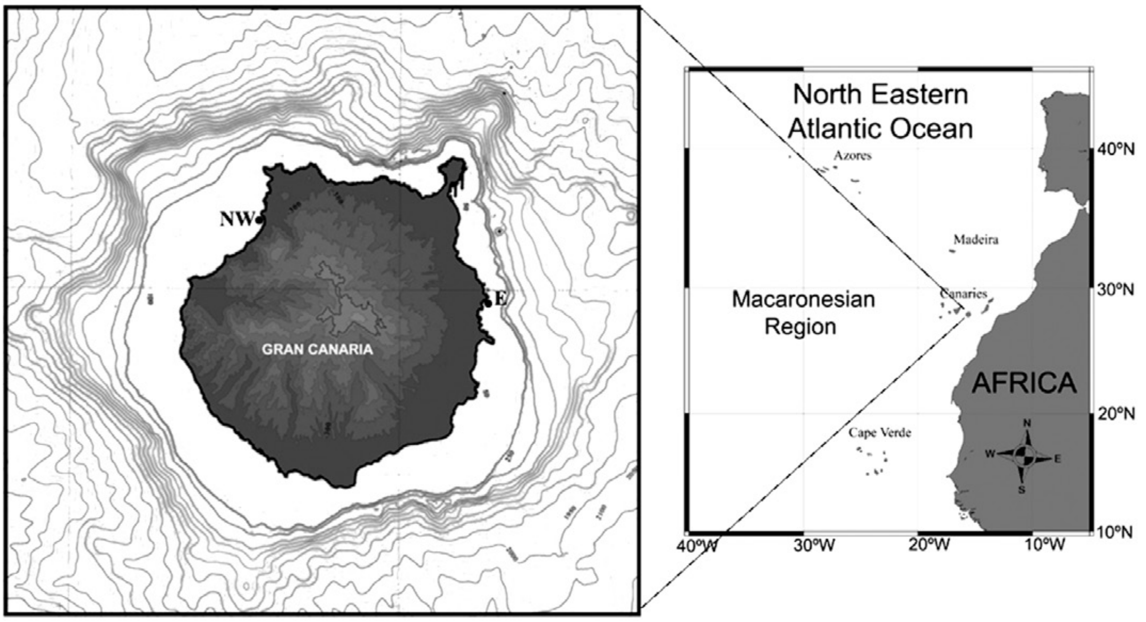

Fig. 1. – Location of study localities at Gran Canary Island (eastern Atlantic Ocean).

Biological sampling

A total of 629 specimens were collected, from January to December 2012 at Telde (east of the island, Fig. 1), through bottom trapping carried out by the local artisanal fleet. Traps were deployed between 18 and 30 m depth, either individually or in strings of 2-3 traps along a fishing rope. The number of days on which traps were placed on the seafloor varied between 3 and 10. For each individual, the total length (TL, mm), total weight (TW, g), and gutted weight (GW, g) were recorded. The sex and stage of sexual maturation (EMS) were recorded by a macroscopic examination of the gonads. Gonads were first removed and weighed to the nearest 0.01 g (GNW). Maturity stages were classified as immature (I), developing (II), spawning (III), regressing (IV) and regenerating (V) (Brown-Peterson et al. 2011). The sagittae otoliths were used to determine fish age. They were extracted from all individuals, cleaned and stored dry in plastic vials.

Age and growth

The right otolith was selected to determine fish age. As otolith weight is considered as an indicator of fish growth rate (e.g. Pawson 1990, Fletcher 1991, Cardinale et al. 2000), the criterion was based on the absence of significant differences in mean weight between left and right otoliths (Student t-test, t=0.0098, p=0.992, n=200).

First, whole otoliths were immersed in a 1:1 glycerin–alcohol solution and observed under a stereomicroscope (NIKON SMZ 1000) using reflected light and a dark background. This method, however, did not provide reliable age estimates, so a random subsample of 200 otoliths was selected to perform the study through sectioning. For that, whole otoliths were embedded in epoxy resin and two or three transverse sections (1 mm thick) were cut through the central region with a slow-speed circular saw (Buehler, ISOMET-TM) to obtain a section that included the otolith core. Otolith sections were then mounted on a glass slide using Crystalbond as a mounting media and polished using decreasing grit abrasive paper (3M Lapping Film). Sections that included the core were examined under a compound microscope with transmitted light (Axioplan, Zeiss; Carl Zeiss Inc., Oberkochen, Germany) connected to a digital camera (ProgRresTM C10 plus; Jenoptik, Jena, Germany). Under transmitted light, the core and opaque bands appear as dark rings, and the wider translucent bands as clear or hyaline rings. The count path of the annuli was from the nucleus towards the tip of the inner face next to the sulcus, where the deposition of seasonal rings appeared clearly defined (Fig. 2a).

To assess the precision of readings, one experienced reader counted opaque bands without knowledge of fish size at least twice. To minimize reading bias, the two readings were separated 2-3 months after randomization in the process of readings. When readings differed, a third reading was taken. An otolith was only considered unreadable, and therefore excluded from the analysis, when the differences between readings did not improve after this procedure. The coefficient of variation (CV=SD⁄mean) was used to measure precision of annuli counts together with a paired t-test to statistically compare differences between readings (Chang 1982, Campana 2001). To assess the yearly pattern of deposition of otolith annuli, the appearance of each otolith margin was recorded as opaque or translucent. The timing of annulus formation was examined by plotting the percentage occurrence of otoliths with a peripheral opaque band as a function of the sampling month (Morales-Nin 1992). January 1 (peak spawning; see results) was considered the birthdate, hence their annuli count was assigned to equal age. Finally, the von Bertalanffy growth equation was used to describe the growth of the species; it was fitted to the observed individual length-at-age data, rather than the frequently used mean length-at-age, to show individual growth variability:

$$L = L_{\infty}\,[1 - e^{-k\,(t - t_0)}]$$

where L is the TL (cm), L_{∞} is the asymptotic length, *k* is the growth coefficient, t is the age (years) and t_0 is the hypothetical age at which length is zero. To better estimate growth parameters, ages of smallest individuals (undifferentiated) were used for both sexes (García-Mederos et al. 2010). Hotelling's T^2 test was used to compare growth parameters between males and females (Cerrato 1990, Gordo 1996).

A multiple linear regression model was used to evaluate whether age determination was predicted by otolith weight, otolith diameter and fish size (Boehlert 1985, Schwamborn and Ferreira 2002). All variables used in the multiple linear regression were log-transformed to conform the assumptions of linearity, i.e. normality and homogeneity of variances (Zar 1996).

Reproductive biology

The spawning pattern was assessed from monthly changes in the frequency of the maturity stages and the gonadosomatic index (West 1990):

$$GSI = 100\,(GNW / GW)$$

Size at first maturity was based on the examination of males and females in mature phases (phase III, phase IV, or phase V) and immature individuals collected during the spawning period. The TL of all individuals was used to estimate the size at first maturity (L_{50}), defined as the size at which 50% of all fish are at sexually mature phases. Maturity curves were adjusted using the logistic curve (Pope et al. 1975):

$$P = 100 / (1 + \exp\,(a + b\mathrm{TL}))$$

where P is the percentage of mature individuals as a function of size class (TL), and *a* and *b* are specific parameters which can change during the life cycle. A logarithmic transformation was initially applied to calculate the parameters *a* and *b* by means of linear regression. An Analysis of Covariance (ANCOVA) was used to compare the curves of maturity between sexes.

The sex ratio of the population (males: females), and the sex ratio by size intervals (10 mm) were determined. Sex ratios were tested statistically for significant deviations from the expected 1:1 ratio via chi-square tests (α=0.05).

Abundance patterns

Spatial and temporal variation in the abundance of *S. lurida* was studied from visual censuses carried out on a monthly basis between January and December 2012, at two randomly selected localities (Fig. 1). One locality is in the northwest (NW, Agaete, 28°5'57.58"N, 15°42'33.48"W) and the other in the east of the island (E, Telde, 27°59'21.68"N, 15°22'12.96"W); visual counts were performed between 0.2 and 5.8 m depth. Only individuals >2 cm (TL) were counted to optimize the in situ identification. On each sampling occasion, n=5 replicated 25 m transects were haphazardly surveyed during daylight hours. The abundance of fish within 2 m of either side of each transect (100 m^2) was recorded on waterproof paper by the same diver, according to standard procedures for the study region (Boyra et al. 2004, Tuya et al. 2004). Individuals were categorized as juveniles (TL<4 cm), sub-adults (TL 6-8 cm) and adults (TL>10 cm) based on morphological characteristics, fundamentally related to their colouration and body size (Mapstone and Wood 1975). This approach was subsequently endorsed by our data (see results). Concurrently, the diver counted on his way back the number of large (>1 m) and small (<1 m) topographic elements of the rocky substrate (i.e. cracks, crevices, caves, holes per 100 m^2), and visually estimated the percentage cover of algae, following standardized procedures via the Linear Point Intercept sampling technique (Ohlhorst et al. 1988). The type of substrate was recorded every metre along the 25 m long transect (i.e. 25 points per transect). Water temperature on the bottom was registered using an underwater thermometer.

Differences in the total abundance of juveniles, subadults and adults among months (fixed factor) and localities (random factor) were tested through ANOVAs from square root transformed data; this was necessary to avoid heterogeneous variances. Multiple linear regressions tested whether the number of small and large topographic elements (100 m^{-2}), the type of substrate, and the algal cover (per transect) affected abundances of the damselfish over time. To retain variables with good explanatory power, the Akaike information criterion (AIC) routine was used as a selection criterion for each model (the smaller the value the better the model, Anderson and Legendre 1999), and the contribution of each independent variable to each model was described with partial r^2 values. Collinearity diagnoses among independent (predictive) variables were carried out through Spearman-rank-correlations. All analyses were based on a 'forward' selection procedure.

RESULTS

Population structure

Fish ranged in size from 56 to 157 mm TL, and weighed between 3.9 and 76.6 g TW. A total of 419 males, 113 females and 110 immature specimens (gonads were characterized by small, thin and translucent filaments) were identified. Significant differences (Student t-test, t=11.22, p=0.002) were found between the mean sizes of sexes; males were larger than females (Table 1). The size and weight distributions differed significantly between males and females (Kolmogorov-Smirnov test, length: d=6.00, p<0.0001; weight: d=5.67, p<0.0001).

Table 1. – Summary statistics of the size (cm) and weight (g) ranges of *S. lurida* according to sex. SD, standard deviation.

Variable	Males				Females			
	n	range	mean	SD	n	range	mean	SD
Total length (cm)	419	7.5-15.7	13.542	7.65	113	7.9-11.4	12.244	11.51
Total weight (g)	419	8.9-76.6	54.28	8.39	113	10.4-67.2	42.60	10.61

Table 2. – Number of males and females of *S. lurida* by 10 mm size (TL) class intervals; the chi-square statistic to test for significant departures of the sex ratio from the hypothetical 1:1 ratio are included. *, significant for $p<0.05$.

TL (mm)	Males	Females	Sex ratio	χ^2	p
70	1	1	1:1.00	0	1.000
80	1	2	1:0.50	0.333	0.564
90	-	-	-	-	-
100	0	6	-	-	-
110	6	10	1:1.66	1.000	0.317*
120	58	65	1:1.12	0.389	0.528
130	216	20	1:0.09	162.780	0.000*
140	119	3	1:0.02	110.295	0.000*
150	6	0	-	-	-

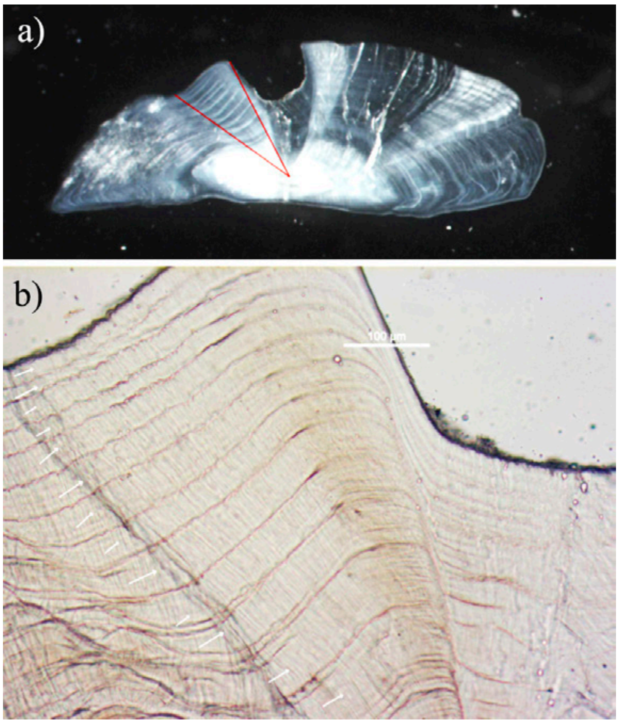

Fig. 2. – Otolith transverse sections showing the selected zone for ageing and the nucleus (a, 40× under reflected light) and annual rings for an individual of 13 years (b, 100× under transmitted light).

The overall ratio of males to females was 1:0.26; the hypothesis of uniformity between sexes was therefore rejected ($\chi^2=180.5$, $p<0.05$). Females were found in most size intervals, but males were more abundant in the larger size interval (130-140 mm) (Table 2).

Growth

The readings coincided for 171 otoliths (85%) and were dissimilar for the remaining 29 (15%). There was no significant difference in age estimation between readings (CV=2.7%; t=–0.094, p>0.05). The growth rings, opaque and translucent, were usually well visible (Fig. 2). Marginal zone analysis showed a pattern of alternating narrow translucent zones and wide opaque zones, forming one annulus per year. Otoliths with an opaque edge (faster growth) were more abundant (52.9-87.5%) from November to March (spawning season, see below), while otoliths with a translucent edge (slower growth) were more common during the remaining months (Fig. 3).

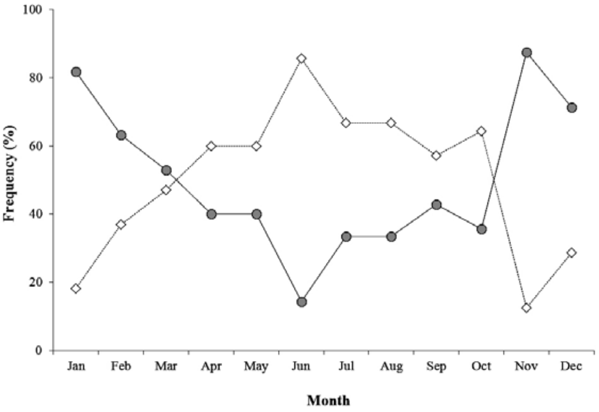

Fig. 3. – Monthly changes in otolith frequency with opaque (grey circles) and translucent (diamonts) edges.

Fish ranged in age from 0 to 18 years; the age of most fishes was between 8 and 10 years. Females reached higher maximum ages (18 years) than males (14 years). Significant differences in mean sizes between sexes were obtained from V and X age classes (Supplementary material, Table S1). A considerable variability in the length-age relationship indicated considerable differences in individual growth. The growth curve obtained by age-at-length data was well described through a von Bertalanffy growth fit, attaining a determination coefficient (r^2) of 0.439 for males and 0.707 for females (Fig. 4, Table 3). Significant differences were found between the von Bertalanffy growth curves of both sexes (Hotelling's T^2-test, $= 68.654>T_0^2{}_{0.05,3.181} = 8.515$).

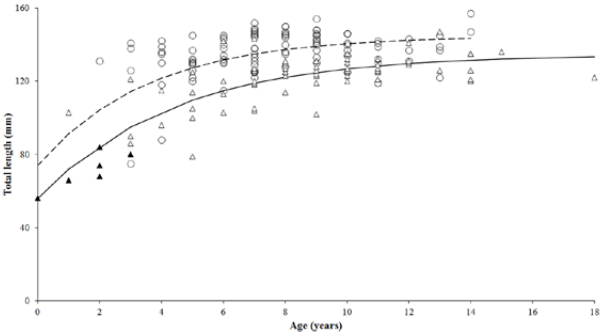

Fig. 4. – Fitted von Bertalanffy growth curves for males (circles, dashed curve) and females (triangles, undashed curve). Black triangles denote immature individuals.

Table 3. – Von Bertalanffy growth parameters for males and females. CL, 95% confidence limits for L; K, growth rate (year^{-1}); L, asymptotic length (mm); n, number of individuals; t_0, time (year). Values in brackets are standard errors.

Sex	n	L	K	t_0	r^2	CL
Males	117	144.87 (4.12)	0.28 (0.06)	–2.55 (0.87)	0.439	136.70-153.04
Females	78	134.61 (4.27)	0.23 (0.05)	–2.32 (0.72)	0.707	126.08-143.14

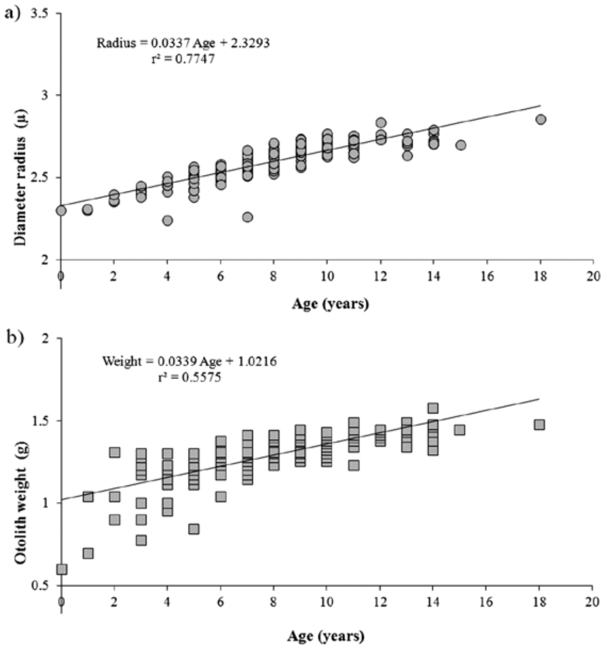

Fig. 5. – Relationships between the age and diameter (a) and weight (b) of otoliths.

Partial regression coefficients indicated that radius diameter (r^2-partial=0.775, t=13.728, p<0.001) and otolith weight (partial r^2=0.5575, t=6.367, p<0.001) were significant predictors of fish age (Fig. 5). By contrast, fish length did not contribute to explaining variation (partial r^2=0.338, t=–0.728, p=0.338).

Reproduction

Males in phase III were observed from November to May, with a maximum peak in February (Fig. 6a). The maximum occurrence of spawning females (phase III) also occurred from November to March, including a peak in February (Fig. 6b). The presence of regressing females (phase IV) was observed from February to August. Females at immature, regressing and developing/regenerating phases (V, I and II, respectively) were found throughout the entire year. A slight increase in phase III females was observed in May, which would likely result in spawning activity during June, suggesting the possibility of a secondary breeding season (Fig. 6b). For males, the GSI increased from November to May, including a peak in January (0.258) (Fig. 6c). The GSI of females also increased from November to May, with a peak of maximum activity in February (3.897) (Fig. 6d). Overall, integration of EMS and GSI results

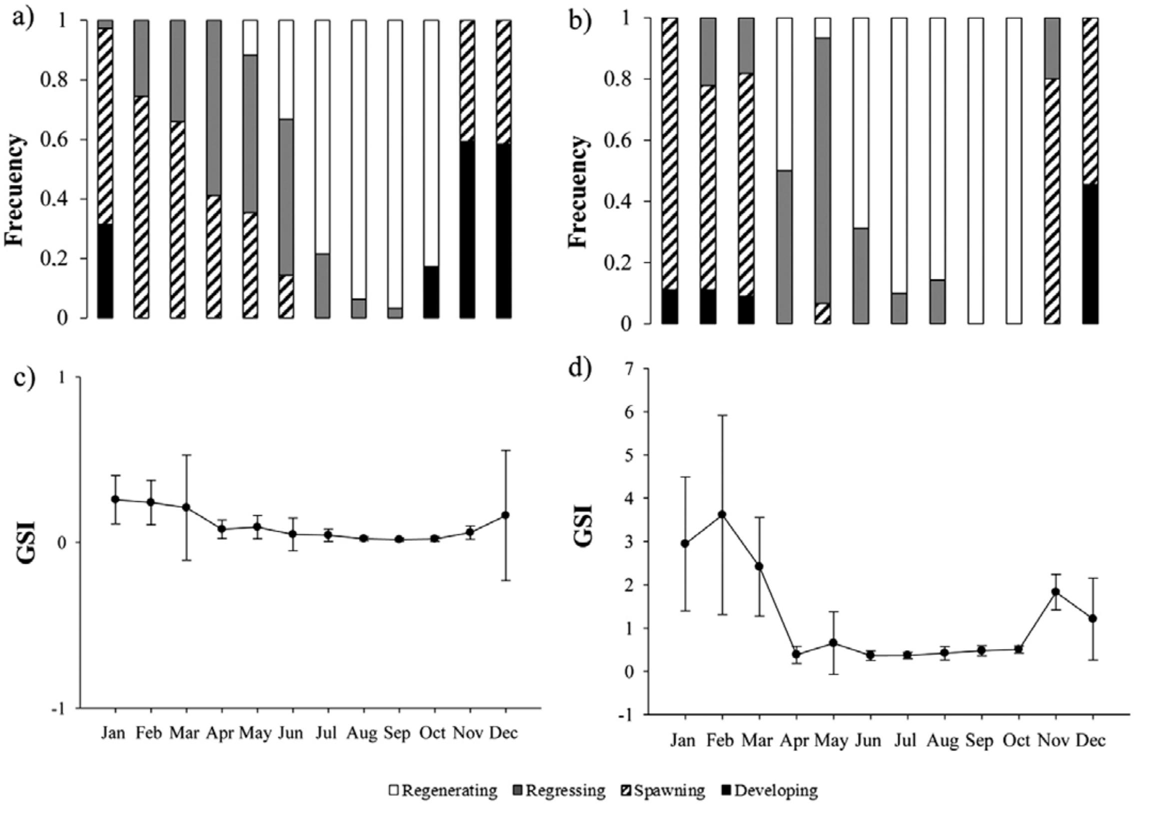

Fig. 6. – Monthly variation of maturity stages and the gonadosomatic index (GSI, mean±SD) for males (a and c) and females (b and d).

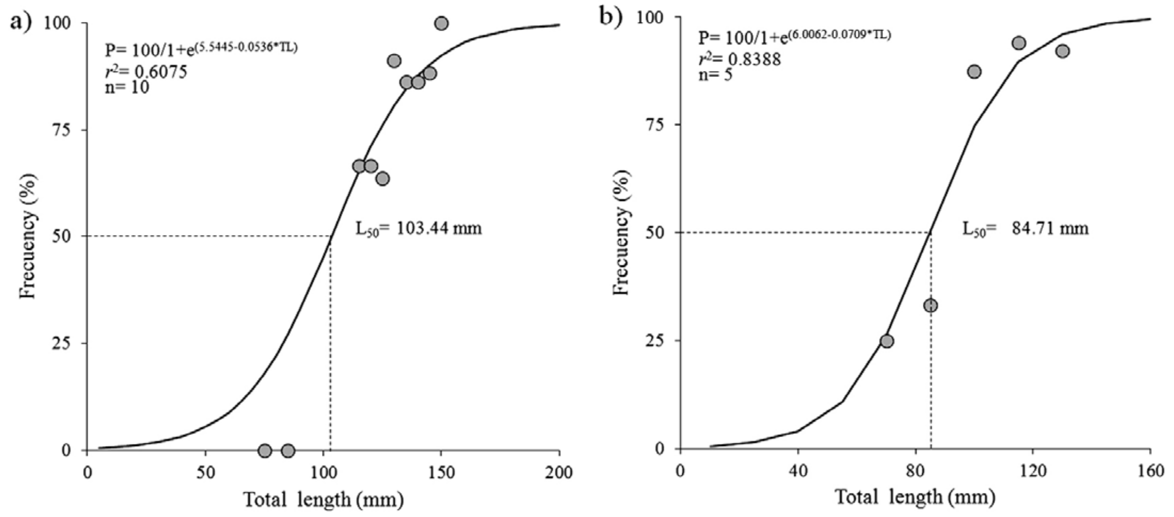

Fig. 7. – Sexual maturity curves and sizes at first maturity ($L_{50\%}$) for males (a) and females (b).

with maturity phases throughout the year indicated a spawning season from November to May. The maturity curves were clearly different between males and females (ANCOVA, F=34.811, p<0.001); the size at which 50% of individuals are mature was 103.44 mm TL for males and 84.71 mm TL for females (Fig. 7).

Abundance and recruitment patterns

The abundance of juveniles, sub-adults and adults varied inconsistently over time between localities (ANOVA: Locality × Month, p<0.05, Table 4). However, juvenile abundances were significantly higher in

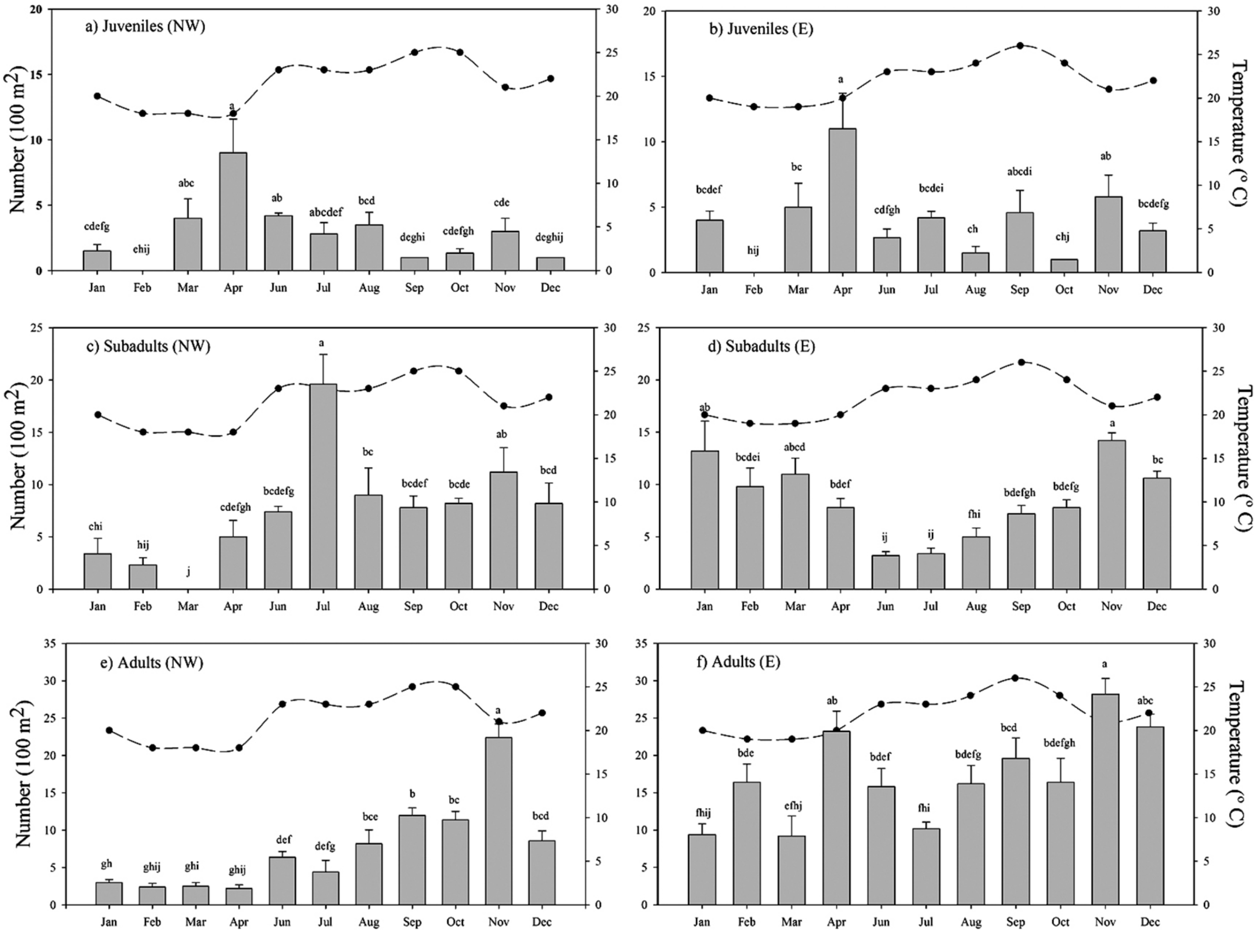

Fig. 8. – Mean (±SE) abundances of individuals (ind/100 m²), including juveniles (a, b), sub-adults (c, d) and adults (e, f). Water temperature at the bottom (full circles) throughout the study is also included.

Table 4. – Results of two-factor ANOVA testing for differences in the abundance of individuals between localities (fixed factor) and months (random factor). *, significant for p<0.05.

	df	MS	F	p
Juveniles				
Locality	1	3.8101	7.3188	0.0076*
Month	10	5.9679	2.4785	0.0858
Locality × Month	10	2.4079	4.6253	0.0002*
Residual	88	0.5206		
Sub-adults				
Locality	1	4.7961	14.0104	0.0006*
Month	10	2.7779	0.4310	0.9102
Locality × Month	10	6.4447	18.8265	0.0002*
Residual	88	0.3423		
Adults				
Locality	1	65.7911	160.9795	0.0002*
Month	10	7.3129	4.3504	0.0166*
Locality × Month	10	1.6810	4.1130	0.0002*
Residual	88	0.4087		

April at both localities (9.0±2.6 ind/100 m^2 at Agaete; 11.0±2.7 ind/100 m^2 at Telde, Fig. 8a, b). The abundance of sub-adults attained higher mean values in July at Agaete (19.6±2.8 ind/100 m^2), while the larger values were observed between November and January (14.2±0.7 ind/100 m^2, 13.2±2.8 ind/100 m^2, respectively) at Telde (Fig. 8c,d). Adults peaked in abundance at similar times at both localities; November (22.4±1.8 ind/100 m^2) at Agaete and November-December (28.2±2.1 ind/100 m^2, 23.8±1.7 ind/100 m^2, respectively) at Telde (Fig. 8e, f).

The percentage of sandy cover in the case of juveniles and adults, and the percentage cover of algae for sub-adults, accounted for the largest contribution to variability in fish abundances at Agaete. However, the number of small topographic elements was the largest contributor to variation in the abundance of sub-adults and adults at Telde (Supplementary material, Table S2). For the majority of specimens, the best models provided by the AIC routine included both the number of small topographic elements with algae and with sandy cover, i.e. patterns of abundance were, in most cases, affected by these two descriptors of the habitat (Table S2). Juvenile abundance was significantly predicted by the presence of large topographic elements at Telde (Table S2), i.e. juveniles were particularly abundant on high relief areas.

DISCUSSION

The Canary damsel, *Similiparma lurida*, is quite similar in size (157 mm TL) to other pomacentrids from the Macaronesian archipelagos, such as *C. limbata* (120 mm SL) and *S. hermani* (160 mm SL), but smaller than *A. saxatilis* (229 mm TL), *C. chromis* (250 mm TL) and *A. taurus* (250 mm TL) (Froese and Pauly 2015). Our findings clearly indicated that this species is of early rapid growth, because it reached half of its asymptotic length within the first year. In pomacentrids, small-sized species seem to have a faster growth (Dulčić and Kraljević 1995, Tzioumis and Kingsford 1999, Wilson and Meekan 2002), although it may be a response to unpredictable recruitment success (Longhurst 2006). Moreover, differences in growth were obtained between sexes: males grow faster (0.28 $years^{-1}$) than females (0.23 $years^{-1}$), favouring the presence of males in larger sizes. Although this is not uncommon for many fishes, it is particularly important for fish species with nuptial behaviour, in which males have to defend their territories and care for their offspring (Breder and Rosen 1966, Dulčić and Kraljević 1995, Bracciali et al. 2014, Allen et al. 2006). Some studies have also indicated that fish size is correlated with social dominance, which additionally favours the acquisition of food, mate choice, retention and reproductive success (e.g. Hoffman 1985, DeMartini 1988, Folkvord 1991, Webster and Hixon 2000, Hobbs and Munday 2004, Fero and Moore 2008). From an ecological perspective, a sexual variability of certain life-history traits may represent a trade-off, the costs paid in the currency of fitness when a beneficial change in one trait is linked to a detrimental change in another (Charnov and Krebs 1973, Stearns 1989, Lester et al. 2004). Fast growth may involve a cost in terms of reproduction, as early maturing occurs at a larger size; when growth is delayed, however, maturing occurs at a smaller size (Stearns and Koella 1986, Charnov 2008, this study).

Alterations in somatic growth are not always reflected in otolith morphometry, due to continuous growth and metabolic non-dependence between the two processes (Reznick et al. 1989, Fowler and Doherty 1992, Secor and Dean 1992, Xiao 1996). Many studies have indicated that otolith thickness, or weight, can explain 80-95% variation in fish age (Fletcher 1991, Newman et al. 1996, Labropoulou and Papaconstantinou 2000). However, Pawson (1990) concluded that this technique has a limited application in ageing fish from wild populations with highly variable growth rates. Schwamborn and Ferreira (2002) found a linear correlation (partial r^2=0.739) between otolith weight and age of the pomacentrid *Stegastes fuscus*, but they recommended that the high variability of otolith weight-at-age hampered the use of this variable for an accurate prediction of age. In our study, otolith thickness provided a better relationship with age than weight. This is most likely because the otolith weight may underestimate the age of older fish (Beckman et al. 1991, Wilson et al. 1991, Ferreira and Russ 1994, Worthington et al. 1995, Newman et al. 1996, Tuset et al. 2004).

There are many spawning strategies by marine fishes, including variation at daily, lunar and seasonal scales (Robertson 1991). Our results demonstrated that *S. lurida* has a long spawning period (ca. 7 months) that coincides with an increase in fish growth and the appearance of denser otolith rings. For pomacentrids, seasonal cycles of spawning and recruitment can be synchronized, particularly when one main spawning peak dominates the spawning period (Robertson 1990). This occurred for the population of *S. lurida* at Gran Canaria Island; recruitment of juveniles reached a maximum in April, immediately after the main peak of spawning (February). This outcome suggests that the duration between gamete release and the appearance of recruits >2 cm is about 2 months. This result sounds plausible, given the fact that larval dispersion in most pomacentrids is reduced (10-24 days, Thorrold and Milicich 1990, Nemeth 2005), and that males guard fertilized eggs for only a few weeks (Thresher 1984, Asoh and Yoshikawa 2002, Bessa and Sabino 2012). Some authors have suggested that some variability in the time of recruitment may arise as a result of several spawning acts, or that larval duration varies due to environmental uncertainty (Robertson 1990, Thorrold and Milicich 1990). The fact that recruitment patterns were studied in shallower waters (0.2-6 m) relative to collections of specimens via fishing traps (18-30 m) does not seem to disturb interpretations, as the habitat is the same: rocky reefs on infralittoral bottoms.

The present study also highlighted the influence of habitat structure on the spatial and temporal variability in the abundance of juveniles, sub-adults and adults of *S. lurida* on shallow-water bottoms. The paramount role of habitat structure (e.g. substratum composition) as a driver of fish distribution and abundance has been widely reported (Luckhurst and Luckhurst 1978, Friedlander and Parrish 1998, García-Charton and Pérez-Ruzafa 2001, Tuya et al. 2009, Tuya et al. 2011). In general, our results suggest that rocky bottoms covered with algae interspersed with sandy patches seem an ideal habitat for *S. lurida*. This pattern, however, varied between localities. At Agaete, different habitat elements contributed to explaining variation in the abundances of sub-adults and adults, in particular the presence of small topographic elements and algal cover. A positive influence of algal cover may be explained by the fact that damselfish territories need to contain algae where females deposit their eggs (Knapp et al. 1995, Navarrete-Fernandez et al. 2014), which are further protected by males. Small-sized topographic elements, on the other hand, provide protection against predators. The presence of large topographic elements contributed to explaining the presence of juveniles at this locality. The tendency of juveniles to seek refuge after recruitment in the benthos, as way to avoid predation, has been reported for a range of reef fish species (Scharf et al. 2006, Leitão et al. 2008), including damselfishes (Almany 2004). Hence, large ledges and outcrops, which we have included here as large topographic elements, seem to provide an ideal habitat for juveniles, which tend to concentrate in these areas. The positive influence of sandy cover on juvenile abundances may be an artefact, as large ledges and outcrops typically reduce water flow and ease sedimentation in their surroundings. Taken together, these outcomes may be indicative of a change in habitat use by *S. lurida* with ontogeny (e.g. an ontogenetic niche shift, Wilbur 1980). Ontogenetic shifts in microhabitat preferences by juveniles and adults of another pomacentrid (*Stegastes planifrons*) have also been registered (Lirman 1994); in particular, adults exhibit a preference for foliose coral heads, whereas juveniles exhibit a preference for dead foliose coral heads. At Telde, however, the number of small topographic elements exclusively contributed to explaining the abundances of sub-adults and adults. This fact may be explained by the presence of more homogenous bottoms at this locality. Therefore, the discrepancy in results between the two localities indicates that between-location variation in habitat composition and structure may affect partitioning of habitat niches between juvenile and adult populations of reef damselfishes.

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http://www.icm.csic.es/scimar/supplm/sm04343esm.pdf

Table S1. – Age-length key for *S. lurida* at Gran Canaria Island. n, number of individuals; SD, standard deviation; TL, total length; *, significant differences.

Table S2. – Results of multiple linear regression analyses testing for the relationship between the total abundances of juvenile, subadult and adult individuals and structural elements of the habitat for each locality. The Akaike information criterion routine was used to retain variables with good explanatory power.

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Life-history strategies of a conspicuous reef fish, the Canary damsel *Similiparma lurida* (Pomacentridae) in the northeastern Atlantic

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Supplementary material

Table S1. – Age-length key for *S. lurida* at Gran Canaria Island. n, number of individuals; SD, standard deviation; TL, total length; *, significant differences.

TL (mm)	Age classes (years)																		
	0	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI	XVII	XVIII
55	1																		
60																			
65		1	1																
70																			
75				1		1													
80			1	1															
85				1	1														
90				1															
95					1														
100		1				1	1	1		1									
105						1		1											
110						1	1												
115					2		1	3		1		2							
120				1		2	1	2	1	2	2	1		2	1				1
125				1		3		8	6	2	4	5	1	1	1				
130			1		1	4	5	2	2	3	4	3	3						
135				1	3	1	1	3	2	1	2	1	1	2	2	1			
140				1	1		4	2	2	4	2	2	2						
145				1			1	5	3	5	3			2	1				
150								1	2	1									
155															1				
Total	1	2	3	9	9	14	15	28	18	20	17	14	7	7	6	1	0	0	1
Males																			
n			1	5	7	9	11	18	10	13	8	7	3	4	2				
mean			133.0	125.0	126.9	128.6	134.7	136.6	142.1	142.5	139.4	131.7	137.0	135.8	152.0				
SD				28.84	18.82	5.20	8.68	9.94	7.20	6.47	7.33	9.76	6.00	9.77	7.07				
Females																			
n		1		3		5	4	9	8	7	9	6	4	2	4	1			1
mean		103.0		99.0		104.6	119.5	122.3	126.9	121.9	127.6	127.5	132.8	123.0	129.3	136.0			122.0
SD				19.16		17.18	16.54	10.32	2.85	9.55	4.67	2.59	5.56	4.24	6.95	-			-
																			-
Student t-test		-	-	1.368	-	3.988*	2.366*	3.481*	5.603*	5.755*	4.008*	1.018	0.958	1.694	3.755*	-			-

Table S2. – Results of multiple linear regression analyses testing for the relationship between the total abundances of juvenile, sub-adult and adult individuals and structural elements of the habitat for each locality. The Akaike information criterion routine was used to retain variables with good explanatory power.

Total	Juveniles	Sub-adults	Adults
Agaete			
X_1 = small topographical elements	X_1 = sandy cover	X_1 = algal cover	X_1 = sandy cover
X_2 = algal cover	X_2 = large topographical elements	X_2 = small topographical elements	X_2 = small topographical elements
X_3 = sandy cover		X_3 = sandy cover	X_3 = algal cover
$Y = -0.676+0.089X_1+ 0.399X_2+0.07X_3$	$Y = -0.536+0.117X_1+0.175X_2$	$Y = 0.262+0.248X_1+0.034X_2+0.051X_3$	$Y = -0.401-0.097X_1+0.045X_2+0.167X_3$
$r^2 = 0.551$	$r^2 = 0.322$	$r^2 = 0.4771$	$r^2 = 0.446$
Telde			
X_1 = small topographical elements with algae	-	X_1 = small topographical elements with algae	X_1 = small topographical elements with algae
$Y = 49.77+0.254X_1$		$Y = 0.99+0.153X_1$	$Y = 28.887+0.202X_1$
$r^2 = 0.307$		$r^2 = 0.129$	$r^2 = 0.314$