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Life history traits of the sand stargazer *Dactyloscopus tridigitatus* (Teleostei: Blennioidei) from south-eastern Brazilian coast

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Individuals of the sand stargazer Dactyloscopus tridigitatus *were collected monthly over a period of one year in an urban-sandy beach in south-eastern Brazil. We sampled 57 males, 64 females, and 6 juveniles, indicating a sex-ratio of approximately 1:1. Total length and weight did not differ significantly between sexes, showing no sexual dimorphism in size. The growth of* D. tridigitatus *was highly positive allometric and the correlation coefficient was significant for both sexes. Males were observed carrying two egg clumps under each enlarged pectoral fin during most of the year. In contrast, females showed a more restricted reproductive period, concentrated during the austral rainy season. The number of eggs in each clump carried by males did not differ significantly from the number of vitellogenic oocytes of mature females. The number of eggs carried by males was weakly correlated to male total length; however, female fecundity was strongly correlated to female total length.* Dactyloscopus tridigitatus *consumed a high variety of prey items, including crustaceans, annelids, molluscs, teleosts, insects and eggs. Isopods were the most important component of the diet followed by polychaetes and amphipods. We concluded that promiscuous breeding, paternal care behaviour and invertivorous feeding habits seem to be important traits for the species' success in the studied habitat.*

Keywords: marine fish, Dactyloscopidae, population structure, reproduction, feeding

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INTRODUCTION

The suborder Blennioidei comprises 883 species, 130 genera and six families of marine fish widely distributed in tropical and warm temperate coasts (Patzner *et al.*, 2009). According to these authors, they generally occur in shallow habitats and have a wide variety of forms, behaviours and ecological niches. Most blennioids display a suite of reproductive tactics that include sexual selection, polygamy and paternal care of eggs in sheltered sites (Gibran *et al.*, 2004; Neat & Lengkeek, 2009). They display a great variety of trophic strategies, ranging from lepidophagy through carnivory to algivory and detritivory (Wilson, 2009). This diversity of reproductive and feeding aspects enabled the evolution of different life histories within this group (Gonçalves & Almada, 1998; Oliveira *et al.*, 2001; Hastings, 2002; Awata *et al.*, 2010).

The Dactyloscopidae is a basal group within Blennioidei based on molecular evidence (Stepien *et al.*, 1997). Also called sand stargazers, the members of this family are small inconspicuous sand-dwelling fish inhabiting tropical marine or estuarine waters on the Atlantic and Pacific coasts of the Western Hemisphere (Dawson, 1982; Nelson, 2006). Dactyloscopids comprise at least 48 species included in nine genera that present elongated bodies, eyes on top of the head and cryptic coloration (Hastings & Springer, 2009). They present some unique features, such as ventilation of the gills by a brachiostegal pump and the development of opercular and lateral fimbriae, both traits associated with sand-dwelling habits (Doyle, 1998).

Dactyloscopus tridigitatus Gill, 1859 is one of the most abundant and widely distributed Atlantic dactyloscopids, ranging from southern Florida in the USA to south-eastern Brazil (Dawson, 1982). Like other sand stargazers, this species is completely adapted to live on sandy bottoms, sometimes totally buried in the sand or with only the mouth and eyes exposed, making it very difficult to detect them visually, since their coloration is very similar to that of the adjacent background (Wagner *et al.*, 1976).

Although there are several studies on the presence of *D. tridigitatus* along its area of occurrence (e.g. Wagner *et al.*, 1976; Halpern & Floeter, 2008; Matamoros *et al.*, 2009), none of

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them provide details on reproduction or feeding of this species. Thus, the purpose of the present study is to describe selected life history traits of *D. tridigitatus* living on the surf-zone of an urban beach of south-eastern Brazil, in order to determine population structure, reproduction and diet of this blennioid.

MATERIALS AND METHODS

Study area and sample collection

Praia da Costa (20°20′S 40°16′W) is a dissipative urban-sandy beach located in the municipality of Vila Velha, Espírito Santo State, south-eastern Brazil. Two kilometres long, it is mostly exposed, although its northern portion is protected by rocky reefs, which minimize the wave impacts and provides shelter for many organisms (Figure 1). This region typically has seasonal climate with two defined seasons: dry (April to September) and rainy (October to March) (André *et al.*, 2008).

From May 2005 to April 2006, monthly active searches were carried out during the lowest tide along all the extension of the Praia da Costa's intertidal zone. After detection of the exposed protuberant eyes of the species, dip nets (40 cm in diameter and 1 mm nylon mesh size) were buried in the sand and the individuals collected. The fish collected were handled according to procedures indicated in the Guidelines for Animal Experiments established by the Brazilian College for Animal Experimentation (COBEA) and kept in 10% formalin for one week and preserved in 70% alcohol afterwards. Voucher specimens are in the fish collection of the Museu de Biologia Professor Mello Leitão (MBPML 939, 941, 945, 947, 948, 951, 953 and 955).

Biological analysis

A total of 127 specimens of *Dactyloscopus tridigitatus* was captured and measured (total length (TL) in mm, and mass (M) in g). After dissection, sex determination and gonadal maturation were established based on macroscopic morphology of the gonads (Carvalho *et al.*, 2009). In order to determine fecundity, the mature ovaries were selected and the vitellogenic oocytes were counted under a stereoscopic microscope, as well as the number of eggs in the clumps attached to pectoral fins of males. The diameter of 200 vitellogenic oocytes from each mature female (N = 15) was measured using a micrometric ocular coupled to a stereoscopic microscope.

To determine the diet composition, the gut was cut from the oesophagus to the anus, since the stomach is not evident. All the prey items were identified to the lowest possible taxonomic level. The importance of each prey in the diet was assessed by settling frequency of occurrence and prey wet

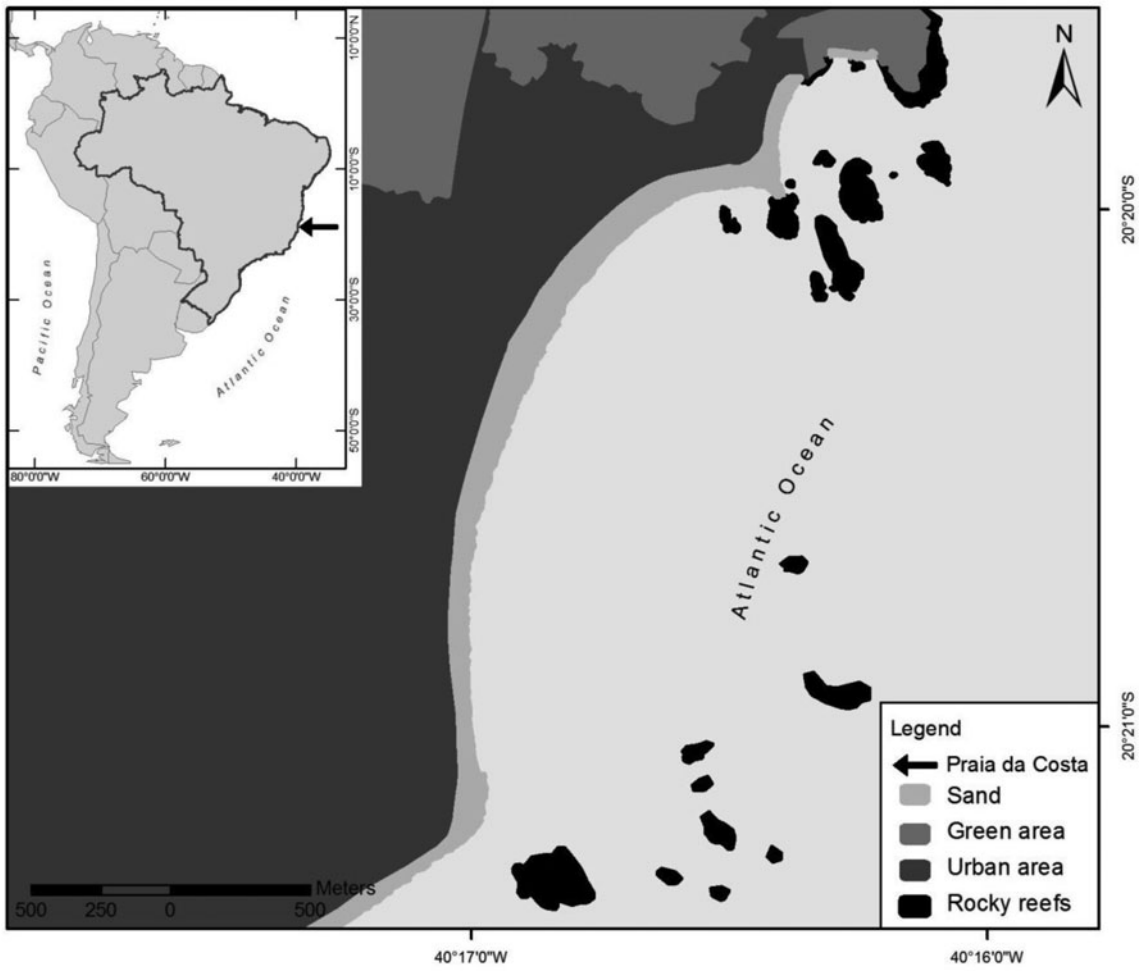

Fig. 1. Location and landscape aspects of the Praia da Costa, Espírito Santo State, south-eastern Brazil.

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weight (to the nearest 0.1 mg) using the alimentary importance index (AII) (Kawakami & Vazzoler, 1980) described by the equation $AII = (Fi \times Wi)/\sum(Fi \times Wi)$, where F*i* and W*i* are the frequency of occurrence (%) and weight (%) of each item, respectively.

Statistical analysis

The Fulton's condition factor (K) was calculated for males and females during the dry and rainy seasons, according to the equation $K = (W/TL^3)100$. The Chi-square test (χ^2) was used to assess the significance of difference in the sex-ratio of males to females through the study period. A one-way analysis of variance test, followed by the Tukey *post-hoc* test, was used to determine the significance of differences of length, mass, condition factor and number of mature eggs between sexes and seasons. The length–weight relationship of *D. tridigitatus* was calculated using the equation $M = aTL^b$, where *a* is a coefficient related to body form and *b* (slope) is an exponent indicating isometric growth when around 3. Parameters *a* and *b* of the exponential curve were estimated by linear regression analysis over ln-transformed data, and the degree of association between the ln Lt and ln M was evaluated by the coefficient of determination (r^2). Pearson's correlation coefficient (r) was used to determine the degree of correlation between the females' fecundity and TL, as well as the degree of correlation between the number of eggs carried by males and TL. Pearson's r was also used to determine the degree of correlation between the vitellogenic oocytes' diameter and female TL.

RESULTS

Population structure

Fish were only found buried in the sandy substrate of intertidal zone sheltered by rocky reefs. No fish was found or collected in the exposed portion of the beach. Throughout the study period, 57 males (44.9%), 64 females (50.4%) and 6 juveniles (4.7%) of *Dactyloscopus tridigitatus* were collected. We found no significant difference in sex-ratio ($\chi^2 = 29.13$, $P = 0.141$) (Figure 2). In the dry season, males varied in TL and M, respectively, from 44.4 to 80.0 mm (mean ± SD = 59.5 ± 13.2 mm) and 0.3 to 3.4 g (1.43 ± 1.3 g), females from 39.5 to 85.3 mm (56.4 ± 10.9) and 0.2 to 4.2 g (0.92 ± 0.9 mm), and juveniles from 30.3 to 39.9 mm (35.8 ± 4.5 mm) and 0.1 to 0.3 g (0.1 ± 0.1 g). In the rainy season, males varied in TL and M from 44.5 to 80.2 mm (61.1 ± 9.3 mm) and 0.3 to 3.5 g (1.3 ± 0.9 g), and females from 40.1 to 73.2 mm (58.0 ± 8.5 mm) and 0.2 to 3.1 g (0.96 ± 0.6 g). No significant differences in the TL ($F = 1.21$, $P = 0.308$) and M ($F = 1.64$, $P = 0.183$) between sexes and seasons were detected (Figure 3A, B). Regarding to condition factor (K) in the dry season, males varied from 0.26 to 0.82 (0.51 ± 0.16), females from 0.23 to 0.68 (0.40 ± 0.12), and juveniles from 0.16 to 0.47 (0.29 ± 0.12). In the rainy season, the K of males varied from 0.27 to 0.73 (0.43 ± 0.12) and females from 0.26 to 0.82 (0.43 ± 0.13). Significant differences in the K values were observed between males and females only in the dry season (Figure 3C) ($F = 3.01$, $P = 0.033$). The parameter *b* of the length–weight relationship of *D. tridigitatus* was 4.06,

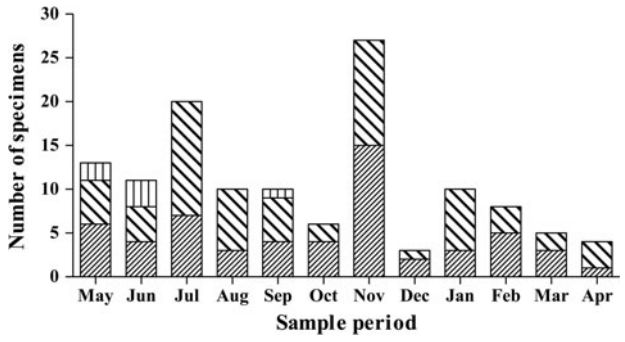

Fig. 2. Number of males (▨), females (▩) and juveniles (▥) of *Dactyloscopus tridigitatus* collected from May 2005 to April 2006 in Praia da Costa, Espírito Santo State, south-eastern Brazil.

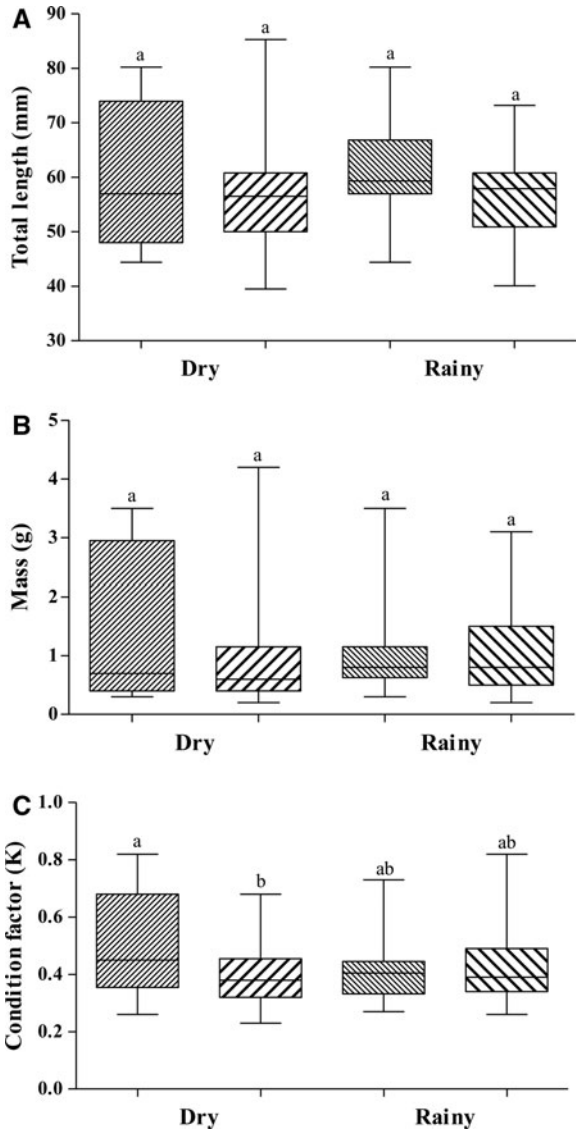

Fig. 3. Mean values ± SD of total length (A), mass (B) and Fulton's condition factor (C) of *Dactyloscopus tridigitatus* during dry (▨ males, N = 25 and females ◪ N = 37) and rainy seasons (▧ males N = 32 and ▩ females N = 27). Values followed by same letters above the bars are not significantly different ($P > 0.05$) by Tukey *post-hoc* test.

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parameter *a* was <0.001 and the coefficient of determination (r^2) was 0.91 ($P < 0.005$) (Figure 4).

Reproduction

In the dry season, 44% of captured *D. tridigitatus* males were in reproductive activity, whilst 10.8% females were in this condition ($\chi^2 = 20.11$, $P < 0.001$). In the rainy season, 56.2% males were in reproductive activity as opposed to 40.7% of reproductive females ($\chi^2 = 2.48$, $P = 0.115$) (Figure 5). Each reproductive male was found carrying two incubating egg clumps under each enlarged pectoral fin (N = 29). The number of eggs found in each egg clump varied from 459 to 922 (590.4 ± 141.4) in the dry season, whilst in the rainy season the number of eggs carried by males varied from 412 to 641 (523.8 ± 62.2). For mature females captured in the dry season, the number of vitellogenic oocytes found in ovaries varied from 408 to 672 (556.3 ± 109.5), whilst in the rainy season the females' fecundity varied from 395 to 589 (507.7 ± 72.6). The number of eggs in each clump carried by males did not differ significantly from the number of vitellogenic oocytes of mature females (F = 1.69, $P = 0.183$) (Figure 6). The smallest egg-carrying male and the smallest mature female measured, respectively, 56.3 mm and 57.2 mm TL. The number of eggs found in each individual clump was weakly correlated to male TL (r = 0.41, $P = 0.025$). In contrast, the number of vitellogenic oocytes was strongly correlated to female TL (r = 0.91, $P < 0.001$) (Figure 7). The diameter of vitellogenic oocytes varied in size from 0.70 to 1.04 mm (0.92 ± 0.08 mm) and was strongly correlated to female TL (r = 0.96, $P < 0.001$) (Figure 8).

Diet composition

Out of the 127 individuals caught, 95 (74.8%) had at least one food item in the digestive tract. Empty guts were found both in dry (N = 14) and rainy seasons (N = 18). All egg-carrying males had empty guts. *Dactyloscopus tridigitatus* consumed a great variety of prey items including crustaceans, annelids, molluscs, teleosts, insects and eggs (Table 1). Although all items reached significant (AII ≥ 0.01) values, crustaceans (AII = 0.74 and 0.61) and Annelida (AII = 0.2 and 0.34) were the most consumed resources during both dry and rainy seasons. Along the dry period isopods (AII = 0.39) were the most important sub-item ingested by the species, followed by amphipods (AII = 0.21) and polychaetes (AII = 0.2). During the rainy season, both isopods and polychaetes ranked first (AII = 0.34), followed by amphipods (AII = 0.11).

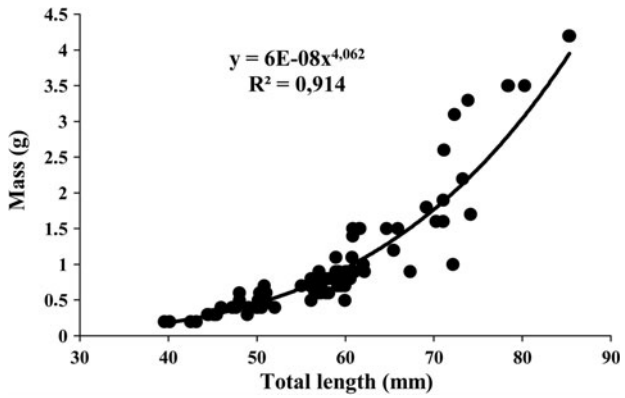

Fig. 4. Length–weight relationship beteween *Dactyloscopus tridigitatus* from a sandy beach in south-eastern Brazil.

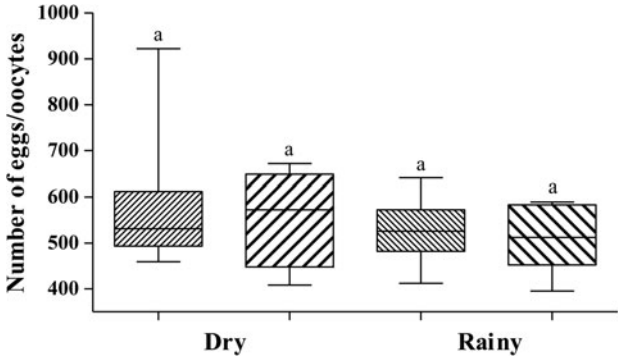

Fig. 6. Mean values ± SD of the number of eggs carried by males and the number of vitellogenic oocytes from the mature ovaries of females of *Dactyloscopus tridigitatus* during dry (▨ males N = 11 and ◪ females N = 4) and rainy seasons (▧ males N = 18 and ◩ females N = 11). Values followed by same letters above the bars are not significantly different ($P > 0.05$) by Tukey *post-hoc* test.

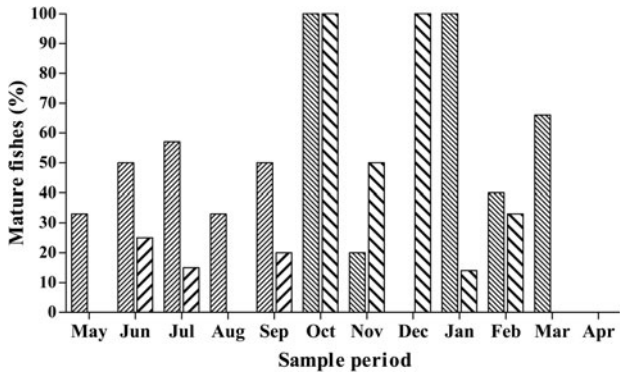

Fig. 5. Relative frequency (%) of mature *Dactyloscopus tridigitatus* during dry (▨ males N = 11 and ◪ females N = 4) and rainy seasons (▧ males N = 18 and ◩ females N = 11) in Praia da Costa, Espírito Santo State, south-eastern Brazil.

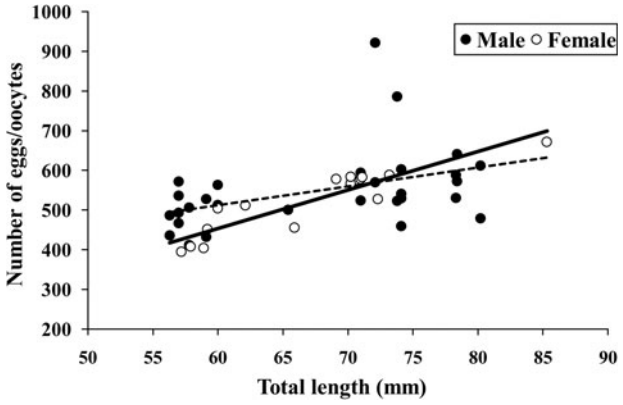

Fig. 7. Correlation between the number of eggs carried by males and the females' fecundity against the total length of *Dactyloscopus tridigitatus* (regression line: dotted for males and solid for females).

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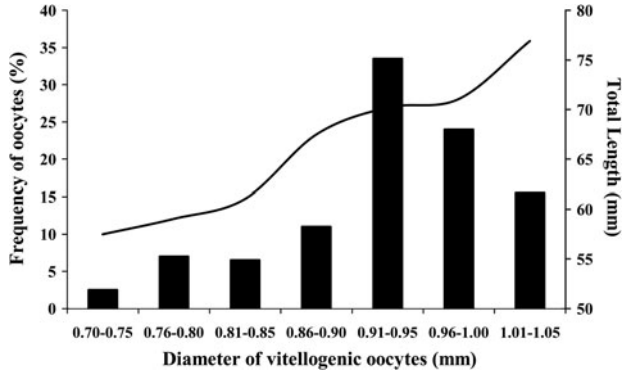

Fig. 8. Frequency (%) of vitellogenic oocytes' diameter from the mature ovaries of females (solid bars) and correlation between the oocytes' diameter and female total length of *Dactyloscopus tridigitatus* (solid line).

DISCUSSION

The finding of *Dactyloscopus tridigitatus* buried in the sand of the intertidal portion protected by rocky reefs is likely related to the fact that sheltered environments serve as refuge from predators for many blennioid fish (Hastings, 1991; Gonçalves & Almada, 1997), and are also useful for reproductive behaviour during the breeding season (Hastings, 2002; Gibran *et al.*, 2004).

Unlike some blennioid species in which males exhibit sexual size dimorphism (Kraak, 1996; Giacomello & Rasotto, 2005), for *D. tridigitatus* this characteristic was not detected in both dry and rainy seasons. In the present study, positive allometric growth ($b > 3$) was observed for *D. tridigitatus*, characterizing an increase in weight greater than the increase in length for both sexes. The high values of the allometric coefficient indicate great investment in growth related to small size of the specimens of population studied. Other blennies in the Blenniidae, Labrisomidae and Tripterygiidae families also have positive allometric growth on the Tropical West Atlantic coast (Macieira & Joyeux, 2009; Camilato *et al.*, 2010).

Males of *D. tridigitatus* were reproductively active in nearly every sampled month, whereas females showed more restricted periods of sexual activity which were concentrated in the rainy season. This can be explained by energy expended by females to produce larger and more costly gametes than males (Andersson, 1994) even with male parental care as an additional energy cost (Oliveira *et al.*, 2001). For most blennies paternal care is habitually egg defence (Almada & Santos, 1995; Gibran *et al.*, 2004) as observed in the present study, in which *D. tridigitatus* males carry only incubating eggs. According to Oliveira *et al.* (2001), this fact allows males to continue breeding over the parental phase, thus their reproductive period is still longer than that of females. These factors usually result in a male-biased operational sex ratio (Kvarnemo & Ahnesjö, 1996; Saraiva *et al.*, 2009), as observed for *D. tridigitatus* in the dry season of the studied beach. However, males and females of the sand stargazer presented similar reproductive rates in the rainy season, although during November and December females reached higher breeding rates. In fact, sex-role reversal can occur in some blenniids in which the number of reproductive females overlaps the number of mature males during the breeding season (Ahnesjö *et al.*, 2001; Shibata & Kohda, 2006; Saraiva *et al.*, 2009).

Polygamy and promiscuity are described for some blennies that display a complex reproductive behaviour (Gonçalves & Almada, 1997; Gibran *et al.*, 2004; Saraiva *et al.*, 2009).

Table 1. Absolute occurrence (O), prey wet weight (W) and alimentary importance index (AII) of the items consumed by *Dactyloscopus tridigitatus* during both dry and rainy seasons.

Item	Sub-item	Dry season (N = 47)			Rainy season (N = 48)		
		O	W	AII	O	W	AII
Mollusca		3	2.3	0.01	2	2.2	0.03
	Bivalvia	2	2	0.01	–	–	–
	Undentified gastropds	1	0.3	<0.01	1	1	0.01
	Littorina ziczac	–	–	–	1	1.2	0.02
Crustacea		43	51.2	0.74	46	33.1	0.61
	Amphipoda	17	5.8	0.21	10	3.7	0.11
	Undentified Brachyura	–	–	–	1	0.3	0.01
	Araneus cribrarius	2	19.5	0.08	1	9.1	0.07
	Callinectes spp.	1	4.3	0.01	2	6.4	0.06
	Pachygrapsus spp.	2	12.2	0.05	–	–	–
	Cumacea	–	–	–	1	0.1	0.01
	Isopoda	20	9.3	0.39	30	13.4	0.34
	Ostracoda	1	0.1	<0.01	1	0.1	0.01
Annelida		6	16.1	0.2	13	31.9	0.34
	Polychaeta	6	16.1	0.2	13	31.9	0.34
Teleostei		3	20.3	0.04	–	–	–
	Anchoviella lepidentostole	1	11.3	0.02	–	–	–
	Gobionellus spp.	1	5.1	0.01	–	–	–
	Trachinotus falcatus	1	3.9	0.01	–	–	–
Insecta		–	–	–	1	0.2	0.01
	Larvae	–	–	–	1	0.2	0.01
Other items		–	–	–	2	0.4	0.02
	Eggs	–	–	–	1	0.1	0.01
	Undentified	–	–	–	1	0.3	0.01

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Perhaps this breeding pattern of blennies can explain the two egg masses carried by *D. tridigitatus* males, which suggests that males mate with more than one female. The suggestion of promiscuity of *D. tridigitatus* is also supported by a weak correlation of the egg clumps' fecundity and the TL of the male, which indicate that male length is not a factor for sexual selection by females. This finding is similar to the blenny *Acanthemblemaria crockeri*, for which the male size is not correlated with the number of eggs received (Hastings, 1988). In contrast, female *D. tridigitatus* fecundity was positively correlated to TL, which indicates that larger females are able to produce more eggs. The vitellogenic oocyte diameter of about 1 mm recorded in mature ovaries of *D. tridigitatus* females is similar to other dactyloscopids (Watson, 1996) and also to the blenny *Labrisomus nuchipinnis* (Gibran *et al.*, 2004).

There is no quantitative data on feeding habits of Dactyloscopidae available in the literature (Wilson, 2009). However, this author classifies the sand stargazers as lie-and-wait predators that prey mainly on small crustaceans. This was the most consumed and important item in the diet of *D. tridigitatus* during both dry and rainy seasons, although it also ingested large amounts of polychaetes. The consumption of molluscs, teleosts, insects and eggs was not as expressive as these two main items, which indicates that they act as complementary resources in the diet of the analysed individuals. Therefore, the results of AII allow us to classify *D. tridigitatus* from Praia da Costa as a predator of mobile benthic organisms; the same trophic category given by Ferreira *et al.* (2007) and Halpern & Floeter (2008) for the same species in their qualitative studies. The absence of food items in the guts of egg-carrying males is a characteristic recorded among other Blennioidei species (Gonçalves & Almada, 1997; Wilson, 2009). We found no egg cannibalism in our study, although filial cannibalism is mentioned for some other Blennioidei (Kraak, 1996; Manica, 2002).

In conclusion, although the species exhibits burrowing behaviour which differentiates it from most of the Blennioidei, the main life history traits for the *D. tridigitatus* from the Praia da Costa are in accordance with the general pattern of this suborder, since this stargazer lives in sheltered habitats, has a long reproductive period, presents both polygamous and parental care behaviour and uses small invertebrates as its main trophic resource.

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REFERENCES

Almada V.C. and Santos R.S. (1995) Parental care in the rocky intertidal: a case study of adaptation and exaptation in Mediterranean and Atlantic blennies. *Reviews of Fish Biology and Fisheries* 5, 23–37.

Andersson M. (1994) *Sexual selection*. Princeton: Princeton University Press.

André R.G.B., Marques V.S., Pinheiro F.M.A. and Ferraudo A.S. (2008) Identificação de regiões pluviometricamente homogêneas no estado do Rio de Janeiro, utilizando-se valores mensais. *Revista Brasileira de Meteorologia* 23, 501–509.

Ahnesjö I., Kvarnemo C. and Merilaita S. (2001) Using potential reproductive rates to predict mating competition among individuals qualified to mate. *Behavioral Ecology* 12, 397–401.

Awata S., Miura S., Seki S., Sagawa T., Sato N. and Sakai K. (2010) Seasonal changes in reproductive and physical condition, sexual dimorphism, and male mating tactics in the jewelled blenny *Salarias fasciatus*. *Ichthyological Research* 57, 161–168.

Camilato V., Simon T., Pinheiro H.T., Pimentel C.R. and Joyeux J-C. (2010) Length–weight relationships for some cryptobenthic reef fishes off Guarapari, south-eastern Brazil. *Journal of Applied Ichthyology* 26, 463–464.

Carvalho P.A., Paschoalini A.L., Santos G.B., Rizzo E. and Bazzoli N. (2009) Reproductive biology of *Astyanax fasciatus* (Pisces: Characiformes) in a reservoir in south-eastern Brazil. *Journal of Applied Ichthyology* 25, 306–313.

Dawson C.E. (1982) Atlantic sand stargazers (Pisces: Dactyloscopidae), with description of one new genus and seven new species. *Bulletin of Marine Science* 32, 14–85.

Doyle K.D. (1998) Phylogeny of the sand stargazers (Dactyloscopidae: Blennioidei). *Copeia* 1, 76–96.

Ferreira C.E.L., Ferreira C.G.W., Rangel C.A., Mendonça J.P., Gerhardinger L.C., Filho A.C., Godoy E.A., Luiz-Jr O. and Gasparini J.L. (2007) Peixes Recifais. In Creed J.C., Pires D.O. and Figueiredo M.A.O. (eds) *Biodiversidade marinha da Baia da Ilha Grande*. Brasília: MMA/SBF, pp. 291–322.

Giacomello E. and Rasotto M.B. (2005) Sexual dimorphism and male mating success in the tentacled blenny, *Parablennius tentacularis* (Teleostei: Blenniidae). *Marine Biology* 147, 1221–1228.

Gibran F.Z., Santos F.B., Santos H.F. and Sabino J. (2004) Courtship behavior and spawning of the hairy blenny *Labrisomus nuchipinnis* (Labrisomidae) in south-eastern Brazil. *Neotropical Ichthyology* 2, 163–166.

Gonçalves E.J. and Almada V.C. (1997) Sex differences in resource utilization by the peacock blenny. *Journal of Fish Biology* 51, 624–633.

Gonçalves E.J. and Almada V.C. (1998) A comparative study of territoriality in intertidal and subtidal blennioids (Teleostei, Blennioidei). *Environmental Biology of Fishes* 51, 624–264.

Halpern B.S. and Floeter S.R. (2008) Functional diversity responses to changing species richness in reef fish communities. *Marine Ecology Progress Series* 364, 147–156.

Hastings P.A. (1988) Correlates of male reproductive success in the browncheek blenny, *Acanthemblemaria crockeri* (Blennioidea: Chaenopsidae). *Behavioral Ecology and Sociobiology* 22, 95–102.

Hastings P.A. (1991) Flexible responses to predators in a marine fish. *Ethology Ecology & Evolution* 3, 177–184.

Hastings P.A. (2002) Evolution of morphological and behavioral ontogenies in females of a highly dimorphic clade of blennioid fishes. *Evolution* 56, 1644–1654.

Hastings P.A. and Springer V.G. (2009) Systematics of the Blennioidei and the included families Chaenopsidae, Clinidae, Labrisomidae and Dactyloscopidae. In Patzner R.A., Gonçalves E.J., Hastings P.A. and Kapoor B.G. (eds) *The biology of the blennies*. Enfield, NH: Science Publishers, pp. 3–30.

Kawakami E. and Vazzoler G. (1980) Método gráfico e estimativa de índice alimentar aplicado ao estudo de alimentação de peixes. *Boletim do Instituto Oceanográfico* 29, 205–207.

Kraak S.B.M. (1996) Female preference and filial cannibalism in *Aidablennius sphynx* (Teleostei, Blennidae); a combined field and laboratory study. *Behavioural Processes* 36, 85–98.

Kvarnemo C. and Ahnesjö I. (1996) The dynamics of operational sex ratios and competition for mates. *Trends in Ecology and Evolution* 11, 404–408.

Macieira R.M. and Joyeux J-C. (2009) Length–weight relationships for rockpool fishes in Brazil. *Journal of Applied Ichthyology* 25, 358–359.

Manica A. (2002) Filial cannibalism in teleost fish. *Biological Reviews* 77, 261–277.

Matamoros W.A. Schaefer J.F. and Kreiser B.R. (2009) Annotated checklist of the freshwater fishes of continental and insular Honduras. *Zootaxa* 2307, 1–38.

Neat F. and Lengkeek W. (2009) Sexual selection in blennies. In Patzner R.A., Gonçalves E.J., Hastings P.A. and Kapoor B.G. (eds) *The biology of blennies*. Enfield, NH: Science Publishers, pp. 249–278.

Nelson J.S. (2006) *Fishes of the world*. 4th edition. Hoboken, NJ: John Wiley & Sons, Inc.

Oliveira R.F., Canario A.V.M. and Grober M.S. (2001) Male sexual polymorphism, alternative reproductive tactics, and androgens in combtooth blennies (Pisces: Blenniidae). *Hormones and Behavior* 40, 266–275.

Patzner R.A., Gonçalves E.J., Hastings P. and Kapoor B.G. (eds) (2009) *The biology of blennies*. Enfield, NH: Science Publishers.

Saraiva J.L., Barata E.N., Canário A.V.M. and Oliveira R.F. (2009) The effect of nest aggregation on the reproductive behavior of the peacock blenny *Salaria pavo*. *Journal of Fish Biology* 74, 754–762.

Shibata J. and Kohda M. (2006) Seasonal sex role changes in the blenniid *Petroscirtes breviceps*, a nest brooder with paternal care. *Journal of Fish Biology* 12, 203–214.

Stepien C., Dillon A., Brooks M., Chase K. and Hubers A. (1997) The evolution of blennioid fishes based on an analysis of mitochondrial 12S rDNA. In Kocher T. and Stepien C. (eds) *Molecular systematics of fishes*. San Diego, CA: Academic Press, pp. 245–270.

Wagner H.J., Menezes N.A. and Ali M.A. (1976) Retinal adaptations in some Brazilian tide pool fishes. *Zoomorphology* 83, 209–226.

Watson W. (1996) Blennioidei. In Moser H.G. (ed.) *The early stages of fishes in the California Current Region*. California Cooperative Oceanic Fisheries Investigations, pp. 1148–199.

and

Wilson S.K. (2009) Diversity in the diet and feeding habits of blennies. In Patzner R.A., Gonçalves E.J., Hastings P.A. and Kapoor B.G. (eds) *The biology of blennies*. Enfield, NH: Science Publishers, pp. 139–162.

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