

A comparative study of territoriality in intertidal and subtidal blennioids (Teleostei, Blennioidei)

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Synopsis

This paper presents a comparative analysis of territoriality in three intertidal (*Lipophrys pholis*, *Coryphoblennius galerita*, *Salaria pavo*) and two subtidal (*Tripterygion delaisi*, *Parablennius pilicornis*) blennioid fishes. Focal-animal observations of males guarding eggs showed that: (i) intertidal species had smaller territories that were less frequently patrolled; (ii) in subtidal species feeding was limited to the territory, while in intertidal fishes a substantial proportion of the feeding acts occurred outside the defended area; (iii) intertidal species spent less time out of the nest and showed a lower level of locomotory activity; (iv) subtidal species were subjected to a higher number of territorial intrusions with more species intruding their territory, some of them potential egg predators; (v) subtidal species performed several water column displays that played a significant role in courtship, while in intertidal fishes these displays are almost absent. Signalling without the presence of a female was almost absent in intertidal species. It is argued that intertidal fishes minimize the time spent out of the nest and the loss of contact with the substrate, features that may be of high survival value in conditions of strong turbulence. Although intertidal species have a reduced time available for feeding, this may be compensated by lower levels of locomotory activity, territorial defense and risk of egg predation.

Introduction

Blennioid fishes are among the most abundant fish groups in tropical and warm temperate rocky coasts, occurring both in intertidal and subtidal habitats. Therefore, they provide an excellent opportunity to investigate the ways in which intertidal conditions affect the behaviour of fishes that occupy such habitats (Almada & Santos 1995). Their suitability for this type of study is further emphasized by their small size and ease of observation and by the fact that, the males at least, are territorial during the breeding season, which allows detailed observations of individual fishes for long periods.

There is a considerable body of literature concerning the territorial behaviour of blennioid fishes (Fishelson 1963, 1975, Stephens et al. 1970, Nursall 1977, 1981, Wirtz 1978, Almada et al. 1983, 1987, 1992, 1994, Lindquist 1985, Santos 1985, 1992, Hastings 1986, Patzner et al. 1986, Koppel 1988, Santos et al. 1989).

There are, however, few detailed comparative studies on the differences in territorial structure between intertidal and subtidal species. Almada & Santos (1995) showed that the basic features of reproductive behaviour, namely male breeding territoriality and parental care, are common to both intertidal and subtidal blennioid fishes. They suggest

that intertidal fishes tend to differ from their subtidal relatives by having courtship and agonistic behaviour patterns that minimize the loss of contact with the substrate, a feature that is probably adaptive in conditions of marked turbulence. Almada et al. (1992) suggested that intertidal blennies may experience reduced egg predation and less territorial intrusions by potential egg eaters, compared to subtidal equivalents. This situation may offset the costs due to the limited time available to feed, imposed by the tidal cycle. This view is in accordance with the more general hypothesis of Gibson (1988) and Horn & Gibson (1988) that rocky intertidal resident fishes are subjected to less severe predation pressure, at least by aquatic predators.

Almada et al. (1992) showed that unguarded egg masses of *Lipophrys pholis* may survive for up to 5 days without predation. Moreover, it is known that subtidal species may visit the intertidal to spawn, leaving the egg masses unguarded during low tide (e.g. DeMartini 1978, Middaugh et al. 1981, Potts 1985). These findings also suggest a reduction of egg predation in intertidal habitats.

In this paper, we present comparative data on the territoriality of the breeding males of five blennioid species, three intertidal (*Lipophrys pholis*, *Salaria pavo* and *Coryphoblennius galerita*) and two subtidal (*Parablennius pilicornis* and *Tripterygion delaisi*).

Material and methods

Data were collected at Arrábida coast (38° 28' N, 8° 59' W) and Ria Formosa (36° 59' N, 7° 51' W), in Portugal, during the years 1986, 1987, 1993 and 1994. At Arrábida, the study site consists of vertical cliffs with boulders and large rocks that become exposed at low tide. At Ria Formosa, the study site is situated inside a lagoon, and the only hard substrates available are bricks in which the males of *S. pavo* establish nests. In both sites wave action is very reduced. Both study areas were previously characterized by Almada et al. (1992, 1994).

Behavioural observations were conducted by skin- and scuba-diving. We performed focal-animal observations (Altmann 1974) of territorial males

guarding eggs, during the breeding season of each species: *C. galerita* – February/March to September/October (Almada et al. 1996); *L. pholis* – October/November to March (Almada et al. 1990a, Faria et al. 1996); *S. pavo* – April/May to September/October (Almada et al. 1994); *T. delaisi* – January/March to August/September; and *P. pilicornis* – February/March to August/September. The amount of focal observation time was: *C. galerita* = 8 h 13 min (n = 23); *L. pholis* = 17 h 51 min (n = 22); *S. pavo* = 31 h 7 min (n = 65); *T. delaisi* = 7 h 20 min (n = 22); and *P. pilicornis* = 7 h 36 min (n = 23).

The area around each nest was arbitrarily divided in four quadrants (upper, lower, left and right), and taking the nest as centre, a series of concentric circles with 10 cm distance between each radius was drawn. The successive locations that a fish visited during each observation period were recorded on a plastic sheet. We also recorded the different behavioural categories performed by the fish in each location, based on the descriptions provided by Fishelson (1963), Wirtz (1978), Almada et al. (1983, 1987, 1992) and Patzner et al. (1986). The area defended against intruders was considered as the territory.

In these observations the time unit used was one minute and the following data were recorded: (i) frequency of excursions out of the nest, their duration, locations visited and the activities performed by the fish during each excursion; (ii) appearance of intruders, their species, the location of their closest approach to the nest and whether they withdrew without apparent reaction by the resident male or left after agonistic action of the territorial fish. For more details on the behavioural observations see Almada et al. (1990b, 1992, 1994, 1995).

The nests mean height to the hydrographic zero were similar in the intertidal species studied (*C. galerita*, *L. pholis* and *S. pavo*). Almada et al. (1992) determined that the average diurnal submersion time obtained for *L. pholis* was 5h 34min. This value was used to calculate the daily rates of patrolling, intrusions and total movement in the intertidal species (for details on this method see Almada et al. 1992). For subtidal species (*T. delaisi* and *P. pilicornis*), these rates were calculated based on the daylight hour period in the peak of the breeding season (14 h in May).

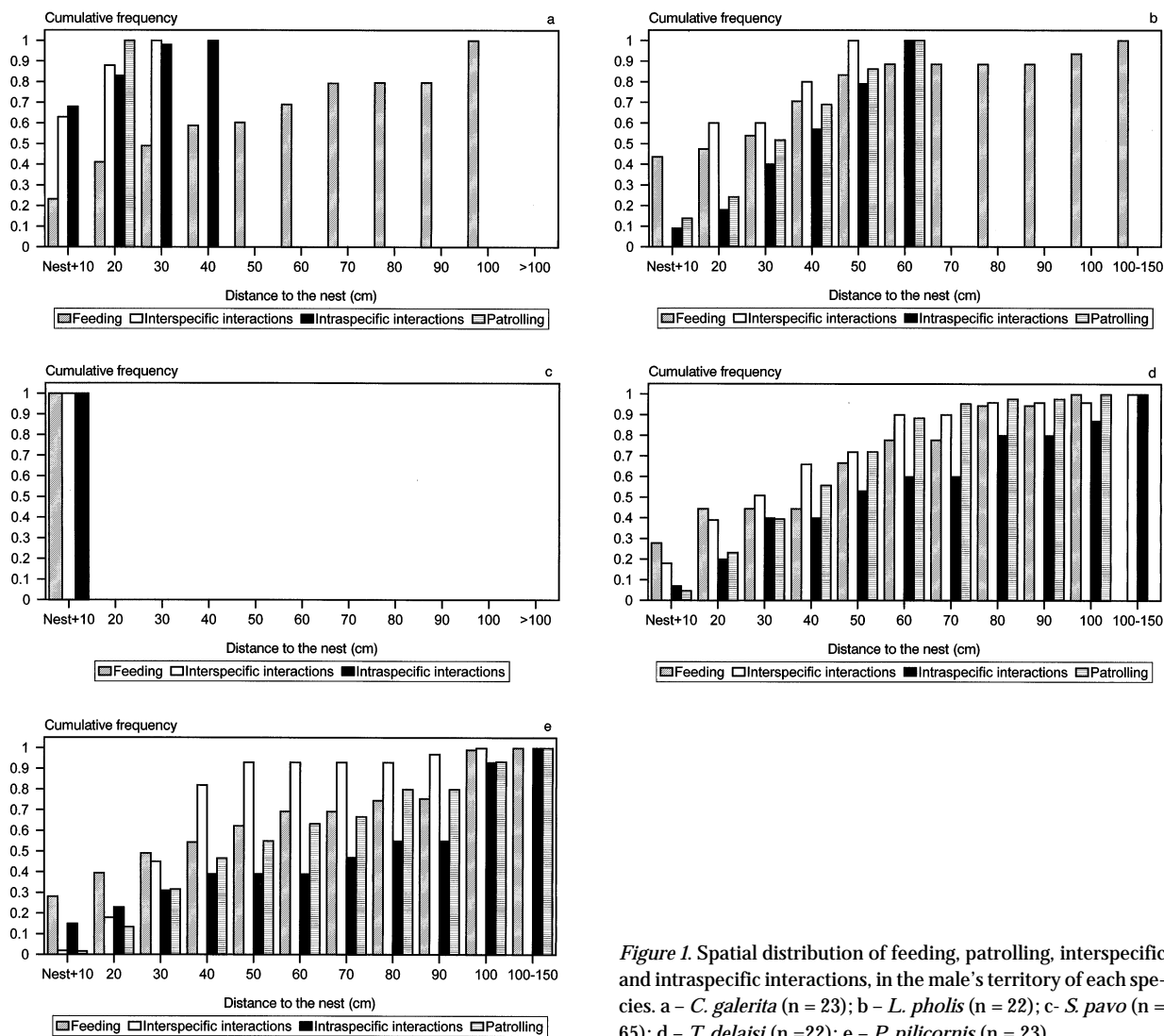


Figure 1. Spatial distribution of feeding, patrolling, interspecific and intraspecific interactions, in the male's territory of each species. a - *C. galerita* (n = 23); b - *L. pholis* (n = 22); c - *S. pavo* (n = 65); d - *T. delaisi* (n = 22); e - *P. pilicornis* (n = 23).

Statistical analysis was performed using the PC computer program STATISTICA for Windows 4.0 (Copyright Statsoft 1993) and the simulation statistical program ACTUS (Estabrook & Estabrook 1989) designed for the analysis of contingency tables. This program uses random numbers to simulate 1000 tables, each with the same row and column totals of the original table. Each simulated table is compared with the original data table. Values smaller than 50 are one-tailed significant ($p < 0.05$). The significance of χ^2 is assessed by the number of times out of 1000 that the value of χ^2 for the simulated table is equal to or greater than that for the original table (Estabrook & Estabrook 1989).

Results

The spatial distribution of feeding, patrolling, intra and interspecific intrusions as a function of the distance to the nest for each species, is shown in Figure 1.

In *S. pavo*, all activities (including feeding) are concentrated in an area of less than 10 cm from the nest. In this species, nests are densely aggregated in bricks and each nest may be surrounded by several others in the same brick. Territoriality is restricted to the nest itself (Almada et al. 1994, 1995, Gonçalves et al. 1996). The breeding males of the two other intertidal species (*L. pholis* and *C. galerita*)

Table 1. a – Number of interspecific and intraspecific intrusions that occurred in the male's territory of each species. b – Statistical analysis using ACTUS.

a	Interspecific intrusions		Intraspecific intrusions	
<i>C. galerita</i> (n = 23)	34		64	
<i>L. pholis</i> (n = 22)	34		50	
<i>T. delaisi</i> (n = 22)	72		19	
<i>P. pilicornis</i> (n = 23)	99		25	

b	(i) Interspecific intrusions	Intraspecific intrusions	(ii) Interspecific intrusions	Intraspecific intrusions
<i>C. galerita</i> (n = 23)	0*	1000	1000	0*
<i>L. pholis</i> (n = 22)	4*	1000	996	0*
<i>T. delaisi</i> (n = 22)	991	1*	12*	1000
<i>P. pilicornis</i> (n = 23)	999	0*	3*	1000

(i) cases in which simulated values did not exceed observed values; (ii) cases in which observed values did not exceed simulated values. $\chi^2 = 73.81$, d.f. = 3, $p < 0.001$. For details of ACTUS see Estabrook & Estabrook (1989).

* $p < 0.05$ (one-tailed).

have territories smaller than those of *P. pilicornis* and *T. delaisi*. Indeed, the shortest distance to the nest at which intruders could penetrate is smaller in intertidal fishes (*C. galerita*: mean = 15.2 cm, s.d. = 8.3, range = 10–40 cm, n = 42 interactions; *L. pholis*: mean = 38.2 cm, s.d. = 15.9, range = 10–60 cm, n = 28 interactions; *T. delaisi*: mean = 42.6 cm, s.d. = 27.3, range = 10–100 cm, n = 47 interactions; *P. pilicornis*: mean = 43.4 cm, s.d. = 25.3, range = 10–100 cm, n = 64 interactions; Kruskal-Wallis: H (3, n = 181) = 57.27, $p < 0.001$). The radius of the defended area was: *C. galerita* = 40 cm; *L. pholis* = 60 cm; *S. pavo* = 10 cm; *T. delaisi* = 100–150 cm; *P. pilicornis* = 100–150 cm. In addition, patrolling is significantly more

frequent in subtidal species, being absent in *S. pavo* and extremely rare in *C. galerita*. The mean individual patrolling rates per day were: *L. pholis* = 20.6 (s.d. = 13.3, range = 2.9–44.5, n = 7), *T. delaisi* = 164.2 (s.d. = 159.9, range = 42–630, n = 11), and *P. pilicornis* = 144.7 (s.d. = 83.4, range = 33.6–336, n = 17) (Kruskal-Wallis: H (2, n = 35) = 15.29, $p < 0.001$).

The spatial distribution of the feeding acts is another feature that distinguishes intertidal and subtidal species. In intertidal species, a substantial proportion of the feeding acts occurred out of the defended area (*C. galerita* = 51%, *L. pholis* = 13%), while in subtidal species territories and home range coincide (Figure 1).

Table 2. Total number of intrusions in the male's territory of each species.

Intruders	<i>C. galerita</i> (n = 21)	<i>L. pholis</i> (n = 17)	<i>T. delaisi</i> (n = 17)	<i>P. pilicornis</i> (n = 20)
<i>C. galerita</i>	64	33	–	–
<i>L. pholis</i>	19	50	–	–
<i>T. delaisi</i>	–	–	19	3
<i>P. pilicornis</i>	–	–	8	25
Other blennioids	3	–	9	2
Wrasses	–	–	32	29
Gobies	–	–	15	3
Sea breams	9	–	–	60
Clingfishes	–	–	8	–
<i>Atherina</i> sp.	–	–	–	2
Crabs	3	1	–	–

Table 3. a – Number of minutes spent inside and outside the nest by the parental male of each species. b – Statistical analysis using ACTUS.

a	Total observation time (min)	Inside the nest (min)	Outside the nest (min)
<i>C. galerita</i> (n = 23)	493	366	7
<i>L. pholis</i> (n = 22)	1071	949	14
<i>S. pavo</i> (n = 65)	1867	1801	6
<i>T. delaisi</i> (n = 22)	440	153	129
<i>P. pilicornis</i> (n = 23)	456	97	90

b	(i) Inside	Outside	(ii) Inside	Outside
<i>C. galerita</i> (n = 23)	168	1000	850	0*
<i>L. pholis</i> (n = 22)	27*	1000	976	0*
<i>S. pavo</i> (n = 65)	0*	1000	1000	0*
<i>T. delaisi</i> (n = 22)	1000	0*	0*	1000
<i>P. pilicornis</i> (n = 23)	1000	0*	0*	1000

(i) cases in which simulated values did not exceed observed values; (ii) cases in which observed values did not exceed simulated values. $\chi^2 = 1353.86$, d.f. = 4, $p < 0.001$. For details of ACTUS see Estabrook & Estabrook (1989).

* $p < 0.05$ (one-tailed).

The proportion of interspecific in relation to intraspecific intrusions was significantly higher in subtidal species (Table 1). In addition, the estimated numbers of interspecific and total intrusions occurring per day were also higher in subtidal species. The mean interspecific intrusion rates per day were: *C. galerita* = 34.4 (s.d. = 15.5, range = 16.7–50.1, n = 16), *L. pholis* = 22.6 (s.d. = 24.0, range = 2.8–83.5, n = 13), *T. delaisi* = 136.5 (s.d. = 81.9, range = 42–336, n = 16), and *P. pilicornis* = 210.2 (s.d. = 128.1, range = 42–462, n = 20) (Kruskal-Wallis: H (3, n = 65) = 42.77, $p < 0.001$); and the mean total intrusion rates per day were: *C. galerita* = 72.8 (s.d. = 31.1, range = 16.7–133.6, n = 21), *L. pholis* = 46.7 (s.d. = 51.1, range = 5.6–200.4, n = 17), *T. delaisi* = 224.8, s.d. = 221.2, range = 42–1008, n = 17), and *P. pilicornis* = 263.2 (s.d. = 135.1, range = 67.2–504, n = 20) (Krus-

kal-Wallis: H (3, n = 75) = 45.30, $p < 0.001$). Subtidal species also suffered intrusions by many non-blennioid fishes. Among them were potential egg predators like the clingfish *Lepadogaster candollei* (see Almada et al. 1987) and several wrasses (Table 2).

The nesting males of subtidal species spent a greater proportion of time out of the nest, when compared with intertidal ones (Table 3). In addition, the daily total amount of movement was also significantly higher in subtidal species. The mean individual total amount of movement per day was: *C. galerita* = 43.42 m (s.d. = 43.90, range = 3.34–133.60 m, n = 16), *L. pholis* = 33.66 m (s.d. = 35.18, range = 0.56–101.87 m, n = 12), *S. pavo* = 21.10 m (s.d. = 25.04, range = 1.67–70.14 m, n = 11), *T. delaisi* = 113.77 m (s.d. = 152.18, range = 8.35–705.60 m, n = 20), and *P. pilicornis* = 152.10 m (s.d. = 85.68,

Table 4. Water column movements performed by each species in courtship or other contexts.

	Courtship		Total	
	Male	Female	Male	Female
<i>C. galerita</i>	0	0	0	2
<i>L. pholis</i>	0	0	1	0
<i>S. pavo</i>	0	0	0	0
<i>T. delaisi</i>	79	0	141	2
<i>P. pilicornis</i>	69	0	98	21

Table 5. Percentage of courtship acts performed with or without the presence of a female.

	Number of courtship acts	Female present (%)	Female not present (%)
<i>C. galerita</i>	19	84.2	15.8
<i>S. pavo</i>	524	100	0
<i>T. delaisi</i>	44	31.8	68.2
<i>P. pilicornis</i>	30	33.3	66.7

range = 30.06–374.08 m, $n = 23$) (Kruskal-Wallis: $H(4, n = 82) = 38.14, p < 0.001$). Similarly, the maximum distance to the nest at which the fishes could be observed was significantly higher in subtidal species. The mean maximum distance from the nest was: *C. galerita* = 38.7 cm (s.d. = 34.8, range = 10–100 cm, $n = 23$), *L. pholis* = 32.3 cm (s.d. = 35.2, range = 0–100 cm, $n = 22$), *S. pavo* = 12.9 cm (s.d. = 37.2, range = 0–200 cm, $n = 65$), *T. delaisi* = 66.0 cm (s.d. = 27.4, range = 30–100 cm, $n = 20$), and *P. pilicornis* = 97.0 cm (s.d. = 36.9, range = 40–200 cm, $n = 23$) (Kruskal-Wallis: $H(4, n = 153) = 82.53, p < 0.001$).

The two groups also differ in some details of their behaviour patterns. Subtidal species performed numerous behaviour patterns that involved movements in the water column, namely in courtship and agonistic displays, while these elements were extremely rare in intertidal fishes (Table 4). In addition, courtship signalling in the absence of a nearby female was common in subtidal species and almost absent in intertidal ones (Table 5). In *L. pholis*, courtship was too rarely observed to be quantified.

One interesting feature shared by the two groups, is that all species performed more radial than tangential displacements, that is, they performed more displacements involving the nest and the peripheral locations, than movements between peripheral locations (Mann-Whitney U-test: *C. galerita* $Z = 4.69, p < 0.001$; *L. pholis* $Z = 3.47, p < 0.001$; *T. delaisi* $Z = 3.67, p < 0.001$; *P. pilicornis* $Z = 4.69, p < 0.001$). When compared with tangential movements, radial displacements minimize the amount of time spent away from the nest.

Discussion

The intertidal habitats of rocky coasts tend to experience much greater turbulence than habitats located well below the tidal influence. Many of the findings presented in this paper can be interpreted as representing adaptations of intertidal fishes to turbulent conditions. When compared to subtidal species, they defend smaller territories, present a reduced total amount of activities, signalling and other behaviour patterns that involve movements in the water column are almost absent, and they stay

more time inside the nest. These findings are in accordance with the hypothesis of Almada & Santos (1995) that turbulence is a prevailing pressure that affects many aspects of intertidal fish behaviour.

For a fish living in turbulent conditions, the risk of being dislodged by water movements and even wounded is likely to be high. Nursall (1977) stated that '*Ophioblennius atlanticus*, in its turbulent habitat, faces physical difficulties. Individuals bearing minor abrasions on the body are not uncommon. It is common for redlip blennies to bear puncture wounds from the spines of *Diadema antillarum*'. Some behavioural features of the intertidal species studied in this paper, suggest that they are minimizing the time spent out of the nest and the loss of contact with the substrate. Nevertheless, it is interesting to note that Phillips (1977) noted that *Istioblennius zebra*, a fish that lives in high intertidal pools that remain quiet for long periods, performs several behaviour patterns that involve loss of contact with the substrate. A similar situation occurs in *Parablennius sanguinolentus* at Azores (Santos 1985, 1992). These water column displays play a significant role in courtship and other social interactions in other blennioids living in low turbulence areas (e.g. Fishelson 1975).

Almada et al. (1992) showed that, for *L. pholis*, the mean time available for feeding was very short (5 h 34 min per day). This corresponds to the period when territories are underwater during daylight hours. The same applies to *C. galerita* and *S. pavo*, since their nests are located in similar heights on the shore. Subtidal species are likely to be able to feed during all daylight time (about 14 h in the peak of the breeding season). However, this does not necessarily mean that the males of intertidal species have to cope with higher energetic costs associated with territorial defense and parental care. Indeed, they may reduce their metabolism when out of water (e.g. Laming et al. 1982), and the small territory size, lower level of intrusions and reduced locomotor activities, may also contribute to save energy.

If the predation pressures are smaller in the intertidal, the benefits of breeding in this zone may further offset the costs imposed by the reduced time available for feeding. Our data show that, unlike intertidal species, subtidal fishes suffer territorial in-

trusions by several potential egg predators. Moreover, the fact that several fish species visit the intertidal to spawn, leaving their egg masses unguarded (e.g. *Enophrys bison*, DeMartini 1978, *Menidia menidia*, Middaugh et al. 1981, *Crenilabrus melops*, Potts 1985), is also in agreement with this hypothesis. It was also observed that when a parental male is removed from his nest, subtidal species suffered almost immediate egg predation (unpublished data), while in intertidal species, egg masses can survive several days unharmed (Almada et al. 1992). We suggest that this hypothesis can be further investigated using other fish lineages, besides blennioids, that contain species subjected to different degrees of turbulence. Gobiids, cottids and gobiocids could provide good opportunities for this type of studies.

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References cited

- Almada, V.C., E.N. Barata, E.J. Gonçalves & R.F. Oliveira. 1990a. On the breeding season of *Lipophrys pholis* (Pisces: Blenniidae) at Arrábida, Portugal. *J. mar. biol. Ass. U.K.* 70: 913–916.
- Almada, V.C., H. Carreiro, C. Faria & E.J. Gonçalves. 1996. The breeding season of *Coryphoblennius galerita* in Portuguese waters. *J. Fish Biol.* 48: 295–297.
- Almada, V.C., J. Dores, A. Pinheiro, M. Pinheiro & R.S. Santos. 1983. Contribuição para o estudo do comportamento de *Coryphoblennius galerita* (L.) (Pisces: Blenniidae). *Memórias do Museu do Mar – série Zoológica* 2: 1–166.
- Almada, V.C., G. Garcia & R.S. Santos. 1987. Padrões de actividade e estrutura dos territórios dos machos parentais de *Parablennius pilicornis* Cuvier (Pisces: Blenniidae) da costa portuguesa. *Análise Psicológica* 2: 261–280.
- Almada, V.C., E.J. Gonçalves, R.F. Oliveira & E.N. Barata. 1992. Some features of the territories in the breeding males of the intertidal blenny *Lipophrys pholis* (Pisces: Blenniidae). *J. mar. biol. Ass. U.K.* 72: 187–197.
- Almada, V.C., E.J. Gonçalves, R.F. Oliveira & A.J. Santos. 1995. Courting females: ecological constraints affect sex-roles in a natural population of the blennioid fish *Salaria pavo*. *Anim. Behav.* 49: 1125–1127.
- Almada, V.C., E.J. Gonçalves, A.J. Santos & M.C. Baptista. 1994. Breeding ecology and nest aggregations in a population of *Salaria pavo* (Pisces: Blenniidae) in an area where nest sites are very scarce. *J. Fish Biol.* 45: 819–830.
- Almada, V.C., R.F. Oliveira, E.N. Barata, E.J. Gonçalves & A.P. Rito. 1990b. Field observations on the behaviour of the breeding males of *Lipophrys pholis* (Pisces: Blenniidae). *Portugaliae Zoologica* 1: 27–36.
- Almada, V.C. & R.S. Santos. 1995. Parental care in the rocky littoral: adaptation and exaptation in Atlantic and Mediterranean blennies. *Rev. Fish Biol. Fish.* 5: 23–37.
- Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour* 49: 227–267.
- DeMartini, E.E. 1978. Spatial aspects of reproduction in buffalo sculpin, *Enophrys bison*. *Env. Biol. Fish.* 3: 331–336.
- Estabrook, C.B. & G.F. Estabrook. 1989. ACTUS: a solution to the problem of small samples in the analysis of two-way contingency tables. *Historical Methods* 22: 5–8.
- Faria, C., V.C. Almada & E.J. Gonçalves. 1996. Juvenile recruitment, growth and maturation of *Lipophrys pholis* (Pisces: Blenniidae), from the west coast of Portugal. *J. Fish Biol.* 49: 727–730.
- Fishelson, L. 1963. Observations on littoral fishes of Israel. I. Behaviour of *Blennius pavo* Risso (Teleostei, Blenniidae). *Israel Journal of Zoology* 12: 67–80.
- Fishelson, L. 1975. Observations on the behaviour of the fish *Meiacanthus nigrolineatus* Smith-Vaniz (Blenniidae) in nature (Red Sea) and in captivity. *Aust. J. Mar. Freshwat. Res.* 26: 329–341.
- Gibson, R.N. 1988. Patterns of movement in intertidal fishes. pp. 55–63. *In: G. Chelazzi & M. Vannini (ed.) Behavioural Adaptations to Intertidal Life*, Kluwer Academic Publishers, Dordrecht.
- Gonçalves, E.J., V.C. Almada, R.F. Oliveira & A.J. Santos. 1996. Female mimicry as a mating tactic in males of the blennioid fish *Salaria pavo*. *J. mar. biol. Ass. U.K.* 76: 529–538.
- Hastings, P.A. 1986. Habitat selection, sex ratio and sexual selection in *Coralliozetes angelica* (Blennioidei: Chaenopsidae). pp. 785–793. *In: T. Uyeno, R. Arai, T. Taniuchi. & K. Matsuura (ed.) Indo-Pacific Fish Biology: Proceedings of the Second International Conference on Indo-Pacific Fishes*, Ichthyological Society of Japan, Tokyo.
- Horn, M.H. & R.N. Gibson. 1988. Intertidal fishes. *Scient. Amer.* 258: 54–60.

- Koppel, V.H. 1988. Habitat selection and space partitioning among two Mediterranean blenniid species. *P.S.Z.N.I., Marine Ecology* 9: 329–346.
- Laming, P.R., C.W. Funston, D. Roberts & M.J. Armstrong. 1982. Behavioural, physiological and morphological adaptations of the shanny (*Blennius pholis*) to the intertidal habitat. *J. mar. biol. Ass. U.K.* 62: 329–338.
- Lindquist, D.G. 1985. Depth zonation, microhabitat, and morphology of three species of *Acanthemblemaria* (Pisces: Blennioidea) in the Gulf of California, Mexico. *P.S.Z.N.I.: Marine Ecology* 6: 329–344.
- Middaugh, D.P., G.I. Scott & J.M. Dean. 1981. Reproductive behavior of the Atlantic silverside, *Menidia menidia* (Pisces, Atherinidae). *Env. Biol. Fish.* 6: 269–276.
- Nursall, J.R. 1977. Territoriality in redlip blennies (*Ophioblennius atlanticus* – Pisces: Blenniidae). *J. Zool.* 182: 205–223.
- Nursall, J.R. 1981. The activity budget and use of territory by a tropical blenniid fish. *Zool. J. Linn. Soc.* 72: 69–92.
- Patzner, R.A., M. Seiwald, M. Adlgasser & G. Kaurin. 1986. The reproduction of *Blennius pavo*. V. Reproductive behaviour in natural environment. *Zool. Anz.* 216: 338–350.
- Philips, R.R. 1977. Behavioural field study of the Hawaiian rock-skipper, *Istiblennius zebra* (Teleostei, Blenniidae). I. Ethogram. *Z. Tierpsychol.* 43: 1–22.
- Potts, G.W. 1985. The nest structure of the corkwing wrasse, *Crenilabrus melops* (Labridae: Teleostei). *J. mar. biol. Ass. U.K.* 65: 531–546.
- Santos, R.S. 1985. Estrutura e função dos territórios em machos de *Blennius sanguinolentus* Pallas (Pisces: Blenniidae). *Memórias do Museu do Mar – Série Zoológica* 3: 1–45.
- Santos, R.S. 1992. Behavioural ecology, phenology and ethology of an intertidal blenny, *Parablennius sanguinolentus parvicornis* (Valenciennes in Cuvier & Valenciennes 1836) (Pisces: Blenniidae), from the Azores. Ph.D. Thesis, University of Liverpool, Liverpool. 293 pp.
- Santos, R.S., V.C. Almada & A.J. Santos. 1989. Field experiments and observations on homing and territoriality in intertidal fishes. pp. 622–632. *In: R.J. Blanchard, P.J. Brain, D.C. Blanchard & S. Parmigiani* (ed.) *Ethoexperimental Analysis of Behavior*, Kluwer Academic Publishers, Dordrecht.
- Stephens, J.S., R.K. Johnson, G.S. Key & J.E. McCosker. 1970. The comparative ecology of three sympatric species of California blennies of the genus *Hypsoblennius* Gill (Teleostomi, Blenniidae). *Ecol. Monogr.* 40: 213–233.
- Wirtz, P. 1978. The behaviour of the Mediterranean *Tripterygion* species (Pisces, Blennioidei). *Z. Tierpsychol.* 48: 142–174.