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Distribution of juvenile blennies (Pisces, Blenniidae) in small tide-pools: result of low-tide lottery or strategic habitat selection?

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Abstract. The distribution of juvenile blennies in small tide-pools in southern Portugal was investigated. Young *Coryphoblennius galerita* (15—30 mm total length) were frequent: approximately 4 individuals per 1000 cm² of surface were counted in inhabited tide-pools, which were on an average larger, deeper and containing more algae cover than uninhabited tide-pools (minimum water volume: 0,23 litres). Larger tide-pools contain more and larger specimens, but are relatively less densely populated.

Countings in identical tide-pools on successive days suggest considerable inter tide-pool movement of juvenile *C. galerita*, but tide-pool fidelity was also observed. It is suggested that both strategies are of adaptive value in the intertidal habitat. *C. galerita*, *Lipophrys pholis* and *Lipophrys pavo* were the only fish found in small tide-pools (maximum water volume: 47 litres).

Key words. Pisces, juvenile Blenniidae, *Coryphoblennius galerita*, *Lipophrys pholis*, tide-pools, habitat preference, Algarve, Portugal.

Introduction

Most of the approximately 300 species of the family Blenniidae live in the rocky littoral zone of the world's oceans. 13 species are known to occur on the Atlantic coast of Portugal (Albuquerque 1956, Almeida et al. 1980, Almeida & Gomes 1978, Zander 1987).

Two of these species (*Coryphoblennius galerita* and *Lipophrys pholis*) inhabit the upper littoral tidal zone on the Portugese coast (Arruda 1979, 1990) and can easily be found in tide-pools. Both species have interested marine biologists for some time. Literature on their biology is relatively abundant (among others: Fives 1980, Gibson 1972, Qasim 1957). The striking tidal activity rhythm of *C. galerita*, probably an adaptation to its "pseudo-amphibious" behaviour (Soljan 1932, Heymer 1982, Zander 1983, Louisy 1987), was described by Gibson (1970). The occurrence of *C. galerita* in tide-pools was qualitatively investigated by Almada et al. (1983) for Portuguese sites. The vertical distribution of *C. galerita* was measured quantitatively by Gibson (1972) for a site in Brittany (France), but the latter author found too few *C. galerita* for further analysis.

Some questions concerning the presence of *C. galerita* in tide-pools remain open: Do *C. galerita* select the tide-pools where they stay during low tide according to certain criteria (e. g. size of tide-pool)? What role do tide-pool fidelity and inter tide-pool movement play?

Material and methods

At the beach of Canavial (Praia do Canavial) east of Lagos (southern Atlantic coast of Portugal), 62 small tide-pools with a total surface of 38 417 cm^2 and a total volume of 115,23 litres were inspected during low tide in summer (July/August). Tide-pools of different size formed an irregular pattern on the surface of large, partly eroded limestone boulders that cover the eastern part of the beach just beneath the steep cliffs that form the coastline. Distances between tide-pools on each boulder varied from a few centimetres to some metres, but boulders were up to 50 metres apart. All the tide-pools examined were covered with water for approximately six hours during high tide and lay exposed for another six hours during low tide.

Inhabited tide-pools and tide-pools with no fish were irregularly distributed on the surfaces of the boulders. They were similarly exposed to the tide and, as most tide-pools were situated on the flat surfaces of the boulders, the sun.

The tide-pools were measured to the nearest cm (length and width) and 0,5 cm respectively (maximum depth). A photograph was taken of each tide-pool in order to allow subsequent measurements and assessment of algae cover. Tide-pool surfaces were simply calculated by multiplying length and width, volumes by multiplying surface and half of maximum depth (assuming this to be the approximate average depth).

Juvenile blennies in the tide-pools were caught, counted for each tide-pool, measured to the nearest 5 mm and released. Dense algae or *Mytilus* cover was searched in order to find hidden blennies. 24 of the above mentioned tide pools, situated on a single large boulder at the western end of the beach, were inspected on six successive days and all fish found in them were counted.

Juvenile *C. galerita* of tide-pools No. 44 and No. 62 were fixed in 4 % formalin and deposited at the Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn (Germany) for further investigation. Species names in this paper are used according to Zander (1987).

Results

Occurrence of juvenile blennies in tide-pools

Of the 62 tide-pools inspected, 23 contained blennies. 110 individuals were *C. galerita* (ranging from 15 to 30 mm total length), 2 were *L. pholis* (15 mm, 50 mm total length) and one specimen was relatively large *Lipophrys pavo* (60 mm). Other fish species could not be found.

Table 1 lists 23 tide-pools inhabited by blennies according to number of blennies and volume of tide-pools. size of inhabited tide-pools varies considerably (0,23 l to 46,5 l). 13 of 23 occupied pools contained thick algae mats, where juvenile blennies could hide. Average volume of water per individual, considering all tide-pools, is 4,4 l.

The number of blennies increases with size of tide-pools. Surfaces of tide-pools show a significant positive correlation with the number of blennies they contain (Spearman rank correlation coefficient: r_s = 0,62; n = 23, P <0,05). Tide-pool volume and number of blennies have an even higher positive correlation (Spearman rank correlation coefficient: r_s = 0,72; n = 23; p <0,001). Fig. 1 shows the relation between tide-pool surface and number of juvenile *C. galerita* found in occupied tide-pools. The comparison with expected blenny numbers on the basis of average density of blennies in occupied tide-pools (4,11 individuals/1000 cm^2 surface) illustrates that smaller pools tend to be more densely populated than larger ones (surface area >1000 cm^2). The total surface of tide-pools without blennies amounted to

Table 1: Tide-pools inhabited by Blenniid fishes.

N	le cm	w cm	d cm	surface cm^2	volume	algae	gal 15 mm TL	gal 20 mm TL	gal 25 mm TL	gal 30 mm TL	gal total number	pho total number
7	16	10	6	160	0,48	80	1				1	0
57	21	15	4	315	0,63	40		1			1	0
30	18	14	5,5	252	0,69	0	1				1	0
33	25	15	4,5	375	0,84	0	1				1	0
46	22	19	4,5	418	0,94	60	1				1	0
3	33	25	5	825	2,01	0		1			1	1
54	50	20	5	1000	2,50	50	1				1	0
39	31	25	7,5	775	2,91	30	1				1	0
58	25	15	4,5	375	0,84	90	1	1			2	0
4	25	22	8	484	1,94	0	1		1		2	1
5	17	11	2,5	187	0,23	0	1	1	1		3	0
50	22	17	4	374	0,75	60	2	1			3	0
8	30	15	4,5	450	1,01	0	2	1			3	0
19	26	26	4,5	676	1,52	20	3				3	0
26	27	18	4	486	0,97	0	4				4	0
55	42	42	6	1764	5,29	90	3	1			4	0
44	25	25	4	625	1,25	80	5				5	0
6	40	35	3,5	1400	2,45	80	4	1			5	0
10	60	23	5,5	1380	3,80	0	4	2			6	0
45	40	40	9	1600	7,20	10	4	2			6	0
41	32	25	7	800	2,80	0	4		2	1	7	0
62	92	35	9	3220	14,49	100	6	6	1	4	17	0
38	133	70	10	9310	46,55	0	17	12	2	1	32	0
total				27251	102,09		67	30	7	6	110	2

N = number of tide-pool; le = length of tide-pool, w = width of tide-pool, d = depth of tide-pool; surface = approximate surface of tide-pool, volume = approximate volume of tide-pool (surface x ½ depth) in litres; algae = algae cover in %; gal = *C. galerita*; pho = *Lipophrys pholis*; pavo = *Lipophrys pavo*, TL = total length

11 166 cm^2. Given the average density of 4,11 blennies per 1000 cm^2 surface in the occupied tide-pools, all these "empty" pools combined should be expected to contain 46 blennies.

In comparison to pools with juvenile blennies, uninhabited pools are significantly more shallow ($P < 0{,}005$; $n = 62$, Welch test) and contain less water volume ($P < 0{,}05$; $n = 62$, Welch test). Large algae that could offer hiding places are rare (only 5 of 39 uninhabited tide-pools, see "algae cover" in Tab. 1, 2).

On the other hand, presence of algae cover in otherwise suited tide-pools fairly well predicts presence of juvenile blennies in a tide-pool (Cole's interspecific association coefficient: $C = 0{,}278$, see Lorenz 1992).

Inter tide-pool movement of blennies

When 24 tide-pools on a very large boulder at the western end of the beach were inspected on six successive days, only 6 of them contained blennies. The remaining 18 small tide-pools on that boulder were never occupied.

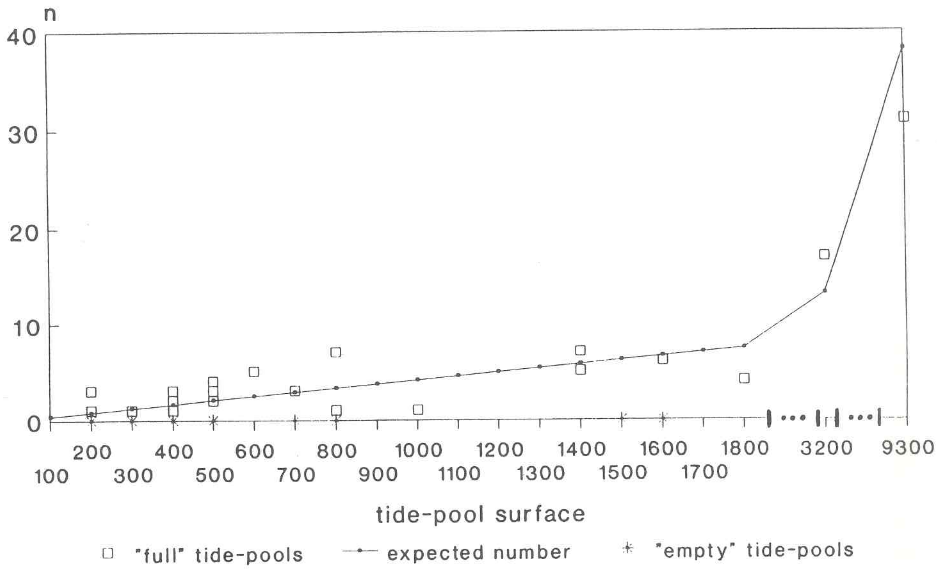

Fig. 1: Tide-pool surface (cm^2) and numbers of *C. galerita* in tide-pools. Note that the rise in tide-pool surface is not proportional after 1800 cm^2. Expected number calculated as product of average number of blennies and surface area.

4 tide-pools were inhabited continuously, 2 with interruptions. Total number of blennies varied from 8 to 15 individuals. Occupation of a given tide-pool varied considerably. Between tides, individuals must have changed tide-pools. Those tide-pools which were never occupied showed typical characteristics of empty tide-pools as mentioned above.

Observations with snorkelling gear during high tide showed adult individuals (exceeding 60 mm total length) of *C. galerita* and *L. pholis* on the surface of the boulders which were searched during low tide. None of these fish were found during low tide in the tide-pools.

Discussion

Theoretically, intertidal fishes could simply find themselves caught in some water aggregation between the rocks. This kind of coincidental tide-pool settlement is improbable because small, shallow and bare tide-pools are in general not occupied by blennies and the uninhabited tide-pools do not contain the number of blennies that should be expected if surface area were responsible for the "gathering" of blennies. Furthermore tide-pools do not contain all the size-classes of blenniid fish active at high tide in the same area.

It must be concluded that tide -pools are indeed actively selected and tide-pool occupation by juvenile blennies is not a coincidental phenomenon. It seems likely that juvenile *Coryphoblennius galerita* decide against occupying small and shallow

Table 2: Tide-pools without blennies..

N	l cm	w cm	d cm	surface cm²	volume l	algae cover %
1	20	11	4	220	0,44	0
2	44	34	3	1 496	2,24	0
9	15	15	4,5	225	0,51	0
11	8	5	1	40	0,02	0
12	12	12	1,5	144	0,11	0
13	10	6	1	60	0,03	0
14	13	6	1	78	0,04	0
15	20	9	1	180	0,09	0
16	10	9	1	90	0,05	0
17	12	10	1	120	0,06	0
18	8	6	2	48	0,05	0
20	84	18	1,5	1 572	1,18	0
21	26	19	2	494	0,49	0
22	17	10	0,5	170	0,04	0
23	16	8	2,5	128	0,16	0
24	12	5	1	60	0,03	0
25	14	8	2	112	0,11	0
27	8	8	1	64	0,03	0
28	7	6	1,5	42	0,03	0
29	28	13	2	364	0,36	0
31	12	8	1,5	96	0,07	0
32	15	11	3	165	0,25	0
34	13	10	1	130	0,07	0
35	11	11	1	121	0,06	0
36	17	14	2	238	0,24	0
37	21	15	2	315	0,32	0
40	43	18	4	774	1,55	0
42	23	12	3	276	0,41	0
43	10	8	0,5	80	0,02	0
47	19	13	2	247	0,25	30
48	22	23	2	506	0,51	0
49	17	15	3,5	255	0,45	0
51	12	12	4	144	0,29	0
52	20	15	2	300	0,30	80
53	25	28	2	700	0,70	0
56	23	16	4	368	0,74	50
59	16	15	1	240	0,24	20
60	20	6	2	120	0,12	0
61	24	16	2,5	384	0,48	50
total				11 166	13,14	

N = number of tide-pool; le = length of tide-pool, w = width of tide-pool, d = depth of tide-pool; surface = approximate surface of tide-pool, volume = approximate volume of tide-pool (surface x ½ depth) in litres; algae = algae cover in %.

tide-pools with little cover offered by algae. The larger a tide pool is, the more (and larger, see table 1) blennies it is likely to contain. Bennett & Griffiths (1984) found a similar relationship between pool size and number of fish for South African rock-pools. In laboratory studies, Richkus (1981) found preference of a tide-pool fish for deeper potholes. The results of countings of blennies on successive days indicate that juvenile blennies frequently change the tide-pools they inhabit between low tides. Certain individuals stay for a number of days in the same tide-pool, but fluctuation on a local scale (between neighbouring tide-pools) and on a larger scale (between distant tide-pools on different boulders) must be considerable. The occurrence of relatively fewer but bigger individuals of *C. galerita* in larger tide-pools is possibly the result of intraspecific confrontations. In New Zealand intertidal fish Mayr & Berger (1992) observed how size predominantly affected contest outcome.

Obviously, a large tide-pool offers in general a safer refuge: temperature is more constant, and large pools are more difficult to exploit for predators such as sea-gulls. Consequently, active preference for large tide-pools should be of adaptive value to tide-pool fish. This means that tide-pool fish should move between rock-pools. During high tide this is obviously easy enough, and even during low tide *C. galerita* could be observed trying to crawl across the rock surface to another tide-pool. Migration between small tide-pools seems to be characteristic of juvenile *C. galerita* and *L. pholis* (Almada et al. 1983). Other tide-pool fish show a similar "exploration" behaviour together with a certain fidelity to particular pools (Beckley 1985, Marsh et al. 1978). As Richkus (1978) already suggested, such a dynamic explorational behaviour is possibly an adaptation to the rapidly changing, high-risk environment that tide-pools offer their inhabitants.

On the other hand, a certain "pool fidelity" may have evolved as a guarantee for finding safe cover (between algae, rock crevices etc.) during low tide (Bennett & Griffiths 1984). Inter tide-pool movement and pool fidelity should have found an evolutionary balance.

It would be rewarding to continue research on the question of tide-pool occupation by juvenile blennies on a wider spatial and temporal scale. The present investigation coincided with a phase of recruitment of juvenile *C. galerita*, as the commonness of very small individuals suggested. What is the situation like in other seasons? Ethological observations could confirm the hypotheses that intraspecific aggression between individuals (as observed in clinid fish by Marsh et al. 1978) is responsible for relatively less denser settlement of larger tide-pools which are occupied by larger individuals.

Obviously, a lot remains to be investigated in the small world of tide-pools.

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Zusammenfassung

Das Vorkommen juveniler Schleimfische (Pisces, Blenniidae: *Coryphoblennius galerita*, *Lipophrys pholis*, *Lipophrys pavo*) in Fluttümpeln an der Südküste Portugals bei Lagos wurde untersucht. Nicht von Blenniiden besetzte Fluttümpel waren im allgemeinen kleiner, flacher und ärmer an Versteckmöglichkeiten bietendem Algenbewuchs. In Wasseransammlungen von weniger als 0,23 l Volumen konnten keine Fische gefunden werden. Volumen und — in geringem Maße — Oberfläche der Fluttümpel waren signifikant positiv mit der Anzahl

juveniler Blenniiden korreliert. Die Verteilung juveniler *C. galerita* in Fluttümpeln zeigt, daß die Tiere mit einsetzender Ebbe aktiv Wasseransammlungen einer bestimmten Mindestgröße aufsuchen. Bei Überprüfungen von Fluttümpeln an aufeinanderfolgenden Tagen zeigte sich, daß juvenile Blenniidae bei Flut einerseits die Fluttümpel wechseln, andererseits eine gewisse Standorttreue zeigen. In ihrem wechselhaften Lebensraum dürfte ein bestimmtes Verhältnis zwischen beiden Verhaltensweisen die optimale Überlebensstrategie darstellen.

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