Journal of Fish Biology (1998) 53, 1263–1273
Article No. jb980795

Patterns of agonistic behaviour, shelter occupation and habitat preference in juvenile *Lipophrys pholis*, *Coryphoblennius galerita* and *Gobius cobitis*

C. FARIA*, V. ALMADA AND M. DO CARMO NUNES
Unidade de Investigação em Eco-Etologia, Instituto Superior de Psicologia Aplicada, R. Jardim do Tabaco 44, P-1100 Lisboa, Portugal

(*Received 31 January 1998, Accepted 1 August 1998*)

The patterns of agonistic behaviour and substratum preferences were investigated in captive groups of juveniles of *Lipophrys pholis* (Blenniidae), *Coryphoblennius galerita* (Blenniidae) and *Gobius cobitis* (Gobiidae). In monospecific groups, size was an excellent predictor of the rank attained by each individual. In heterospecific groups, both *C. galerita* and *L. pholis* were dominant over *G. cobitis* of similar size, and *C. galerita* dominated *L. pholis*. Although *G. cobitis* showed higher rates of activity and of attacks per minute, and a higher ratio of attacks over threats, all these measures were depressed in the presence of either blenniid. In both blennies, in monospecific groups, the dominance rank of each fish was a good predictor of the time spent inside shelters. *G. cobitis* occupied preferentially the sandy substratum both in mono- and heterospecific groups. Both blennies, when in monospecific groups, occupied preferentially the rocky substratum, with *C. galerita* showing the highest level of selectivity. In nature, *C. galerita* also showed a marked preference for rocky substrata, while *G. cobitis* was especially abundant in mixed bottoms. *L. pholis* occupied an intermediate position. In the blenniids studied, competition for access to shelter may be one major functional consequence of agonistic behaviour in non-reproductive contexts.

Key words: Blenniidae; Gobiidae; intertidal fishes; substratum selection; agonistic behaviour; shelter use.

INTRODUCTION

There have been several attempts to use laboratory experiments, in which animals of different species are induced to behave agonistically to each other, in order to examine the role of interspecific aggression in determining the relative abundance of species in a community (Bergamo *et al.*, 1988; Pickett & Maxson, 1988; Rahel, 1989; Itzkowitz, 1990; Sano, 1990; Walls, 1990; Mesa, 1991; Clarke, 1992; Hazlett *et al.*, 1992; Hori *et al.*, 1993; Nakano & Tanaka, 1994). These studies have yielded mixed results. Although in some cases the outcomes of interspecific agonistic encounters are in agreement with that expected from the relative abundance and niche partitioning between two species, in other cases the results of these tests are poor predictors of the relative competitive abilities of the species in nature. One of the potential problems with this type of study is that standard test situations, in which pairs of animals are induced to interact, have little in common with the environments to which the organisms are adapted.

In rocky intertidal fishes, agonistic behaviour has been documented in many species (Guitel, 1893; Soljan, 1932; Qasim, 1956; Gibson, 1968, 1969, 1971;

---

*Author to whom correspondence should be addressed. Tel.: +351 1 8863184; fax: +351 1 8860954.

0022–1112/98/121263+11 $30.00/0

Koppel, 1988; Santos *et al.*, 1989; Almada *et al.*, 1992). The best documented cases relate agonistic behaviour with inter-male competition and parental care, but in several species it has been demonstrated that agonistic behaviour is present in both sexes and even in juvenile fishes (Gibson, 1969, 1982).

In these non-reproductive contexts the presence of agonistic behaviour does not imply that the fishes are territorial, and Gibson (1968) suggested the concept of diffuse territoriality as a more appropriate way to describe social interactions in groups of juveniles of *Lipophrys pholis*. Instead of defending well-defined areas, each fish may visit and defend several hiding places and the more dominant fishes tend to have priority of access to these places, forcing the subordinates to leave them. It is likely that the priority of access to shelter sites may be one important function of non-reproductive agonistic behaviour in intertidal fishes.

One of the few studies on interspecific aggression in intertidal fishes, reports the results of tests using pairs of fishes of two species from New Zealand (Mayr & Berger, 1992). Although the authors found that one of the species in the laboratory tends to dominate the other, they suggest that differences in microhabitat preferences may reduce the likelihood of interspecific aggression in the wild.

Lipophrys pholis (L.), *Coryphoblennius galerita* (L.) and *Gobius cobitis* (Pallas), are major components of the rocky intertidal fish fauna on western European shores, and are frequently found together in the same tide-pools (Gibson, 1972; Milton, 1983). *Gobius paganellus* (L.) and *Lipophrys trigloides* (Valenciennes) are also present in these communities, but at least in our study area, they are present only in very low numbers in pools (Arruda, 1990).

The agonistic behaviour of *L. pholis* and *C. galerita* has been described by Gibson (1968), and Almada *et al.* (1983, 1992) respectively. That of *G. cobitis* has been studied by the authors and will be described elsewhere (Faria *et al.*, 1998).

Despite the phylogenetic differences between gobiids and blenniids, the three species share similar patterns of aggression, namely threatening, advancing, charging, chasing, biting, retreating and fleeing (Gibson, 1968; Almada *et al.*, 1983, 1992 for definitions).

In this paper we present data on agonistic interactions observed in captive groups of *L. pholis*, *C. galerita* and *G. cobitis*. The observations were aimed to test the following hypotheses.

1. In heterospecific groups, there are interspecific differences in the ability of the fishes to achieve dominance.
2. The rank attained by each individual, in a monospecific group, affects positively its access to shelter.
3. The three species differ in their patterns of use of different substratum types, which may affect their likelihood of interacting with members of other species.

MATERIALS AND METHODS

OBSERVATIONS IN CAPTIVITY

From October 1993 to September 1994, 18 groups of *L. pholis*, *C. galerita* and *G. cobitis* were observed in tanks of 118 × 28 × 27 cm. The tanks were subjected to natural illumination and temperature (range 10–25° C), and were equipped with biological filters. Fishes were fed with pieces of common cockle. The bottom of each tank was divided into six similar-sized patches of three different types of substratum (sand, rock and gravel). In each patch there were some stones covered with algae that could be used as shelters. The relative position of the patches of the different substrata was assigned randomly each time a new group was started. These patches were divided further into two halves, one in the front and one in the rear of the tank, by an imaginary grid to facilitate the study of activity patterns. Thus, 6 × 2 cells were formed, four of which were occupied by each substratum type.

A total of 428 h of focal observations (Martin & Bateson, 1990) was made in nine monospecific groups (three for each species) and nine heterospecific groups (combinations of the three species, two at a time). The observations were based on groups of six juveniles (3–7 cm L_T), to avoid the possible effect of reproductive behaviour. Each group stayed in captivity for periods of 17 days, but no observations were made in the first 7 days (habituation period). On subsequent days, daily observations were made (2–4 h per day = 24 h per group). The habituation period of a week was chosen since in previous studies (Almada *et al.*, 1983; Faria *et al.*, 1993), it was found that after 7 days the fishes moved actively, interacted frequently with each other, and responded immediately to the presence of food. We assume that these findings were indicators of habituation to the conditions of captivity.

The fishes were recognized individually by their relative size and the peculiarities of their colour patterns. For practical reasons the time unit used was 30 s, since it was found that units of shorter duration made observation and recording very difficult. For each fish, its location at the beginning of each 30-s period was noted. For this purpose, it was considered that the fish could be either in one of the 12 cells of open substratum, or in one of the six shelters available in the tank. If the fish changed location during the same 30-s unit, only the first position was considered for location purposes, although the total number of location changes occurring during each observation period was used as a measure of activity.

The sequences of agonistic behaviour in which the focal fish participated were recorded. A fish was classified as the loser of an encounter if at the end of the interaction it withdrew or fled from the opponent, or was threatened or attacked without retaliation. When both fishes withdrew without an apparent asymmetry, the outcome was classified as inconclusive. To make data from different groups comparable, the size (total length) of each fish was expressed as relative size in relation to the other members of the group. To calculate the dominance rank of each fish in its group we followed the procedure described in Appleby (1983).

OBSERVATIONS IN THE FIELD

In order to study the distribution of the fishes by different substrata in the field, non-destructive samples were taken monthly from 27 tide-pools (nine pools with sandy bottom, 14 with rocky bottom and four with mixed gravel and rocky bottom), at Parede and São Pedro do Estoril (38°41′ N, 9°22′ W), near the mouth of the Tagus river (Lisbon), from January to December 1994. During each inspection, all the fishes that could be collected with a 20-cm hand-net were taken from the tide-pool. For each fish, species and total length (L_T) were recorded. After inspection, all fishes were returned to their original pool.

To calculate the area of each pool, a grid divided in square cells of 10 × 10 cm, was placed over the pool and the number of cells that fell over the surface of the pool was counted. The areas of the pools of a given substratum type were added and the number of fishes of each species present on that substratum were also summed, to compute the densities of fishes per square meter of each type of substratum.

Data analysis was performed using the computer program Statistica for Windows (version 4.5) (Copyright 1983, Statsoft Inc.). χ^2 goodness-of-fit tests were performed using Adersim (Almada & Oliveira, 1997).

TABLE I. Correlation between length of each fish and its rank in the hierarchies observed in monospecific groups ($n=6$)

Group:	1		2		3	
	r_s	P	r_s	P	r_s	P
G. cobitis	0·94	<0·01	1·00	<0·001	1·00	<0·001
L. pholis	0·94	<0·01	1·00	<0·001	1·00	<0·001
C. galerita	0·94	<0·01	0·94	<0·01	1·00	<0·001

RESULTS

AGONISTIC BEHAVIOUR PATTERNS

In the two blenniids, the most frequent threat behaviour involves raising the head and the anterior part of the body, and erecting the median fins, a display that in *C. galerita* is emphasized frequently by small lateral turnings of the head to one or both sides. In *G. cobitis* the threat display also involves erection of al median fins and is emphasized further by elements that increase the apparent siz of the head. The branchiostegal membrane is extended fully while the opercul are opened. The anterior part of the fish may be raised by the sucker, or the hea may be pointing ahead and slightly downwards. In all three species, a defeate individual may press the head and body against the substratum with folded fins In addition, the two blenniids may perform a submissive posture in which th defeated fish rolls over onto a flank, and slowly withdraws from the opponen (Gibson, 1968).

DOMINANCE, SIZE AND SPECIES IDENTITY

Since size is known to be a strong predictor of dominance in some of thes species (Gibson, 1968; Almada *et al.*, 1983), the assessment of possibl interspecific differences in the ability to achieve dominance must take into acoun the effect of size.

In all monospecific groups, relative size was an excellent predictor of th dominance rank attained by each individual (Table I). In all heterospecifi groups with *G. cobitis* however, the dominance rank was related mainly to th species (Table II), and fishes of a given species defeated heterospecific opponent of slightly larger size. This pattern was consistent among groups, with *C. galerit* clearly dominating *G. cobitis*, and also *L. pholis*, that in turn, dominated *cobitis*. This is evident also if Tables I and II are compared, since all th correlation coefficients between rank and size, of heterospecific groups includin *G. cobitis*, were substantially smaller than those from monospecific groups. Thu hypothesis one is confirmed.

In monospecific groups *G. cobitis* showed higher rates of agonistic interaction displacement, and attacks over threats, than did both blenniids (Table III Indeed, although a significant fraction of the variance was explained b intergroup differences, significant differences between species were detected als (Table IV). When the several possible pairs of species were compared, significan differences were found between *G. cobitis* and any of the blennies (Tukey HS test: agonistic interactions and displacement: *G. cobitis*/*C. galerita* $P<0{\cdot}00$

TABLE II. Correlation between species and length of each fish and its rank in the hierarchies observed in heterospecific groups ($n=6$)

Group:	Variable	1		2		3	
		r_s	P	r_s	P	r_s	P
G. cobitis/*C. galerita*	Species	0·77	NS	0·83	<0·05	0·78	NS
	Length	0·57	NS	0·60	NS	0·49	NS
L. pholis/*C. galerita*	Species	0·25	NS	0·02	NS	0·41	NS
	Length	0·77	NS	0·83	<0·05	0·83	<0·05
L. Pholis/*G. cobitis*	Species	0·83	<0·05	0·83	<0·05	0·77	NS
	Length	0·60	NS	0·53	NS	0·51	NS

TABLE III. Rates of agonistic interactions, displacement and attacks over threats per species, observed in monospecific groups ($n=18$)

	G. cobitis		*L. pholis*		*C. galerita*	
	Mean	S.D.	Mean	S.D.	Mean	S.D.
Agonistic interactions	75·61	20·89	10·78	5·31	17·22	10·73
Displacement	0·78	0·31	0·47	0·33	0·39	0·31
Attacks/threats	5·02	6·06	1·53	1·67	1·91	2·64

TABLE IV. Results of nested ANOVA, testing the effect of group and species on rates of agonistic interactions, displacement and attacks over threats, observed in monospecific groups (acos data transformation)

	Source	d.f.	F	P
Agonistic interactions	Group	45	13·67	<0·001
	Species	45	115·82	<0·001
Displacement	Group	45	3·30	<0·01
	Species	45	18·32	<0·001
Attacks/threats	Group	45	1·54	NS
	Species	45	4·97	<0·05

G. cobitis/*L. pholis* $P<0{\cdot}001$; attacks over threats: *G. cobitis*/*C. galerita* $P<0{\cdot}05$; *G. cobitis*/*L. pholis* $P<0{\cdot}05$). In heterospecific groups however, *G. cobitis* was involved in a significantly lower rate of agonistic interactions than in monospecific groups (Table V). This difference between mono- and heterospecific groups is still significant, even if the value of the probability is raised to compensate for the repeated use of some of the data (Martin & Bateson, 1990). Thus, the species that was more aggressive and active when in monospecific groups was at a disadvantage when in heterospecific groups.

TABLE V. Results of nested ANOVA, testing the effect of type of group on rate of agonistic interactions of *G. cobitis* (acos data transformation)

Source	d.f.	*F*	*P*
Group	26	8·39	<0·001
Mono/heterospecific	26	77·72	<0·001

TABLE VI. Correlation between time spent in shelters of each fish and its rank in hierarchies observed in monospecific groups ($n=6$)

Group:	1		2		3	
	r_s	*P*	r_s	*P*	r_s	*P*
G. cobitis	0·66	NS	0·94	<0·01	0·31	NS
L. pholis	0·89	<0·05	0·99	<0·001	0·94	<0·0
C. galerita	0·83	<0·05	0·83	<0·05	0·84	<0·0

DOMINANCE AND CONTROL OVER SHELTERS

In both blennies, the dominant fishes spent more time than the subordin in shelters (Table VI). In *G. cobitis*, the correlations between dominance r and time spent in shelters were not significant, but approached signific (Table VI). This finding suggests that for juvenile blennies agonistic behav can be related functionally to the control over shelters, while for *G. cobitis* relation does not hold or is much less important. Thus, hypothesis tw confirmed also, a least for both blennies.

SUBSTRATUM PREFERENCES

The three species differed also in their substratum preferences. monospecific groups, *C. galerita* and *L. pholis* used predominantly r substrata, while *G. cobitis* stayed more frequently in open sand (Fig. 1) control for the possibility of effects caused by specificities of the groups analysis of variance was performed, in which the percentage of time spen rock (100 times the number of time units in which each fish was found on rock, over all the units recorded), by the fishes of each species was anal using species identity and group identity as independent variables (Table Only the interspecific differences were significant, while the variability du intergroup differences was clearly unimportant. Posterior pairwise compar revealed a significant difference between *G. cobitis* and *C. galerita*, while *L. p* occupied an intermediate position (Tukey HSD test: *G. cobitis*/*C. ga* $P<0·01$).

To compare the number of fishes of each species observed in all the (Table VIII) of each type, with the number that would be expected if the were indifferent to the nature of the substratum, expected numbers computed, assuming that the number of fishes of each species, occurring

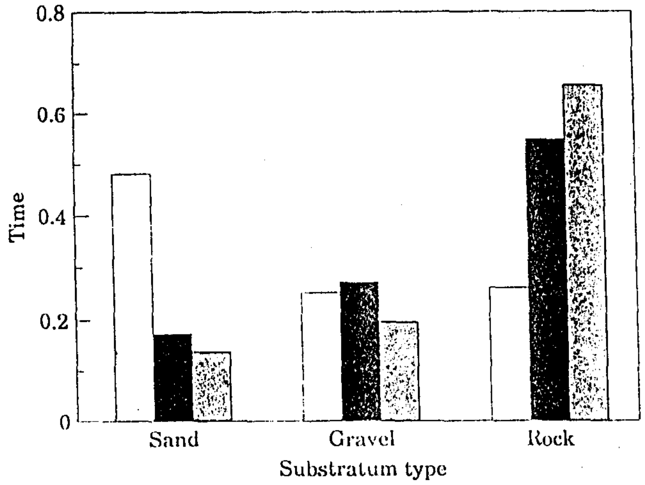

FIG. 1. Distribution of each species in the different substratum types studied in monospecific groups (relative number of intervals of 30 s): ☐, *G. cobitis*; ■, *L. pholis*; ☐, *C. galerita*.

TABLE VII. Results of nested ANOVA, testing the effect of group and species on percentage of time on rock substratum (log data transformation)

Source	d.f.	*F*	*P*
Group	6	0·88	NS
Species	2	5·17	<0·01

TABLE VIII. Number of fishes of each species per m^2, observed in the 27 tide-pools followed from January to December 1994

	Sand	Rock	Mixed substrata
G. cobitis	17	9	13
L. pholis	27	32	116
C. galerita	6	58	6

given substratum type, was a simple function of the proportion of the total area of pools occupied by that substratum. Thus the expected values were calculated as the total number of fishes of each species, collected in all pools, multiplied by the area of the pools of a given substratum type, divided by the total area of all the pools. A χ^2 goodness-of-fit test was then performed using Adersim (*L. pholis*: $\chi^2=469{\cdot}29$, d.f.$=2$, $P<0{\cdot}001$; *C. galerita*: $\chi^2=145{\cdot}05$, d.f.$=2$, $P<0{\cdot}001$; *G. cobitis*: $\chi^2=15{\cdot}36$, d.f.$=2$, $P<0{\cdot}001$). *C. galerita* was significantly more abundant than

TABLE IX. Results of the χ^2 goodness-of-fit test (Adersim) applied to the number of fishes of each species observed in pools with different substrata: (a) cases in which the simulated values did not exceed the observed values; (b) cases in which the observed values did not exceed the simulated values

	Sand	Rock	Mixed substrata
G. cobitis			
(a)	7*	604	1000
(b)	997	551	2*
L. pholis			
(a)	0*	114	1000
(b)	1000	920	0*
C. galerita			
(a)	0*	1000	196
(b)	1000	0*	893

*$P<0{\cdot}05$, one tailed.

expected on rocky substrata, while *L. pholis* and *G. cobitis* were more con
than expected on mixed substrata. All three species were significantl
common than expected on sandy bottoms (Table IX).

The habitat preferences of *L. pholis* and *C. galerita* were related more c
to each other than to *G. cobitis*. Indeed, while the numbers of the two bl
species per pool were correlated positively [Spearman rank correlation (*n*
$r_s=0{\cdot}88$, $P<0{\cdot}001$], that was not true for the co-occurrence of *G. cobiti*
either blenny [Spearman rank correlation ($n=27$): *G. cobitis*/*L. pholis*: r_s=
NS; *G. cobitis*/ *C. galerita*: $r_s=0{\cdot}02$, NS]. Thus, the available evidence su
hypothesis three.

DISCUSSION

The first hypothesis considered in this study was supported, with th
blennies clearly dominating *G. cobitis*. This result raises the question: why
blenniids, especially *C. galerita*, tend to win encounters with gobiids of s
size? For the same length, the goby has a more massive and compact body
obs.). *G. cobitis*, when studied in monospecific groups, also showed a high
of attacks over threats and a higher rate of attacks per minute, th
blenniids. Thus, the factors that give superiority to *C. galerita* require
experimental investigation.

When *C. galerita* were introduced in groups of *Parablennius pilicornis* (C
an extremely aggressive blenny, *C. galerita* were able to avoid attac
survived, apparently by their quick manoeuvres, that allowed them to av
attacks of the larger *P. pilicornis* (pers. obs.). In contrast, other less
blenniids, such as *L. pholis* or *L. trigloides*, would have been killed
pilicornis in a few minutes, if they had not been removed quickly from th

(pers. obs.). It would be interesting to consider the possible effect of the greater agility of the blenniids, minimizing the impacts of attacks by *G. cobitis*, and the possible role of other features of the fighting technique of *C. galerita* and *L. pholis* that may contribute to their superiority over *G. cobitis*.

The present results also provide evidence supporting our second hypothesis, at least regarding the two blennies. Indeed, for *L. pholis* and *C. galerita* one major functional consequence of agonistic behaviour relates to competition for access to shelter sites. This conclusion was supported by the correlation between the dominance rank and the time spent in shelters in monospecific groups. Both blenniid species are benthic and cryptically coloured, and are confined for several hours a day in tide pools. It is likely that ready access to shelter plays a crucial role in predator avoidance. Almada *et al.* (1983) reported that *C. galerita* when disturbed in tide pools, rushed quickly to shelters (small holes and crevices) and that on some occasions, a fish that entered an already occupied shelter was driven away by the occupant, being forced to search for another shelter, increasing the time that it was exposed. The same authors noted that each occupant of a pool seems to be informed about which holes and crevices are available, restricting its displacements to a network of relatively well-defined paths.

Gibson (1968) studied groups of captive juveniles of *L. pholis*, and also concluded that one consequence of dominance is the definition of some sort of order of priority of access to shelter, with the subordinate fishes retreating quickly from a shelter site when dominant individuals approach.

Such a relationship between dominance rank and access to shelter was not conclusively demonstrated in the case of *G. cobitis* in the present study, and the possible functions of agonistic behaviour in juveniles of this fish need further investigation. It is interesting to note that *G. cobitis* lives in pools and channels, where the substratum is less structured, providing little shelter in the form of crevices and holes. Indeed they tend to occupy large pools with frequently eroded rock surfaces and with sand and boulders on the bottom (Gibson, 1972; Arruda, 1990). In such a habitat it is unlikely that defence of access to individual shelters is an economically feasible strategy. Other possible functions of agonistic behaviour, such as competition for food, specially during high tide, when the fishes are more active, and move out of pools (Gibson, 1971; Almada *et al.*, 1983), should be considered in future.

Concerning hypothesis three, the evidence obtained both in the field and in captivity, indicates that the fishes show clear preferences for different substratum types. Since these differences in substratum preferences are observed in monospecific groups, it is not clear from the present results to what extent the differences in fighting capability among species play a role in their ecological segregation.

It is also interesting to note that *C. galerita*, which tended to be dominant over *L. pholis* in the experiments, is consistently less abundant in nature (Milton, 1983; Gibson, 1972). *L. pholis* attains a larger size and has a longer lifespan, thus being more fecund (Qasim, 1956) than *C. galerita*.

L. pholis was shown in this study also to be less selective than *C. galerita* in its choice of microhabitat, both in nature and in captivity. It is likely that the relative superiority of *C. galerita* in aggressive encounters with *L. pholis* is viewed best, in ecological terms, as a means by which a species with smaller size an lifespan is able to coexist with a more fecund and abundant species, by utilizin a restricted type of microhabitat from which it is able, at least partially, t exclude the competitor.

Part of this study was supported by Junta Nacional de Investigação Científica Tecnológica (JNICT) as part of the project PBIC/1313/MAR/92 and Pluriannua Program (UI&D 331/94). CF was also supported by a grant from JNICT (PRAXI XXI/BD/5666/95). We thank R. Gibson for his helpful editorial comments; tw anonymous referees, whose criticisms and suggestions helped to improve the quality o the manuscript; and C. Silva who helped in the field work.

References

Almada, V. C., Dores, J., Pinheiro, A., Pinheiro, M. & Santos, R. S. (1983) Contribuição para o estudo do comportamento de *Coryphoblennius galerita* (L. (Pisces, Blenniidae). *Memórias do Museu do Mar, Série Zoológica* **2,** 1–165.

Almada, V. C., Gonçalves, E. J., Oliveira, R. F. & Barata, E. N. (1992). Some feature of the territories in the breeding males of the intertidal blenny *Lipophrys pholi* (Pisces, Blenniidae). *Journal of the Marine Biological Association of the Unite Kingdom* **72**, 187–197.

Almada, V. C. & Oliveira, R. F. (1997). Sobre o uso de estatistica de simulação e estudos de comportamento. *Análise Psicológica* **15,** 97–109.

Appleby, M. C. (1983). The probability of linearity in hierarchies. *Animal Behaviour* **31** 600–608.

Arruda, L. M. (1990). Population structures of fish in the intermareal ranges of th Portuguese coast. *Vie Milieu* **40,** 319–323.

Bergamo, P., Fiorito, G. & Miralto, A. (1988). An analysis of the agonistic behaviour o *Carcinus mediterraneus* (Czerniavsky) (Crustacea; Decapoda): fighting an ritualization. *Monitore Zoologico Italiano* **22,** 315–322.

Clarke, R. D. (1992). Effects of microhabitat and metabolic rate on food intake, growt and fecundity of two competing coral reef fishes. *Coral Reefs* **11,** 199–205.

Faria, C. , Almada, V. C., Gonçalves, E. J., Gil, M. F., Baptista, C. & Carreiro, H (1998). Notes on the social behaviour of *Gobius cobitis* (Pisces Gobiidae). *Act Ethologica* **1**, 49–56.

Gibson, R.N. (1968). The agonistic behaviour of juvenile *Blennius pholis* L. (Teleostei) *Behaviour* **30,** 192–217.

Gibson, R.N. (1969). The biology and behaviour of littoral fishes. *Oceanography an Marine Biology Annual Review* **7,** 367–410.

Gibson, R. N. (1971). Factors affecting the tidal rhythm of activity of *Blennius pholis* L (Teleostei). *Animal Behaviour* **19,** 336–343.

Gibson, R. N. (1972). The vertical distribution and feeding relationship of intertidal fis on the Atlantic coast of France. *Journal of Animal Ecology* **48,** 189–207.

Gibson, R. N. (1982). Recent studies on the biology of intertidal fishes. *Oceanograph and Marine Biology. Annual Review* **20,** 363–414.

Guitel, F. (1893). Observations sur le moeurs de trois blénidés *Clinus argentatus, Blenniu montagui* et *Blennius sphynx*. *Archives de Zoologie Expérimentale et Générale (série)* **1,** 325–384.

Hazlett, B. A., Anderson, F. E., Esman, L. A., Stafford, C. & Munro, E. (1992) Interspecific behavioral ecology of the crayfish *Orconectes rusticus*. *Journal Freshwater Ecology* **7**, 69–76.

Hori, M., Gashagaza, M. M., Nshombo, M. & Kawanabe, H. (1993). Littoral fis communities in Lake Tanganyika: irreplaceable diversity supported by intricat interactions among species. *Conservation Biology* **7**, 657–666.

Itzkowitz, M. (1990). Heterospecific intruders, territorial defence and reproductiv success in the beaugregory damselfish. *Journal of Experimental Marine Biolog and Ecology* **140**, 49–59.

Koppel, V. H. (1988). Habitat selection and space partitioning among two Mediterranean blenniid species. *Marine Ecology* 9, 329–346.

Martin, P. & Bateson, P. (1990). *Measuring Behaviour, An Introductory Guide.* Cambridge: Cambridge University Press.

Mayr, M. & Berger, A. (1992). Territoriality and microhabitat selection in two intertidal New Zealand fish. *Journal of Fish Biology* 40, 243–256.

Mesa, M. G. (1991). Variation in feeding, aggression and position choice between hatchery and wild cutthroat trout in an artificial stream. *Transactions of the American Fisheries Society* 120, 723–727.

Milton, P. (1983). Biology of littoral blenniid fishes on the coast of south-west England. *Journal of the Marine Biological Association of the United Kingdom* 51, 247–265.

Nakano, S. & Tanaka, T. F. (1994). Intra and interspecific dominance hierarchies and variation in foraging tactics of two species of stream-dwelling chars. *Ecological Research* 9, 9–20.

Pickett, P. E. & Maxson, S. J. (1988). Interspecific interactions of spotted sandpipers. *Wilson Bulletin* 100, 297–302.

Qasim, S. (1956). The spawning habits and embryonic development of the shanny (*Blennius pholis*). *Proceedings of the Zoological Society of London* 127, 144–155.

Rahel, F. J. (1989). Nest defense and aggressive interactions between a small benthic fish (the johnny darter *Etheostoma nigrum*) and crayfish. *Environmental Biology of Fishes* 24, 301–306.

Santos, R., Almada, V. & Santos, A. (1989). Field experiments and observations on homing and territoriality in intertidal blennies. In *Ethoexperimental Approaches to the Study of Behaviour* (Blanchard, R., Brain, P., Blanchard, D. & Parmigiani, S., eds), pp. 223–232. London: Academic Press.

Sano, M. (1990). Patterns of habitat and food utilization in two coral-reef sandperches (Mugiloididae): competitive or noncompetitive coexistence? *Journal of Experimental Marine Biology and Ecology* 140, 209–223.

Soljan, T. (1932). *Blennius galerita* L. poisson amphibien des zones supralittorale et littoral de l'Adriatique. *Acta Adriatica* 1, 1–15.

Walls, S. C. (1990). Interference competition in postmetamorphic salamanders: interspecific differences in aggression by coexisting species. *Ecology* 71, 307–314.