FIELD OBSERVATIONS ON THE BEHAVIOUR OF THE BREEDING MALES OF *LIPOPHRYS PHOLIS* (PISCES: BLENNIIDAE)

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RESUMO: Apresenta-se neste trabalho um etograma dos machos parentais de *Lipophrys pholis* baseado em observações subaquáticas durante duas épocas de reprodução sucessivas. Os comportamentos locomotores e alimentares são descritos. Os padrões de comportamento agonístico observados confirmam as descrições anteriormente publicadas para os juvenis. Como novas descrições assinalam-se : "virar a cabeça na direcção do oponente", "abrir e fechar a boca" e "oscilações verticais da cabeça". Este último elemento só foi encontrado em machos reprodutores parecendo ter um papel importante na corte. Os comportamentos parentais incluem: "rotação sobre o eixo do corpo", "roçar o ventre sobre os ovos", "ventilação caudal" e "remoção de bolhas de ar do interior do ninho". Na baixa-mar os machos parentais permanecem emersos nos ninhos junto dos ovos. Quando perturbados apresentam um conjunto de reacções defensivas e produzem um som característico. Os resultados são discutidos numa perspectiva ecológica e evolutiva.

ABSTRACT: This paper presents an ethogram of the breeding males of *Lipophrys pholis* based on underwater observations during two consecutive breeding seasons. Locomotory and feeding behaviour patterns are described. Agonistic behaviour patterns confirm previous work on captive juvenile fishes. New patterns include: "head turning", "opening and closing the mouth" and "nodding". "Nodding" was only performed by nesting males and seems to be an important element of courtship. Parental behaviour includes: "rotation along the body axis", "skimming", "tail fanning" and "removal of air bubbles from the nest". During low tide the nesting males stay out of water inside the nests. When disturbed they show a number of defensive responses and produce a characteristic sound. The results are discussed in an ecological and evolutionary context.

INTRODUCTION

This paper presents an ethogram of the breeding males of *Lipophrys pholis* (Linnaeus, 1758) in natural waters.

Few data are available on the ethology of this blenniid. Qasim (1956) described spawning and parental behaviour in captivity. Gibson (1967a, 1968) presented a detailed ethogram of the agonistic behaviour of juvenile captive fishes and showed experimentally that this species shows an endogenous tidal rhythm of activity, displaying peaks and lows at high and low tide respectively. Gibson (1971) also showed that this activity rhythm may be kept synchronized with tide if the fish is subjected to cyclical fluctuations in the water pressure. Based on successive recaptures of marked fishes, Gibson (1967b) showed that *L. pholis* has an home range that includes several pools, although individuals seem to visit some pools more frequently then others. Finally, Wirtz (1974, 1975, 1976) and Wirtz & Davenport (1976) studied the physiological effects of social contact in this species.

As data on blenniids living in areas where strong tides prevail are still scarce, it seems of interest to get more information on the natural behaviour of *L. pholis*.

MATERIAL AND METHODS

Observations were conducted both by skin- and scuba-diving at Praia dos Pilotos (Arrábida coast, Portugal: 38° 28' N, 8° 59' W) during the breeding seasons of 1986 and 1987.

The total observation time was about 54 hours (13h 38m of focal observations on 12 nests and 40 hours of *ad libitum* observations). The duration of each observation session varied from 12 to 45 minutes. Observations were distributed in time from mid morning to sunset.

The males of this blenniid establish small breeding territories intertidally, around a hole or a crevice where spawning takes place from December to May. The male guards and cares for the developing eggs. In our study area, we identified 30 nests on the vertical walls of rocks, and it was around such nests that observations were centered.

Nests were also visited during low tide at various times of the year and were checked for the presence of eggs and/or fishes. During diving observations notes were taken with a pencil on plastic sheets.

This study was divided in two phases: (i) in the first one we tried to describe the behavioural repertoire of the breeding males. Thus, observations were randomly distributed on as many nests as possible. The short hand notes taken *in situ* by each of four observers were later confronted in order to provide more objective descriptions. For each description only the elements for which a good agreement between observers could be reached were retained; (ii) in the second phase only the behaviour patterns that had been formally described were recorded, using a predetermined code. Before each dive a sketch of the nest and its surroundings was drawn on a plastic sheet to allow easy coding of the position relative to the nest of the different behavioural acts. The aim of this phase was to get contextual information on the behaviour patterns previous described. Twelve nests, containing eggs, were selected for systematic observations.

RESULTS

1. Non-social behaviour

1.1. Locomotion and associated behaviour

a) Hopping - When moving for short distances the fish "hops". It takes off the substratum with a quick stroke of the pectoral fins and settles after moving for about a body length. It may perform one or few undulations of the body and tail while in motion.

b) Swimming - For longer distances, after taking off with a movement of the pectorals, the fish swims in an anguilliform way.

c) Hovering - A pattern as yet undescribed for *L. pholis*. In mid water, the fish keeps position for a few seconds at an oblique angle, with the head up. This position is maintained by the combined action of undulations of the body and tail with rotatory movements of the pectorals. Afterwards, the fish dives quickly to the substrate. This pattern was of short duration. This action was rarely observed and its meaning is unclear.

d) Raising in mid water - A pattern as yet undescribed for *L. pholis*. At an oblique angle and with the head up, as described above, the fish undulates the entire body ascending in the water column. The movement is intermittent.

Between two bouts the fish goes down slightly, while the angle of the body with the horizontal decreases. This pattern was rarely observed and always with the fish oriented to the observer.

e) Creeping - This behaviour occurs when the fish moves in the nest, both when it is underwater or exposed to air, or out of the nest when the water layer is too thin to allow "hopping" or swimming. In this type of locomotion the fish is in close contact with the substratum and moves backwards or forwards propelled by the pectoral fins and body undulations. The anal fin probably helps in exerting pressure against the irregularities of the substratum.

1.2. Postures outside the nest

We include in this section different kinds of postures that the fish adopts outside the nest.

a) The fish remains still on the substratum with its body closely adjusted to the contours of the substratum surface.

b) The fish remains still with the body forming an "U" or "S" curve that does not fit the topography of the substratum.

1.3. Postures inside the nest

The terminology used for these postures follows that of Phillips (1977) for *Istiblennius zebra*.

a) Head out - The fish remains still inside the nest with its head out.

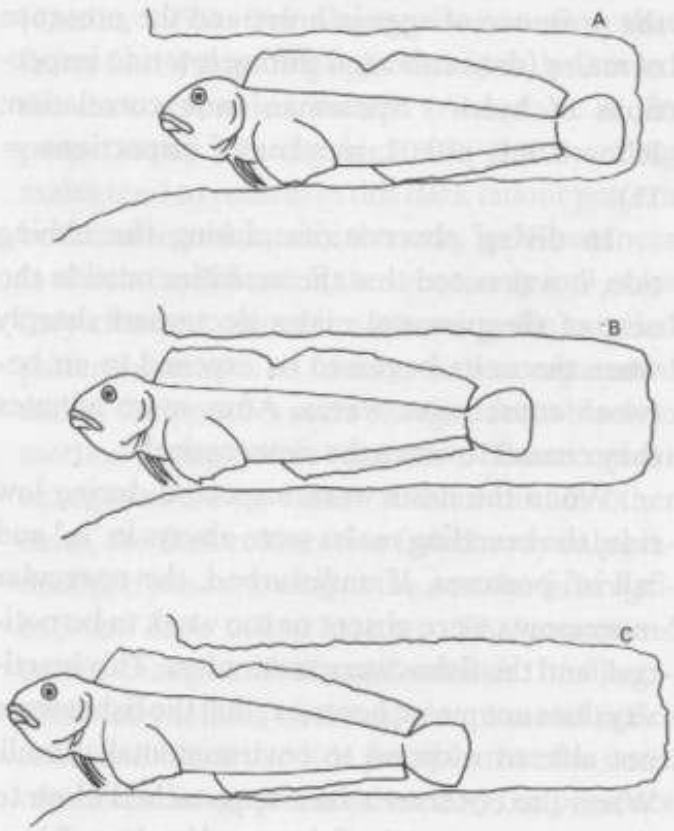
b) Part out - Similar to "head out" with more than half of the body out.

c) In - Only the head is visible just at the nest entrance. It differs from "Head out" in that the head does not protrude from the nest (see Fig. 1).

d) All in - The fish is inside the nest but not visible.

The postures "head out", "part out" and "in", may be adopted with the fish standing on the bottom of the nest or at varying angles, with the abdomen turned to the nest walls. These three postures may be combined with other behaviou-

Figure 1. Schematic illustration of the different postures adopted by the breeding males of *L. pholis* when inside the nest. (A) "In"; (B) "Head out"; (C) "Part out".



ral patterns. When the fish is "all in" (posture d) it cannot be observed.

1.4. Nest entry

There has been considerable discussion about the meaning of the way parental male blenniids enter their nests (Abel, 1964; Wirtz, 1978).

The frequency with which males entered tail first (TF) or head first (HF) was noted ($n = 70$, $HF = 66$, $TF = 4$). It is clear that the males enter predominantly head first (G-test: $n = 70$, $G = 63.64$, $d.f. = 1$, $p < 0.01$). This probably reflects the fact that the nests are not tubelike structures which fit tightly the size of the animal as described for other blenniids (Abel, 1964, 1980).

1.5. Behaviour of the breeding males during low tide

During low tide, the breeding males of *L. pholis* remain inside the nests with the eggs. There is a highly significant correlation between the presence of eggs in holes and the presence of males (data collected during low tide inspections of holes - Spearman rank correlation: $R.S. = 0.961$, $p < 0.01$, number of inspections = 11).

In diving observations during the ebbing tide, it was noted that the activities outside the nest of the parental males decreased sharply when the nests begun to be exposed to air between consecutive waves. After some minutes they ceased to leave the nests entirely.

When the nests were inspected during low tide, the breeding males were always in "in" and "all in" postures. If undisturbed, the opercular movements were absent or too weak to be noticed, and the fishes were motionless. This inactivity does not mean, however, that the fishes were not able to respond to environmental stimuli. When the observer's face approached close to the nest entrance, the fish moved backwards, remaining deeper inside the nest.

In seven instances we prodded the fishes with a piece of wire. In this situation, the fishes reacted quite wildly. The body curved with violent and sudden lateral flexions, remaining curved to one side for several seconds, then flexing suddenly to the opposite side. During these movements, the head was raised and the mouth opened, and the body seemed to be in great muscular tension. Together with these pronounced movements, the fishes bit the wire, produced a clacking sound and showed a high frequency of opercular movements. The direction of the described movements seemed to be independent of the wire position. Although these behaviour patterns were induced by the action of the observer, they may represent a more general pattern of response to intrusions during low tide, for example by crabs.

1.6. Feeding

The feeding acts that were observed typically involved the following sequence: i) the fish settles motionless on the substratum; ii) it performs a quick forward dash, simultaneously lowering the head; iii) it grips a food item that is attached to the substratum; iv) the food item is pulled by raising the head together with a quick vigorous backward movement of the body. The whole sequence lasts a second or less. The feeding acts occur in bouts of a few acts. Between bouts, the fish usually moves to another place.

When food items are too big to be taken whole, the fish may try to detach a fragment by vigorous lateral shaking movements of the head, while the mouth firmly grips the food item.

1.7. Chafing

The fish swims to a hard surface, tilts the body while moving and presses the head, flank or tail against the substratum, after which it resumes normal swimming. In other teleosts it is supposed to be a response to the presence of ec-

toparasites. In *L. pholis* "chafing" is however very frequently performed during agonistic interactions, suggesting that it has signal value in this context. Gibson (1968) already commented on the similarity of form between "chafing" and "submission" in *L. pholis* and on the possibility that "submission" evolved from "chafing" as a "derived activity".

1.8 Defecation

One fish was observed to defecate outside the nest. After taking off the substratum the fish turned 180° along the body axis and while in a "belly-up" position it quivered and a compact mass of faeces was expelled.

2. Social behaviour

2.1. Agonistic behaviour

As the agonistic behaviour repertoire of this species was previously described by Gibson (1968), we will only mention some additional behavioural patterns that emerged from our observations.

2.1.1. Behavioural patterns: new descriptions

a) Head turning - Turning the head towards an intruder was frequently followed by retreat of the intruding fish. So it seems that this behavioural element is a part of the agonistic repertoire of this species. It was always observed with the breeding males in "part out" posture (see Fig. 2a).

b) Nodding - "Nodding" was performed when the fish was in the nest, and consisted of repeated vertical head movements in bouts of 4 to 7. It was often preceded or followed by opening and closing the mouth. This action was performed as the intruding fish was at distances from 20 to 60 centimeters. "Nodding" was usually followed by the retreat of the intruder. In many of the instances that we observed it seemed to be directed to females. On some occasions however, it was performed by a breeding male towards a neighbouring male whose nest was 13 centimeters away (see Fig. 2b).

c) Opening and closing the mouth - This pattern consists of the fish opening and closing the mouth in rapid succession. It may occur as single acts or bouts. In two cases we recorded bouts of 10 and 15 acts in 30 and 60 seconds respectively. In 33% (n=83) of the cases recorded an intruder was present. This behaviour was often associated with other acts such as "nodding", head turning and colour changes. Its association with other agonistic behavioural patterns, its repetition in bouts and the frequent presence of an intruder, suggests that it may be functional as a low intensity display in agonistic interactions.

d) Colour change - The colour patterns of *L. pholis* may vary with background, light intensity and social context (Gibson, 1968), and with the reproductive state (Qasim, 1956). The breeding males are very dark, uniformly coloured, and this makes their whitish lips very conspicuous (Qasim, 1956). Our observations confirm that fishes found guarding eggs consistently showed the dark coloration pattern (Almada *et al.*, in preparation). During high tide the breeding males tend to remain in this dark colour pattern both inside and outside the nest. In 76 instances in which the fishes left the nests, only in 9 cases they changed coloration assuming the mottled pattern common to females and non-parental males. Only once a male changed from black to mottled being inside the nest. These colour changes could be rather sudden but, in other cases, the dark colouration faded away only gradually. Upon returning to the nest the fish regained the dark colour pattern. The process of colour change took about 2 seconds. In all agonistic interactions observed the parental males remained black , so it is possible that the cases of colour change were induced by the presence of the observer.

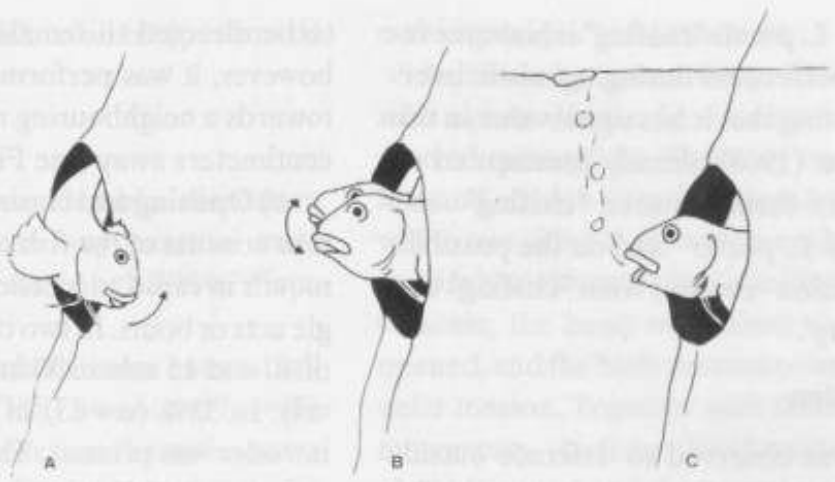


Figure 2. Some behaviour patterns of the breeding males of *L. pholis*. (A) "Head turning"; (B) "Nodding"; (C) "Releasing of air bubbles from the nest".

2.1.2. Organization of agonistic interactions

The summary that follows must be considered with caution because it was based on a low number of agonistic interactions (n = 13):

i) The majority of interactions involve only a small number of behavioural elements (up to 3 different acts).

ii) Overt attack was infrequent occurring only 3 times in 13 interactions.

iii) The majority of interactions (9 in 13) begun with the parental male in "head out" posture.

iv) An important proportion of interactions were decided with approach, or approach and charge only (4 in 10).

v) Two interactions were resolved without the parental male leaving the nest.

vi) We never observed a parental male being attacked by an intruder or any prolonged fight.

vii) The parental male generally returns to the nest soon after the intruder left (8 in 10).

viii) Concerning the identity of the intruder, the majority of interactions involved conspecifics (n = 13; *Coryphoblennius galerita* = 1; *L. pholis* = 12).

Intrusions by neighbour parental males of *Coryphoblennius galerita* released a significantly lower proportion of agonistic responses in males of *L. pholis*, and were frequently ignored (Almada *et al.*, in preparation).

Crabs (i.e. *Pachygrapsus marmoratus* and *Eriphia verrucosa*) were also attacked by vigorous biting and were driven away by this action. It is unclear however, to what extent these attacks are best classified as agonistic rather then predation attempts by the fish.

2.2. Sexual behaviour

In about 54 hours of observation during the breeding season we never observed a complete courtship sequence. This may have been caused either by low frequency of spawning and courtship or by courtship being restricted to very specific periods, for example at dawn or at a particular moon phase, that we may have missed.

On one occasion a black male was in "part out" posture, when a female entered the nest and remained there while the male maintained the "part out" posture. No obvious specialized courtship display were noted. Lack of oxygen forced us to interrupt this observation.

In another instance we observed what ap-

pears to be an unsuccessful courtship attempt. A male was in "head out" when a female, recognizable by its swollen abdomen, approached the nest. When the female was about 20 centimeters away from the nest, the male begun to "nod" in a bout of 5 "nods". The female came closer to the nest (about 10 cm) when the male backed to an "in" posture.

The female, then moved to the nest opening, stopping with the body lying across the entrance and pectorals fully open. After a few seconds the female moved away and stopped at about 30 centimeters from the nest, staying parallel with a neighbour territorial male that had moved into the area. This male performed quick lateral flexions of the body upon which the female moved back to the nest of the first male. The resident male "nodded" 4 times, and the female moved away about 60 centimeters from the nest where it stood still.

Our observations suggest that "nodding" may be involved in the process of courtship as in many other blenniids (see discussion).

2.3. Parental behaviour

a) Rotation along the body axis - The fish may rotate along the body axis remaining still again at an angle of up to 90° or 180° with the standing position. In this case it stays attached to the walls or to the ceiling of the nest.

b) Skimming - Inside the nest in one of the postures mentioned above the fish may move with pronounced lateral flexions of the body, rubbing its ventral part against the inner nest surface, where the eggs are attached. This behaviour is supposed to be related to the care of eggs. Mechanical cleaning of eggs is one of its possible functions (Qasim, 1956).

c) Tail fanning - Like many other blenniids (see Almada *et al.*, 1983 for references), the breeding males perform tail fanning, a behaviour in which the fish stays in "part out" posture while the tail moves regularly from side to side. This behaviour may cause an increase of water circulation in the nest, facilitating oxygenation of the eggs and removal of silt and debris.

d) Removal of air from the nest - This behaviour is probably similar to the removal of debris and small objects (including dead eggs) with the mouth that many blenniids often perform (Wirtz, 1978). In our observations we found that males of *L. pholis* can remove air from inside the nest using this same behaviour. Air removal was observed in two nests. The males disappeared inside the nest, and after emerging released an air bubble. One of the fishes released the bubbles in "head out" posture (see Fig. 2c), while the other male was observed to leave the nest releasing the bubbles at distances that ranged from 20 to 60 centimeters. The first male removed bubbles in bouts of 4 to 6 acts, releasing a single bubble in each movement. The other male performed repeated excursions to release the bubbles (also one at a time). In a period of 4 minutes this male came out 9 times to release bubbles.

This behaviour is particularly interesting. Since the nests of *L. pholis* stay out of water at low tide and the topography of the inner nest surface is irregular, it is probable that air pockets may represent a significant problem for the development of the eggs. These are spawned predominantly on the ceiling and walls of the nest, and if air pockets are retained inside it during high tide, they may prevent many eggs from direct contact with sea water. We also found this behaviour in *Salaria pavo* (Almada *et al.*, in preparation), another intertidal blenniid.

DISCUSSION

Despite considerable disagreement among authors on the limits of the genera and their affinities (see Louisy, 1983), there is a consensus that the species placed in the genus *Lipophrys* are closely related to *Parablennius* and *Salaria* (Louisy, 1983). Generally species of *Parablen-*

nius tend to occur subtidally, while those of *Lipophrys* are predominantly intertidal (Zander, 1972). The species of *Parablennius* that have been studied ethologically, tend to show behavioural elements such as "signal jumping" of *P. rouxi* (Heymer & De Ferret, 1976), *P. pilicornis* (Denoix, 1984; Almada *et al.*, 1987), and *P. incognitus* (Abel, 1964; Louisy, 1983); "loop swimming" of *P. sanguinolentus* (Santos, 1985); "nod-swimming" of *P. zvonimiri* (Wirtz, 1978) and *P. pilicornis* (Denoix, 1984) and "hovering" of *P. pilicornis* (Denoix, 1984; Almada *et al.*, 1987), that involve loss of contact with the substratum and some degree of movement in the water column during the displays. These "water column displays" are probably primitive blennioid patterns that are important in signalling the territories of males to females, and probably to potential rivals. Indeed, this type of behavioural patterns occur in tripterygiids (Shiogaki & Dotsu, 1973; Wirtz, 1978), chaenopsids (Stephens *et al.*, 1966), and in blenniids only weakly related to Parablenniini, like *Meiacanthus* (Nemophini) (Fishelson, 1975) and *Istiblennius* (Salariini) (Phillips, 1977). In contrast, in the genus *Lipophrys* these displays are uncommon or absent. On the other hand, head movements, like "nodding" and "lateral head shaking" observed in *L. canevae* (Abel, 1964), *L. dalmatinus* (Abel, 1980), *L. adriaticus* (Wirtz, 1978) and *L. velifer* (Wirtz, 1978, 1980), often associated with conspicuous head masks (Abel, 1964; Zander, 1975; Papaconstantinou, 1979), tend to play the major role as social signals. Our results in *L. pholis* fall within the general *Lipophrys* behaviour repertoire. We suggest that, reduction of movements in the water column and its compensation by an increase in colour markings, may be associated with the evolution of an intertidal mode of life in this genus. In the intertidal zone, water movement and turbulence may be quite intense, and may have acted strongly in evolution against displays that involve active swimming and loss of contact with the substratum.

Another intertidal blenny common on exposed rocky shores in Europe (*C. galerita*), also lacks "water column displays". In this species the male courts females by "nodding" and threatens conspecifics by wide amplitude head movements (Guitel, 1893; Almada *et al.*, 1983). These kind of displays also have the advantage of allowing the signalling fish to stay in the security of the nest, with only the head and part of the body protruding. In several *Lipophrys* species the fishes are quite small and nest in narrow tubular holes as for example *L. canevae* (Abel, 1964), *L. dalmatinus* (Abel, 1980) and *L. velifer* (Wirtz, 1980). The emphasis on head movements and colour patterns may thus be important in two distinct situations: i) blenniids that live in turbulent waters; ii) blenniids that are very small and nest in narrow tubes that tightly fit their bodies. These are the two conditions where we find species of the genus *Lipophrys*.

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