THE ETHOGRAM OF *PARABLENNIUS SANGUINOLENTUS PARVICORNIS* (VALENCIENNES IN CUVIER & VALENCIENNES, 1836) (PISCES: BLENNIIDAE) FROM THE AZORES

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ARQUIPÉLAGO

SANTOS, RICARDO SERRÃO & JOÃO PEDRO BARREIROS. The ethogram of *Parablennius sanguinolentus parvicornis* (Valenciennes in Cuvier & Valenciennes, 1836) (Pisces: Blenniidae) from the Azores. *Arquipélago*. Life and Marine Sciences 11A: 73-90. Angra do Heroísmo. ISSN 0870-6581.

This paper describes the ethogram of *Parablennius sanguinolentus parvicornis*. The ethogram includes the description of around forty patterns of behaviour illustrated by drawings mostly prepared from video recordings and photographs. The most distinctive features of the ethogram, by contrast with other common intertidal species, are: i) the capacity of the individuals to swim distances over 1 metre at one go, ii) the formation of a clearing in front of or around the nest entrance by the parental male, iii) the incidence of patterns of behaviour that elevate the body in relation to the bottom (highly conspicuous in signal swimming, but also present in all sets of activities in which swimming is used as a mode of locomotion).

SANTOS, RICARDO SERRÃO & JOÃO PEDRO BARREIROS. Etograma de *Parablennius sanguinolentus parvicornis* (Valenciennes in Cuvier & Valenciennes, 1836) (Pisces: Blenniidae) dos Açores. *Arquipélago*. Ciências Biológicas e Marinhas 11A: 73-90. Angra do Heroísmo. ISSN 0870-6581.

No presente artigo concentramo-nos no etograma qualitativo de *Parablennius sanguinolentus parvicornis*. O etograma inclui o descrição de cerca de quarenta padrões de comportamento ilustrados por desenhos baseados em registos *video* e fotografias. Os aspectos mais distinctivos do etograma, em contraste com outras espécies intertidais, são: i) a capacidade dos indivíduos para nadarem distâncias superiores a 1 metro sem contacto com o fundo, ii) a formação, pelo macho parental, de uma clareira em frente e à volta da entrada do ninho, iii) a incidência de padrões de comportamento com elevação do corpo em relação ao fundo (altamente conspícuo na natação sinal, mas também presente em muitas das actividades em que a natação é utilizada como modo de locomoção).

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INTRODUCTION

Blennies have long been the subject of behavioural observations and studies. This is mainly due to their easy adaptability to laboratory conditions, accessibility in the natural environment (intertidal species may be observed without the need of diving equipment), but also because of their rich behavioural repertoire.

Early detailed behavioural observations can be dated back to the end of the last century. GUITEL (1893) produced the first ethogram of two blennies (*Coryphoblennius galerita* and *Aidablennius sphynx*) and a clinid (*Clinitrachus argentatus*), together with some experimental observations on the homing abilities of *C. galerita* and *A. sphynx*. Two other papers, examining orientation and recognition of the nest, appeared during the first half of this century, the first concerning *Blennius ocellaris* (PIÉRON 1914), and the second *Salaria basiliscus* (ROULE 1926). Ethology and behavioural ecology offered the framework for further studies on blennies after 1950 (e.g., ABEL 1955, 1964; QASIM 1956; WICKLER 1957, 1965; ROBINS et al. 1959; FISHELSON 1963; GIBSON 1968; PHILLIPS 1971, 1977; HEYMER & FERRET 1976; NURSALL 1977; 1981; WIRTZ 1978; BERNIER 1982; ALMADA et al. 1983, 1987; LOUISY 1983; MARRARO & NURSALL 1983; JONGE 1985; SANTOS 1985a,b, 1987, 1992; PATZNER et al. 1986;

THOMPSON 1986; HEYMER 1987; HASTINGS 1988a,b; SANTOS & ALMADA 1988; ALMADA 1989; CÔTÉ & HUNTE 1989a,b; JONGE & VIDELER 1989; JONGE et al. 1989; SANTOS et al. 1989; GONÇALVES 1990).

Parablennius sanguinolentus parvicornis is a medium-sized (maximum total length around 18cm) intertidal rock pool dwelling blenny, whose males establish territories during the reproductive season. These territories are based on natural cavities. Females come to these nests for spawning, leaving the eggs to the care of the male. Caring for the eggs is essential for their survival, and constitutes a highly demanding activity. Teleost eggs left on the substratum are at high risk from bacterial and fungal infection. Spawning inside a cavity makes protection against predators easy, but oxygen supply more problematic. Males use a variety of behavioural solutions to overcome these kinds of problems. In addition to successful mating, parental care is essential for reproductive success.

In the present paper we give an account of the ethology of *Parablennius sanguinolentus parvicornis*. A short preliminary ethogram was given by SANTOS (1985a). That work has been largely extended here. The ethogram is illustrated by drawings of most of the behavioural patterns.

MATERIAL AND METHODS

1. Locality

All observations were made in rock pools at Feteira, Island of Faial. Fishes were observed during low tide. At high tide no observations were possible due to considerable wave action in the area.

Flat basaltic platforms are not very common in the Azores. Intertidal pools at these platforms were formed inside "*furnas*" whose top has been eroded by wave action. Their maximum diameter may vary from some centimeters to 30 metres. Their depth may also vary from a few centimetres to, exceptionally, two or three metres. *P. s. parvicornis* uses shallow pools for reproduction, not deeper than 0.75m (SANTOS 1985a, 1992).

2. Behavioural observations

Observations were made during the months of June, July and August, initially in 1985 and the major part, subsequently, in 1987.

Observations were made from outside the pools, but were interrupted under windy and rainy conditions.

Forty hours of quantitative (SANTOS 1985b, 1986, 1992), plus approximately 100 hours of qualitative observations (to build the species ethogram) were made. Video Recording (JVC-GR/A30 in an underwater IKELITE cage) and photography (NIKONOS/IV-A and PENTAX/ Super A inside an underwater IKELITE cage, both with an IKELITE substrobe MV) were also used.

RESULTS

1. PATTERNS OF BEHAVIOUR

1.1. NON-SOCIAL BEHAVIOUR

1.1.1. Non-moving postures

1.1.1.1. Open places

i) The individual keeps stationary on the bottom with both pectoral fins open and pelvic fins either half extended or retracted. The caudal fin is generally closed and slightly raised and turned to one side. The head and the anterior part of the belly are not generally in contact with the bottom. The dorsal fin may be either completely spread out or completely closed. This position is commonly assumed when the animal sits on the bottom and is not frightened. (Fig. 1A).

ii) The individual remains in close contact with any kind of sheltering topographic structure. The body tends to follow the configuration of the rock (Fig. 1B). Most of the time the fins appear retracted. This posture is associated with alarm situations. The degree of adjustment of the body to the substratum, and of the position of fins is probably related to the internal state of arousal of the animal.

1.1.1.2. On cavities and shelters

i. ROLL UP INSIDE (Fig. 2)

The individual is completely inside the cavity and the body is tightly pressed against the walls in an U position .

ii. STARING (Fig. 1C and Fig. 3)

This is the most common posture of a fish when inside a hole or another kind of cavity. The body is inside the hole while the head, or part of it, is outside. This posture can be made with the body in different inclinations, from upright to upside-down postures. The animal regularly changes its position. This posture seems to be related to higher states of vigilance and/or attention to what is happening in the surroundings of the shelter. It is one of the most common postures of parental males.

iii. LYING ACROSS (Fig. 4)

The body of the animal lies across the entrance of the shelter. This behaviour may be related to the possession of a shelter.

iv. PERCHING (Fig. 5)

The body of the fish is supported ventrally on the bottom of a hole or cavity. The head is oriented to the inside, while the body is completely outside. This pattern seems to be used to examine the interior of an actual or potential shelter.

1.1.2. Locomotion

i. SWIMMING (Fig. 6)

As in all other blennies, swimming is of anguilliform type (e.g. ALMADA et al. 1983; SANTOS 1987). Pectoral fins are not used much during swimming. They are mainly used in the initial phase, when the fish lifts from substratum, and for a change in velocity or orientation. The movement is mainly characterized by sinusoidal movements of the body. At higher velocities the pectoral fins are held close to the body. The distance covered without contact with the bottom may frequently be greater than 100cm - a distance not commonly observed in other intertidal blennies (see GIBSON 1970; ALMADA et al. 1983).

ii. LIFT-OFF (Fig. 7)

Before starting swimming, a fish that is on the bottom must lift-off. The movement that enables the fish to lift-off is initiated with coordinated movements of both pectoral fins, together with propulsion of the caudal fin.

iii. LANDING (Fig. 8)

As these fishes are more dense than water, they sink to the bottom when they stop swimming. The animal settles down with the body held rigidly, pectoral fins open, and the posterior part of the body slightly elevated. Pelvic and pectoral fins possibly reduce the impact of landing.

iv. JUMPING (Fig. 9)

This form of locomotion is easily distinguished from short swims by the fact that it is only executed by synchronized movements of the pectoral fins, although a slight movement of caudal fin may also occur. It is common in smaller individuals. This type of movement is always short. The distance covered is usually shorter than the body length. It occurs generally in sequence. The behaviour can be considered as composed of lift-off and landing. It is commonly used during foraging.

v. SKIPPING AND CRUTCHING (Fig. 10)

Skipping only occurs when the animal is in strict contact with the substratum. It involves sinusoidal movements of the whole body. The propulsive force is given by the tail. It is used both to move forwards and backwards.

Crutching is a slower movement involving abduction of both pectoral fins, and slow sinusoidal inflections of the body, which enables the animal to move in permanent contact with the substratum.

Crutching and skipping are forms of locomotion mostly used when the animal moves out of the water. Only crutching is used when the animal is frightened in the water and moves very close to any available sheltering topographic feature.

vi. JUMPING WHEN OUT OF THE WATER

When a fish is out of the water it may jump in an apparently random way. The movements may be very strong, and executed by a rapid contraction

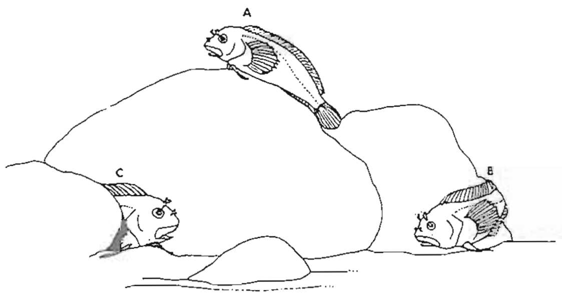

Fig. 1 - Non moving postures: A - Sitting on an open place. B - Leaning against a rock. C - Partially inside a hole.

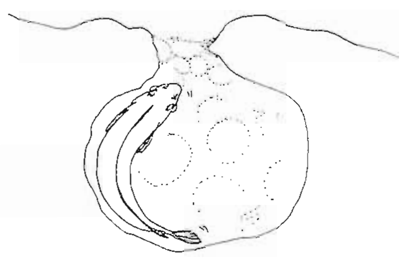

Fig. 2 - Roll up inside.

Fig. 3 - Staring.

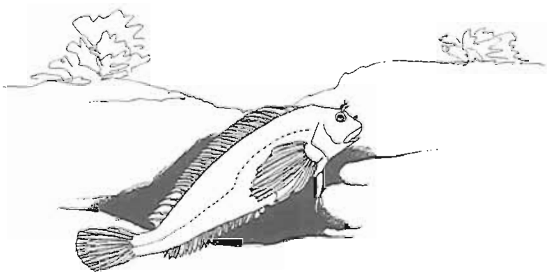

Fig. 4 - Lying across.

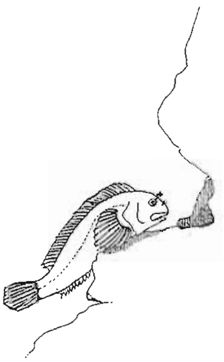

Fig. 5 - Perching.

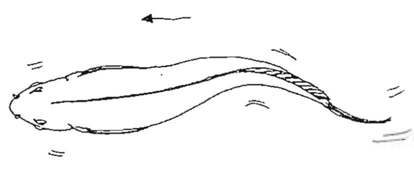

Fig. 6 - Swimming.

of body muscles that lift the animal. The individuals take rests between jumps. Invariably through a sequence of jumps and skips the fishes are able to return to the water. Leaping out of the water is more common at night, when oxygen is depleted in pools due to algal respiration.

P. s. parvicornis may also execute oriented jumps from one pool to another (Fig. 11). Exactly how this is done has never been observed closely. However, we have frequently noticed jumps from pool to pool.

1.1.3. Feeding

i. FEEDING (Fig. 12)

Individuals feed almost exclusively on green algae (*Enteromorpha*, *Ulva*, *Cladophora*). Exceptionally other items, like small crabs, may be found in the stomach. They also react very positively to the offer of soft parts of sea-urchins and limpets. Natural carnivorous feeding was seen only once.

When feeding on algae, the body is seated on the bottom. The head is lowered in relation to the body horizontal axis. Small to large pieces of the algae seem to be broken both with bites, and with a scraping movement.

1.1.4. Movements of unknown function

i. YAWN (Fig. 13)

This behaviour is always made when the fish is resting and seated on the bottom (inside or outside the holes). It spreads its dorsal fin at the same time that it opens the mouth and raises its head. Following this, the animal seems to relax the muscles involved in these movements, closing the mouth, and lowering the head and dorsal fin.

ii. SOUND EMISSIONS

When handled, fish emit short deep sounds that seem to be of frictional origin. The emission and use of sounds by these species for communication was not investigated, neither was their occurrence under natural circumstances. It is known that other species, living in similar circumstances, use sound in intraspecific communication (TAVOLGA 1958).

iii. CHAFING (Fig. 14)

While swimming the fish rotates the body and rubs against any hard feature of the bottom. This is done most of the time after lift- off, and may be done several times in succession. This behaviour could serve to free the fish from ectoparasites, and could also be related to irritation of the skin, due to some kind of cutaneous infection. Chafing could also be related to other types of stressful situations, or may even be an intention movement (*sensu* LORENZ 1970).

1.1.5. Cleaning activities

i. EXCAVATION (Fig. 15)

Potential shelters and shelters in use are easily covered and filled by all kinds of detritus and sand that are deposited in the pools by water movements. Before use by the fish these shelters must be cleaned, and the detritus removed. One method the fish uses is excavation. During excavation the fish is seated on the bottom. It excavates and pushes sand and other material out of the shelter, with the help of synchronized strong movements of both pectoral fins. The fish may also excavate with only one of the pectoral fins with the body slightly inclined to the operating side. The caudal fin can also be used in isolation or combined with pectoral fins.

Excavation is a very important adaptive pattern during the reproductive season, when males occupy nesting shelters.

ii. FANNING (Fig. 16)

Fanning is one of the main activities of parental males. Its main function is not cleaning, and it will be more extensively described under parental behaviour. As a cleaning activity it may contribute to the removal of small particles deposited in the nests and light materials such as faeces.

iii. REMOVAL WITH TRANSPORTION

The fish moves detritus or even small organisms from one place to another by mouth. It is again a behaviour mostly seen in parental males, and mostly related to removal of objects from the nest-

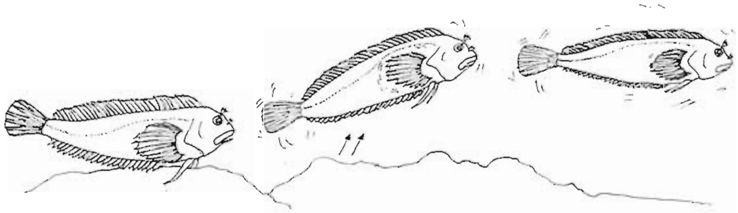

Fig. 7 - Lifting.

Fig. 8 - Landing.

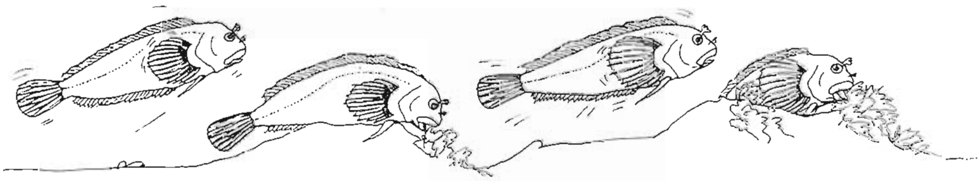

Fig. 9 - Jumping while grazing.

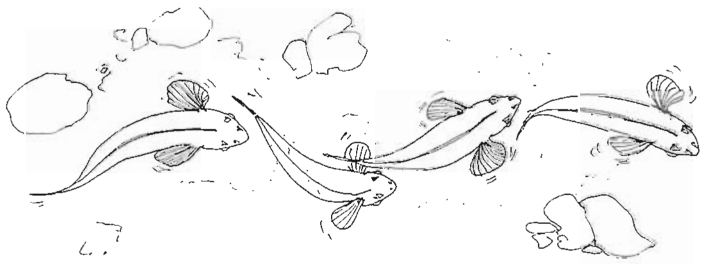

Fig. 10 - Crutching.

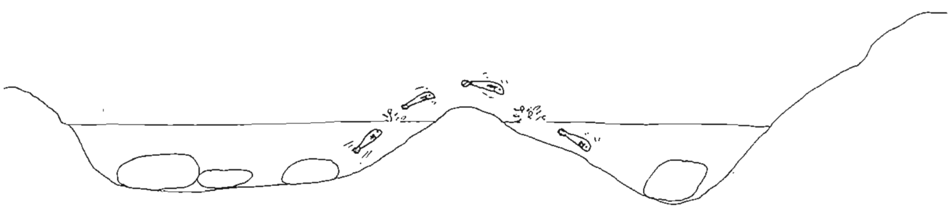

Fig. 11 - Jumping across two tide pools.

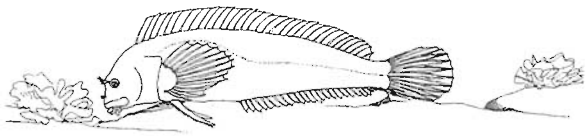

Fig. 12 - Feeding.

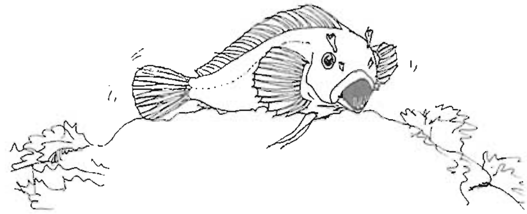

Fig. 13 - Yawn.

Fig. 14 - Chafing.

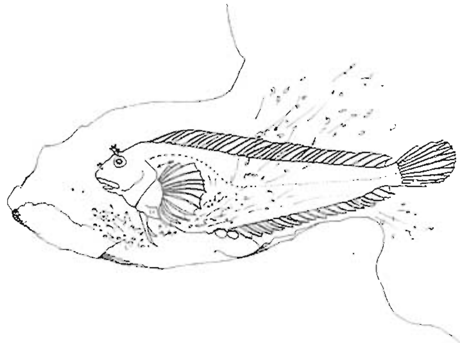

Fig. 15 - Excavation.

Fig. 16 - Fanning.

ing cavity. It is a behavioural pattern that can easily be provoked experimentally, and is best considered in relation to size of material moved.

Loose objects smaller than the mouth of the fish, such as sand, are transported in the mouth and spat out at a variable distance from the shelter. Shells from small molluscs, small hermit crabs and other organisms are also removed from the bottom, clasped by the teeth and released away from the nest (Fig. 17).

Materials and organisms attached to the substratum may be pulled out with the teeth. These include small tufts of algae (e.g. *Padina pavonia*) that are close to the nest entrance, hiding it. It is a pattern mostly observed in parental males. By removing all the algae from a circle, 10cm diameter, around the nest parental males form a distinctive clearing (see below).

Smaller materials and/or organisms that are attached to the walls of the nest are removed by scraping with the teeth (Fig. 18) and are spat out from the nest (Fig. 19). This pattern is mostly used by pre-parental males during the preparation of the walls of the future nest.

Objects bigger than the fish's mouth, such as sea-urchins, stones, large hermit crabs and empty shells are pushed away with the snout, whilst the fish moves by skipping.

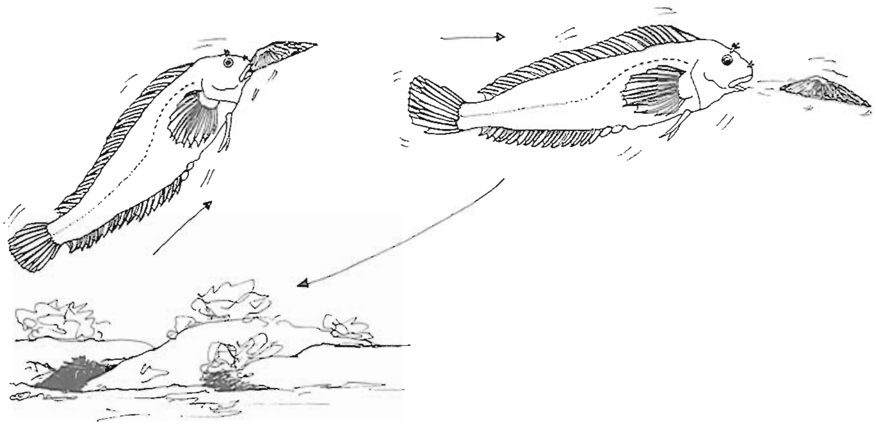

Fig. 17 - Object removal with the mouth (limpet shell).

1.2. SOCIAL BEHAVIOUR

1.2.1. Agonistic behaviour

i. APPROACH

This is a pattern where the fish may swim or jump to approach a conspecific.

ii. CHARGES (Fig. 20 and Fig. 21)

Charges involve fast swimming directed against other fish. The mouth remains open and the head is aligned with the body axis. Normally it precedes a butt or a bite. Before the charge the fish raises its head and looks at the other individual.

iii. BUTTING (Fig. 22)

Butting is a strong impact made with the snout of a fish against the body of another fish. The dorsal fin is erected. It usually follows a charge.

iv. PUSHING

A soft impact is made with the snout of a fish against the body of another fish. It can occur on occasions when the fishes are very close. In this case the fishes move by skipping. It may appear combined with threat elements. It could also be interpreted as a removal pattern in relation to a conspecific.

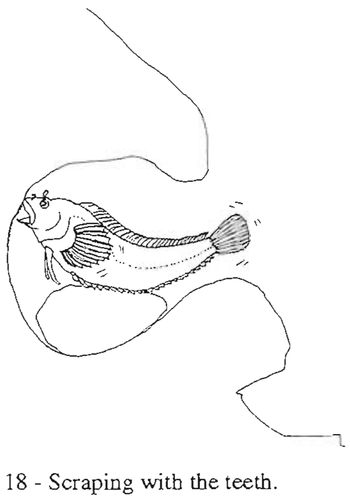

Fig. 18 - Scraping with the teeth.

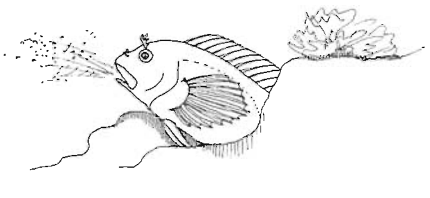

Fig. 19 - Sand spitting.

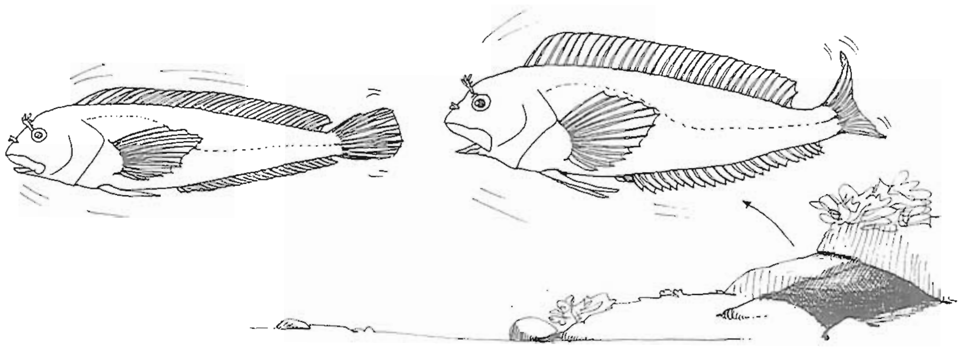

Fig. 20 - Intraspecific charge.

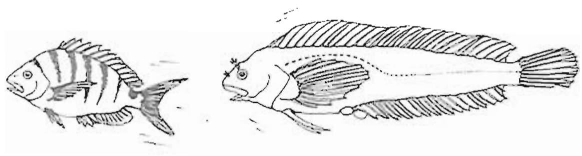

Fig. 21 - Interspecific charge.

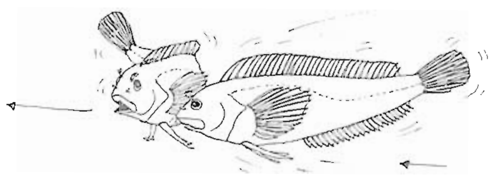

Fig. 22 - Butting.

v. BITE

One of the fishes bites the operculum, the body, or one of the fins of another individual. A variant of this is a mouth to mouth fight (Fig. 23). It usually follows a charge or a pursuit. During high intensity contests the biting fish may hold the other for some seconds. These are the kinds of actions that could provoke injuries in individuals. Fish, mainly parentals, also bite other species, like octopus that approach the nest, and chase them.

vi. WITHDRAWAL (Fig. 24)

This pattern is shown by an intruder and is characterized by a turn away when approaching a territory, or when a dominant male is approaching. A territorial male when approaching a territory of another male, slightly turns away from it, and passes by on the periphery.

vii. PURSUIT

Pursuit is fast swimming of a fish following another fish. It is similar to the initial phase of the charge, and essentially constitutes a more prolonged version. Pursuit only occurs if another individual flees, but a flight does not necessarily imply a pursuit.

viii. FLIGHT

In contrast to the previous pattern, flight is achieved by very fast swimming, and generally follows a pursuit and/or a charge. Fish that are fleeing may jump out of the water for a few centimetres (Fig. 25).

ix. UNDULATION SWING (Fig. 26)

This is one of the two threatening patterns identi-

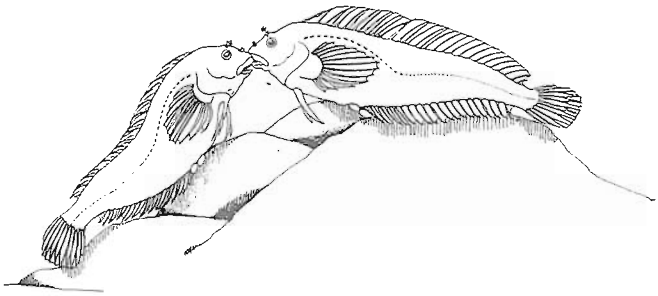

Fig. 23 - Mouth to mouth bite.

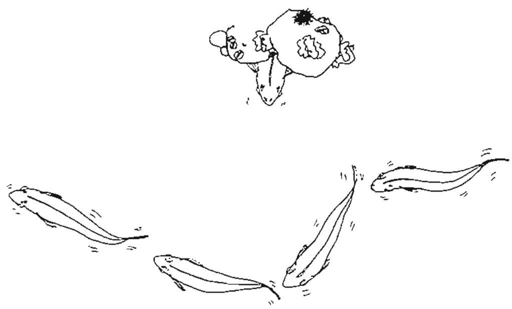

Fig. 24 - Withdrawal when approaching a conspecific territory.

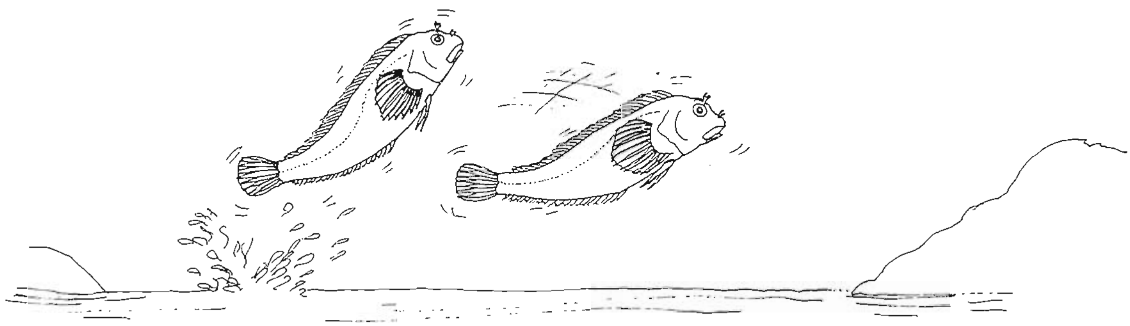

Fig. 25 - Jumping out of the water while fleeing.

fied for this species. The actors very slowly undulate the whole body, from the front to the back. During undulation both fish assume relative positions: head to flank (T relative position), head to head (parallel) and/or head to tail (anti-parallel). At any time the actors may advance slowly or retreat. This situation may also escalate into higher levels of aggression.

X. SWIMMING PRESENTATION (Fig. 27)

This is shown by a parental male against another neighbouring parental male who approaches its territory. While the "intruder" swims slowly close to the territory, the owner charges but does not cross the boundary. After each charge it returns to the centre of the territory. Charge and return last

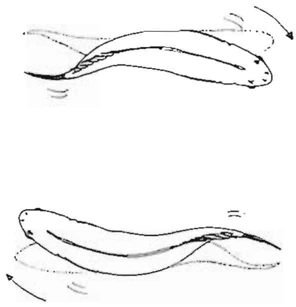

Fig. 26 - Undulation swing.

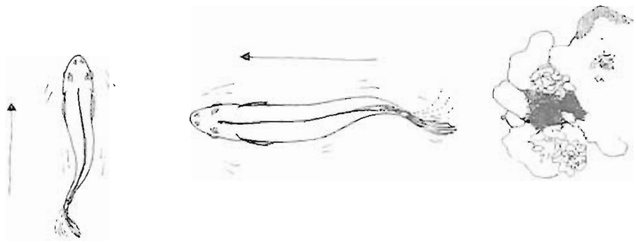

Fig. 27 - Swimming presentation.

while the neighbour continues its approach.

xi. DORSAL PRESENTATION (Fig. 28)

This is a behavioural pattern that clearly inhibits aggression from another individual. It is based on lateral rotation of the body. Sometimes it is so accentuated that the actors can stay seated laterally on the bottom. It may be executed during very slow swimming or when the fish is stationary. It is frequently used by a fish that approaches a territory. Females, when approaching a parental male and when entering the nest for spawning, always show dorsal presentation. Satellite males were also seen to exhibit dorsal presentation.

x. FIGHT

Fights are prolonged interactions between two individuals, and may be of different kinds and intensities. Several of the patterns described above may occur during fights.

1.2.2. Mating and parental behaviour

i. SIGNAL SWIMMING (Fig. 29)

This pattern is exclusively observed in males. The male swims slightly (5 to 15cm) above the bottom, on a oblique (more rarely, vertical) axis. It then turns the head and comes back, describing a circle or a loop. This pattern is mostly performed repeatedly, close to the nest by parental males. It is normally initiated at the nest entrance. The return component is directed to the entrance. It may be executed with or without females present. It can be considered a signalling mating pattern.

Fig. 28 - Dorsal presentation.

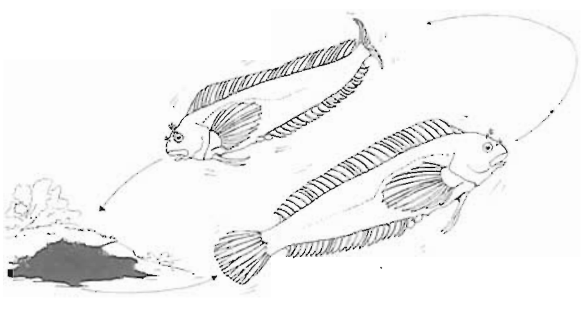

Fig. 29 - Signal swimming.

ii. BACK-AND-FORTH PRESENTATION (Fig. 30)

This is a pattern exhibited by courting males in the presence of females. It is performed with the fish half inside the nest. It then goes back-and-forth in a very rhythmic pattern which may accelerate.

iii. GENTLE BUTT (Fig. 31)

Before the female goes inside the nest the male may approach her and make gentle touches with the snout on her body, as if trying to push her physically towards the nest.

iv. CROSS BARRIER

Before and just after the female enters the nest, the male block the nest with its body for a few seconds by positioning across the entrance.

v. CIRCLING THE FEMALE (Fig. 32)

When the female is at a short distance from the nest the male may swim towards her, circle her, and return again. This may be done repeatedly.

vi. CIRCLING THE NEST (Fig. 33)

The male may also swim in circles around the nest when a female approaches. It is probably a behaviour pattern that shows the localization of the nest for the female.

vii. QUIVERING (Fig. 34)

After the female has entered the nest the male shakes his entire body. This happens several times. Each of the times only lasts a few seconds. It must coincide with sperm release.

viii. RUBBING (Fig. 35)

Parental males rub the ventral part of the body against the internal walls of the nest. This is a pattern of behaviour very common in parental males. They rub the belly over the eggs. The exact function is not clear.

Fig. 30 - Back-and-forth presentation.

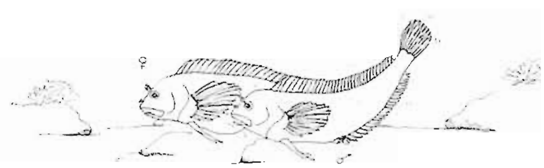

Fig. 31 - Gentle butt.

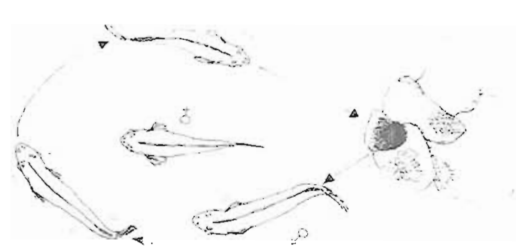

Fig. 32 - Circling the female.

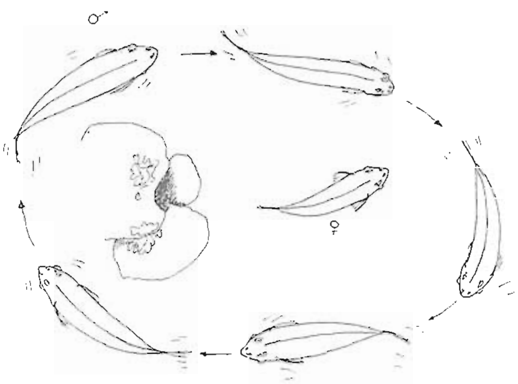

Fig. 33 - Circling the nest.

Fig. 34 - Quivering.

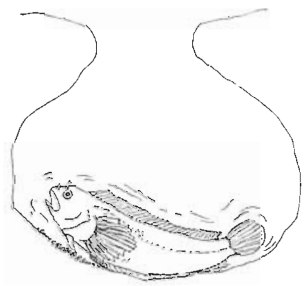

Fig. 35 - Rubbing.

IX. FANNING (Fig. 36 and Fig. 37)

Fanning is the most time and energy consuming behaviour pattern exhibited by parental males. It consists of synchronized or alternating movement of the extended pectoral fins. The males may also make use of the caudal fin in fanning. While fanning, the male may be at the entrance of the nest or completely inside. During caudal fanning alone two thirds of the body (the anterior part) may be outside. This pattern promotes the circulation and renewal of water inside the nest. From timed observations it was apparent that parental males spent 90% of the time inside the nest, most of which (70%) was spent fanning.

2. COURTSHIP AND MATING

Males mate several times during the reproductive season. The nests have clutches of eggs from different females and in different stages of development. Besides the patterns of behaviour directly related to the development and defence of the embryos, males invest a small part of their time in activities related to courtship and mating.

In addition to the regular exhibition of looping, the male watches the territory and reacts promptly to the approach of a female. He can then approach her or initiate a series of back-and-forth presentations at the nest entrance. When the male approaches the female (Fig. 38), he contacts her with the snout, and pushes her slowly. He may return to the nest («showing») and approach the female again. He may also exhibit the cross-barrier position at the nest entrance. These patterns can be repeated several times in sequence. The female may then enter the nest. This is always done in a dorsal presentation. When the female is inside the

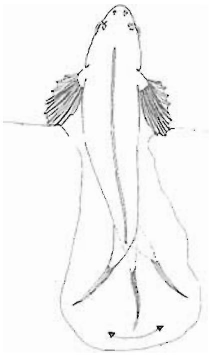

Fig. 36 - Caudal fanning on a vertical hole.

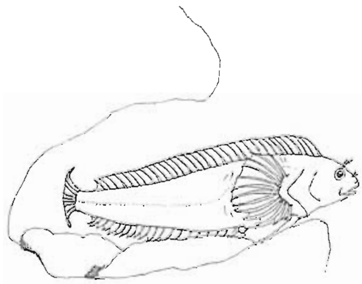

Fig. 37 - Caudal and pectoral fanning on a horizontal hole.

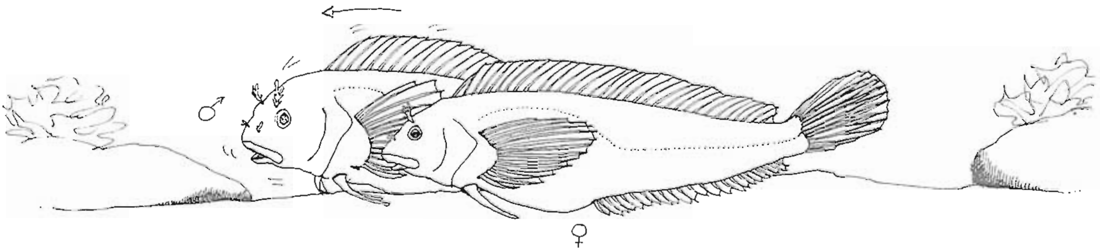

Fig. 38 - Approaching and touching the female.

male closes the entrance using the cross-barrier position and looks inside. He then enters. When inside he appears very excited. Quivering occurs several times. He rubs the walls of the nests and turns frequently, while the female is laying the eggs.

Eggs are laid by the female, one by one, in a single layer.

The male may or may not charge over the female after spawning. The female may also leave the nest after a little time and return later, to the same nest and male. Courtship is rather reduced during repeat mating.

DISCUSSION

1. Patterns of behaviour

Cleaning activities have been described for many species of blennies (see GIBSON 1969). GUITEL (1893) was the first author to refer to them. However, their use in the formation of a clearing in the territories of parental males has never been reported for any other blenny.

They probably constitute an important adaptive trait by which cavities are maintained clean and free from a diverse range of materials and organisms which are frequently transported into them by the tides and waves. Cleaning patterns of behaviour are also present in parental males of the subtidal species *Ophioblennius atlanticus atlanticus* from the Azores (our observations).

A pattern called "*torsão*" described by ALMADA et al. (1983) for *C. galerita* seems to have similarities with undulation, of which it probably constitutes a more advanced, ritualized form. Both types may be considered as ritualizations (*sensu* HUXLEY 1966) phylogenetically established. They may represent a motivational conflict between charge and flight where the characteristic sinusoidal pattern of blennioid locomotion is preserved.

Signal-swimming in *P. s. parvicornis* has obvious structural and functional affinities with patterns described for other species: «loop-swimming» (*Tripterygion melanurus*: WIRTZ 1978), «Fig.-8-swimming» (Tripterygion spp.: WIRTZ 1978), «cerco ao ninho» (*Coryphoblennius galerita*: ALMADA et al. 1983 and *Hypsoblennius* spp.: LOSEY 1976) and «*signalsprung*» (*Parablennius rouxi*: HEYMER & FERRET 1976). In *P. s. parvicornis* it is possible that the formation of a clearing close to the nest opening and signal-swimming are effective in facilitating the attraction of females in an environment where the nests are surrounded by algae clumps.

Back-and-forth presentation is a highly ritualized pattern. The male does not completely leave the nest, neither does it go inside. Like the threaten pattern described above, the present movement seems to be a crystallization of a situation of motivational conflict. A conflict between the motivation to swim towards the female, and the "motivation" to enter/stay in the nest.

Similar ritualized patterns have been described for other closely related species such as the nodding exhibited by *C. galerita* (GUITEL 1893; ALMADA et al. 1983). Again in this case the pattern shown by *P. s. parvicornis* seems to be less evolved from its original components (i.e. from the locomotion patterns of advancing and retreating). In *C. galerita* the movement consists of vertical movements of the head and locomotory components are no longer obvious (ALMADA et al. 1983; SANTOS 1988).

Oxygen is a limiting factor for the survival and development of the embryos. It is directly obtained from the water by the embryo, through the porous chorion, which expels CO_2. In a semi-enclosed place, such as a nesting cavity, the environment could be very quickly saturated with CO_2 expelled by thousands of embryos. Replacement of the water is therefore a matter of life or death for the embryos. All known fish species with parental care of external embryos show fanning (KEENLEYSIDE 1979). Obviously it is also a very characteristic behaviour pattern in many blennies (GIBSON 1969). It is known, from many species, that frequency and intensity of fanning increases with the development of the embryos (KEENLEYSIDE 1979). Fanning constitutes one of the most time consuming activities of parental males (SANTOS 1992). It must have high costs associated with it. The many forms fanning can assume may be associated with the need to alternate the use of different muscles.

2. Behavioural plasticity

In contrast to many other intertidal blennies (e.g. *C. galerita, L. trigloides* and *L. pholis*), in *P. s. parvicornis* some of the patterns of courtship and related behaviour are made by elevating the body in relation to the bottom. *P. s. parvicornis* belongs to a genus (*Parablennius*) in which the majority of species are subtidal (e.g. *P. pilicornis, P. gattorugine, P. ruber*). In the Mediterranean *P. sanguinolentus sanguinolentus* is present below the zone directly swept by wave action (GIBSON 1972; ILLICH & KOTRSCHAL 1990). *P. sanguinolentus parvicornis* has preserved in the intertidal the self-advertisement behaviour of its subtidal relatives. Its intertidal occurrence in the Azores offers an excellent opportunity to study the conditions that can lead subtidal benthic fishes to colonize the tidal zone. It also exemplifies to what extent subtidal benthic blennies are preadapted in many respects, namely in their reproductive style, to colonize the intertidal if the opportunity is available (SANTOS & ALMADA 1988).

The Azores are 900 miles away from the European continent. The dominant species in the northeastern Atlantic rocky intertidal coasts, *Lipophrys pholis*, is rare in the Azores. The rocky subtidal is dominated by the highly territorial species *Ophioblennius atlanticus atlanticus* and the pomacentrid *Abudefduf luridus*, which occupy the available rock surface, and display agressively to other benthic fishes (MAPSTONE & WOOD 1975). It is possible that severe competition in the subtidal zone, and weak competition in the intertidal were important factors leading the Azorean population of *P. s. parvicornis* to occupy rocky intertidal pools where it became dominant (SANTOS 1992). There it is out of reach of benthic predators (e.g. Scorpaenidae, Congridae, Muraenidae).

P. s. parvicornis, while presenting the general features of the reproductive style of rocky intertidal warm temperate residents, shows a number of pecularities that illustrates well the evolutionary plasticity that this breeding pattern can display. The formation of a clearing close to the nest entrance, the patterns of self-advertisement with elevation of the body in relation to the bottom and the reproductive diethism and dimorphism in males are good examples of that plasticity.

Comparison of reproductive styles of fishes in contrasting habitats is an excellent way of exploring the diverse ecology of rocky intertidal habitats. The blennies, with their radiation to a diverse range of habitats, are particularly useful in this respect. This theme is elaborated and discussed in detail by ALMADA & SANTOS (in press).

ACKNOWLEDGEMENTS

The authors acknowledge the field support given by Norberto Serpa and the late Olavo do Amaral. They are also very grateful for the comments of Stephen J. Hawkins and Richard D. M. Nash (Port Erin Marine Laboratory), Robin Gibson (Scottish Marine Biological Association) and Vitor Almada (Instituto Superior de Psicologia Aplicada). The first author also wishes to thank Junta Nacional de Investigação Científica e Tecnológica (JNICT - Ciência) for their support.

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Accepted 5 August 1993.