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Allopaternal care in the redlip blenny

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Territorial male *Ophioblennius atlanticus atlanticus* were found to switch to experimentally deserted nests of other males and adopt their fry. This alloparental care appears to aid in acquiring additional clutches of eggs at the nest site.

Key words: *Ophioblennius atlanticus atlanticus*; alloparental care; Azores.

Several studies have shown the importance of eggs in a nest for increasing the probability of obtaining more eggs in fish with male parental care. Ridley & Rechten (1981) have shown that females of *Gasterosteus aculeatus* L. prefer to mate with males that have eggs in their nests. Jamieson & Colgan (1989) found that the presence of eggs in the nest had an effect of increasing the courting activity of the males of that species. Further evidence of an association between the presence of eggs in the nest and the probability of acquiring more mates by the males came from studies on *Cottus gobio* L. (Marconato & Rasotto, 1983; Marconato & Bisazza, 1986; Bisazza & Marconato, 1988), *Padogobius martensi* (Günther) (Bisazza *et al.*, 1989), *Pimephales promelas* Rafinesque (Unger & Sargent, 1988), *Etheostoma flabellare* Rafinesque (Knapp & Sargent, 1989), *Axoclinus carminalis* (Jordan and Gilbert) (Petersen, 1989), *Hypsypops rubicundus* (Girard) (Sikkel, 1989), and *Aidablennius sphynx* (Valenciennes) (Kraak & Videler, 1991; Kraak & Berghe, 1992). Bisazza *et al.* (1989) and Unger & Sargent (1988) reported the occurrence of allopaternal care. Advantages for the females choosing a male which already cared for eggs (Sikkel, 1989) could be related to: the reduction of losses by predation (Rohwer, 1978; Ridley & Rechten, 1981); increased paternal investment associated with accumulation of clutches (Coleman *et al.*, 1985); and increased attractiveness of the males which show a higher capacity of caring for eggs (Ridley, 1978).

If the presence of eggs constitutes an attractive trait for mating females, males must obtain eggs not only because of their intrinsic value but also because they constitute a means of obtaining more eggs, and thus of increasing their reproductive success. The present paper, reports a case where males acquire other nests from which male owners were removed experimentally; these males cared for the eggs in the adopted nest and continued to spawn with additional females.

The present study was carried out with redlip blenny *Ophioblennius atlanticus atlanticus* (Valenciennes) a territorial inshore marine species with male parental care (Nursall, 1977). Care is given only during the embryonic stages. Larvae are planktonic, with post-metamorphic juveniles adopting a rocky benthic life, thus the probability of kin returning to the same site is extremely low. *O. a. atlanticus* of the Azores occurs in shallow rocky habitats from 0–15 m depth, with higher abundance from 0·5–7·5 m (Patzner *et al.*, 1992; Patzner & Santos, 1993). The breeding season lasts through June and July and spawning occurs during the early morning.

The study site was on the sea side of Horta Harbour breakwater (Island of Faial: 38°31·3′ N; 28°27·2′ W), composed of concrete cubic blocks (2·5 m) arranged in a regular pattern from 1·5 to 10 m depth. Despite their uniform shape, they possess numerous irregularities that form cavities of adequate size for the nests of breeding males of *O. a. atlanticus*. The site, comprising 36 blocks in three vertical rows, together with the location of the nests, was mapped. Twenty parental males were removed by hand nets

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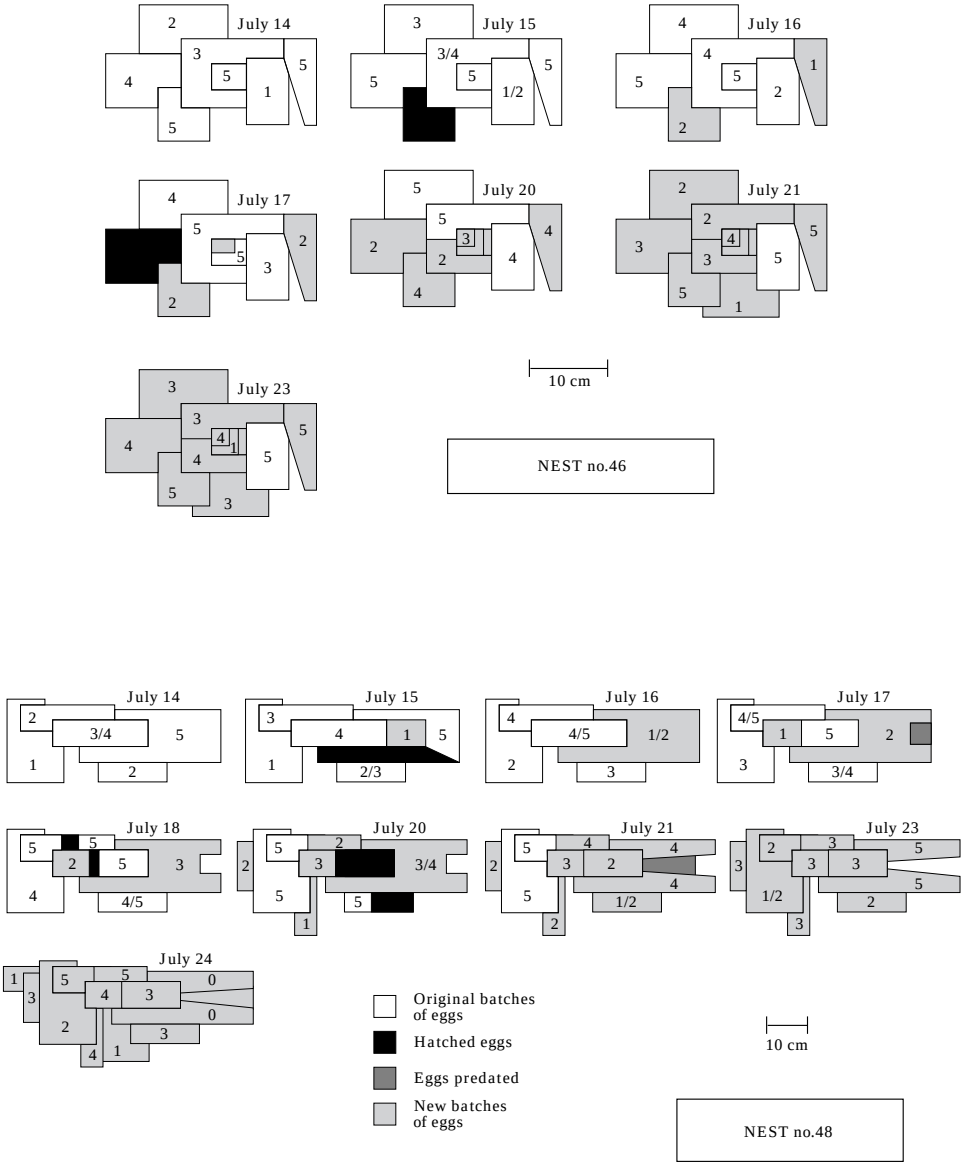

FIG. 1. Stylized representation of the development of batches of eggs in two selected nests after the day the original male owners were removed (July 14) and the subsequent days when the nests were occupied by other males. Numbers in the box refer to different stages of embryo development.

and kept in aquaria in the laboratory. They were returned to the site at the end of the experiments which lasted from 14 July until 10 August 1990. Length and width of clutches of eggs in nests were measured almost every day. Developmental stages of the eggs were ranked in six categories, from 0 (zygote) to 5 (embryos with fully developed eyes and mouth), over the 10 days to hatching (Fig. 1). The boundaries of the egg patches were linearized for the purpose of diagrammmatic representation. Some fishes were tagged (Floy® tags), and others were simply identified by scars or other distinctive patterns.

TABLE I. Number of nests, which were taken over by other males, classified according to the survival of the batches of eggs of the removed parent and the additional spawnings obtained by the adopting male

	No take-over of nest	Additional spawnings after take-over of nest	No additional spawnings after take-over of nest
Original eggs surviving	1	12	3
Original eggs not surviving	3	0	1

Analysis of the data in the text. [Analyses of contingency tables using simulations (Estabrock & Estabrock, 1989) were used to calculate χ^2].

Forty-two matings were monitored in 21 nests. Intrusions by other males were never observed during spawnings. Therefore, there is no reason to suppose that the male adoption of abandoned eggs was related to previous fertilization attempts of those eggs.

An alloparental male significantly increased the chances of the original eggs surviving (1 : 15 *v.* 3 : 1) ($\chi^2 = 9{\cdot}453$, $P = 0{\cdot}005$; Table I). Additional spawnings, after take-over of a nest, were significantly higher if the original eggs survived (1 : 12 *v.* 3 : 0) ($\chi^2 = 11{\cdot}077$, $P = 0{\cdot}004$; Table I). On one occasion, no eggs survived in the nest, yet a male occupied it for 7 days and no spawning occurred, despite the active displays of the male and visits by females which left after rubbing their bellies on the nest wall. Twelve out of 16 nests taken over by alloparental males went on to receive additional clutches of eggs. This number of nests with additional spawnings is significantly greater than that predicted by chance alone (prior probability = 0·5; binomial test $P = 0{\cdot}011$).

Females preferred to spawn close to other batches of eggs and probably chose males based on the quantity of eggs already present in the nest. Since the density of nesters was quite high (mean ± S.D. = 0·4 ± 0·33 nests m^{-2}, with a maximum of 1·25 nests m^{-2} in one of the blocks) the interactions between males and females were frequent, allowing females to assess the quality of neighbouring males easily. The pattern of succession of new batches of eggs showed that females released eggs close to other batches and, in most cases, in areas where eggs had recently hatched (Fig. 1). They seemed to prefer to fill empty spaces left in the middle of patches of eggs. Eggs at the periphery are always more subject to predation (Côté & Hunte, 1989) and parental care is very important for egg survival. The habitat where *O. a. atlanticus* lives is dominated by egg predators [e.g. *Coris julis* (L.), *Thalassoma pavo* (L.), *Diplodus sargus* (L.), and sea urchins]. These predators identify unprotected fry easily, which they consume completely in a very short time. Furthermore, good nesting sites are a limited resource. The upper-surfaces and the lateral sides of the blocks had no nests, and were occupied by the non-nesting males and by the females. Take-over males could have destroyed the eggs present in the adopted nests, but on the contrary they kept and cared for them.

O. atlanticus has been previously studied in the reefs of Barbados, in the Caribbean. Nursall (1977, 1981) and Marraro & Nursall (1983) studied several aspects of the social behaviour and reproductive periodicity of the species. Recently, Côté & Hunte (1989) showed that parental males monitored their own reproductive success; males with lower reproductive success were more likely to switch nesting sites than other males. The reproductive success of those males increased during the period after a switch.

The present observations in the Azores were clearly different from those of Côté & Hunte (1989). In the Caribbean populations of redlip blenny the males switched nests, but did not adopt or care for unrelated eggs. However Nursall's (1977, 1981) and Côté & Hunte's (1989) populations had discrete monthly periods of reproduction. Nest switching happened from one month to the next. The reproductive season in the Azorean population was continuous over 2·5 months, thus creating the opportunity for a male to switch nests or acquire nests while matings and spawnings were in progress.

In this population the eggs seemed to have a clearly epigamic function, increasing the probability of a male obtaining more eggs. Males that took over deserted nests and guarded eggs of other males could be maintained in a population through female selection.

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