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Alternative Male Mating Tactics in *Hypoptychus dybowskii* (Gasterosteiformes): Territoriality, Body Size and Nuptial Colouration

Izumi Akagawa and Muneo Okiyama

Ocean Research Institute, University of Tokyo, 1-15-1 Minamidai, Nakano-ku, Tokyo 164, Japan

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Abstract Reproductive behaviour of *Hypoptychus dybowskii* was studied in the field and aquarium. Two male mating tactics were found. Some males with remarkable nuptial colouration established territories around sargasso weeds, while the remainder schooled. A territorial male began courtship in response to the approach of a gravid female. Several schooling (non-territorial) males followed the gravid female and were often attacked by the territorial male. Egg masses, comprising a mean of 32 eggs of about 2 mm in diameter, were coiled around the branching points of sargasso weeds in the male's territory. Just after spawning by a female, both the territorial male and several non-territorial males rushed to the spawning site to fertilize the eggs; the territorial male, situated nearest to the female, rushed first. Females were never observed to spawn with non-territorial males only. The territorial male frequently picked at the eggs so as to attach them firmly together around the sargasso weeds, for about 30 min after spawning and occasionally thereafter, but never conducted further paternal care such as fanning. Territorial males were not always larger than others, and schooling males in the aquarium suddenly became territorial or vice versa, with rapid changes in body colouration. It is therefore suggested that males alternate two mating tactics depending on their physiological condition, or as a mixed strategy at the individual level.

Many cases of alternative male mating strategies and tactics have been reported in fishes in recent years (Semler, 1971; Warner and Hoffman, 1980; Gross, 1984; Kuwamura, 1987; Chan and Ribbink, 1990; Turner, 1993; Magurran, 1993). For example, male North American sunfish have three types in behaviour. The largest and oldest males establish territories around the nest and undertake parental care, the smallest and youngest males behave as sneakers, and the intermediate males are satellites (Gross, 1982). Generally, large territorial males show brighter or more intense body colouration than others, the relationship between body colouration and female mate choice having often been discussed (Semler, 1971; Houde, 1987; McLennan and McPhail, 1989; Rowland, 1984, 1989; Warner and Schultz, 1992; Magurran, 1993; Turner, 1993).

Reproductive behaviour of Gasterosteidae species, especially the threespine stickleback, *Gasterosteus aculeatus*, has been studied in detail. Males establish mating territories and take care of eggs (Wootton, 1976, 1984; McLennan et al., 1988). However, in the remaining two families in Gasterosteiformes, Aulorhynchidae and Hypoptychidae (Nelson, 1984), little is known regarding reproductive behaviour. Among the Aulorhynchidae, life history and ecological notes on *Aulorhynchus flavidus* (Limbaugh, 1962; Marliave, 1976), and copulational urogenital papilla (Sasaki, 1977) and oviposition into sea squirts by *Aulichthys japonicus* (Yamamoto and Shirai, 1988) have been reported. In *Hypoptychus dybowskii* Steindachner, a monotypic species of Hypoptychidae, living in the coastal waters of northern Japan and Sakhalin (Ida, 1984), a few studies on morphology (Ida, 1976) and reproductive ecology (Ishigaki et al., 1957) have been made. However, almost nothing is known of its reproductive behaviour.

Reproductive behaviour of *H. dybowskii* was studied both in the field and aquarium. This paper describes male mating territories, courtship, spawning and paternal care in *H. dybowskii*, and includes a discussion of alternative male mating behaviour in relation to sexual differences in body size and nuptial colouration.

Materials and Methods

Field work was conducted in Otsuchi Bay (39°20′N, 141°55′E), Iwate Prefecture, Japan. In

this area schools of *Hypoptychus dybowskii* are seen all year round, the reproductive season being from May through June (K. Kawaguchi, pers. comm.). Schools and spawning sites of *H. dybowskii* were searched for throughout Otsuchi Bay from a boat in June 1989. Subsequently, underwater observations on reproductive behaviour were made using SCUBA over two weeks in June, on both sides of the pier (about 500 m long) in front of the Otsuchi Marine Research Center, University of Tokyo. The bottom comprised a sandy layer on rock beds. At intervals of 5–20 m several areas of about 5–10 m^2 were covered with 1–5 stands of sargasso weeds (Sargassaceae spp.) and other seaweeds. The depth was 5–7 m and the water temperature 13–14°C. Observations were conducted in the daytime between 10 h–16 h, about 10 hrs in total. Territorial behaviour and courtship were recorded.

Fishes were captured around the spawning sites by seine net four times in June, 1989. Some (120 males and 96 females) were fixed immediately in 10% seawater-buffered formalin, and subsequently measured for standard length (SL), body weight (BW) and gonad weight (GW). Eggs in the ovary were also examined. The remainder were kept in a holding tank (1 ton) also for further aquarium observations. We collected 112 egg masses attached to sargasso weeds from the spawning sites so as to measure and count the number of eggs per mass.

Of several hundred individuals kept in the holding tank, about two hundred were transfered to a transparent, acrylic aquarium (150×70×50 cm, 500 *l*) 6–12 hrs after every capture, for observation of spawning behaviour. As spawning substrates, two or three stands of sargasso weeds had been planted on one side of the aquarium, with flowing seawater at 14±1°C. Three sets of consecutive observations were conducted for 5–7 hrs, using different captive individuals each time. Many individuals died or weakened badly before and during the observations, and were replaced by others from the holding tank. The establishment of territories, courtship, spawning and paternal care were recorded.

In another series of aquarium observations, whenever a territory was established, the territorial male was soon removed and fixed in 10% seawater-buffered formalin. Nine territorial males were removed one after another, and about 10 hrs after the start of the observation the remaining individuals (148 males and 111 females) were also fixed. Together with the territorial males, these were measured for standard length, body weight and gonad weight.

Results

Egg mass and fecundity

Egg masses of *Hypoptychus dybowskii* were found on the branching points of sargasso weeds (*Sargassum horneri*, *Cystoseira hakodatensis* and other Sargassaceae spp.) standing up 3–7 m from the substrate. Sometimes they were found also on floating sargasso weeds, which might have become detached shortly before. Eggs were slightly depressed, about 2 mm in diameter, and stuck together forming a coil around the branching point. It was impossible to remove an egg without breaking it, because of the strong adhesion between the egg membranes. The number of eggs per egg mass varied from 13 to 84 (mean±SD=31.7±11.2, $n=112$).

Eggs in the ovary comprised three distinctive size classes (Fig. 1), as reported by Ishigaki et al. (1957), suggesting multiple spawning of females. The largest eggs, about 2 mm in diameter, were seemingly almost matured, being translucent and located in the rearmost part of the ovary (Fig. 1). The number of translucent eggs in an ovary was 0–96 (18.9±19.2, $n=96$). Since each egg mass included at least 13 eggs, which seemed the minimum number necessary for effective coiling around sargasso weed, females whose ovary contained more than 12 large, translucent eggs could be regarded as potential spawners. The number of translucent eggs (34.0±14.1, $n=47$) in the ovaries of these females did not differ significantly from the number of eggs (31.7±11.2, $n=112$) in the egg masses ($t=0.99$, df=71.5, $p>0.1$). The number of translucent eggs (>12) in the ovaries was not significantly correlated with body size of females (59.1±4.8 mm SL, $n=47$; $r=0.11$, $p>0.1$). The gonadosomatic indices (GSI) of females ranged between about 10 and 20 (16.29±4.93, $n=96$). Thirty-eight females (39.6%), whose GSI values were small (about 10), lacked translucent eggs, and seemed to have just spawned.

Reproductive behaviour in the field

Male mating territories.—Schools of *Hypoptychus dybowskii*, comprising 100–500 individuals, were observed swimming around in the bay. Concurrently,

one or a few males had established territories in each area covered with several stands of sargasso weeds, at any time during the observation (10h–16h). More than 10 territorial males in total were observed in the study area every day. Within each territory, one to several egg masses were found attached to the branching points of sargasso weeds. Territorial males occasionally pushed the egg masses with their snout, and also pushed other branching points of sargasso in their territories. Each territorial male usually stayed within an area of 1 m or less in diameter around the egg mass, although sometimes swimming about 3–5 m from the centre of its territory. Males seldom moved considerable distances, 10 m or more away from the territory. Any invasion of neighbouring territories by the former was followed almost immediately by their expulsion.

Courtship behaviour.—During observation of the territorial males, schools were seen to pass near the territories on more than 10 occasions. In several of these cases, a gravid female left the school for the territory, followed by several males from the school.

The territorial male began to direct a series of courtship behaviour movements toward the approaching female (Fig. 2). The courtship comprised three phases: "dash and return," "quivering" and "pushing weeds." From a distance of about 5 m, the territorial male dashed to the female, subsequently turning toward his territory. When the female approached to within 1 m of the territory, the male quivered his tail, while bending his body in front of the female's snout. With this display the male slowly led the female to the centre of his territory. When the female came within 15 cm of the sargasso weed, the male began to push the branching points with his snout, in front of the female. Subsequently, the female began to push the branching points with her snout, investigating one after the other, while the territorial male quivered his body beside her. At that time, the males following the female, in addition to some males following a second female, gathered around the courting pair.

During the courtship, the territorial male often attacked the non-territorial males following the female. The territorial males were more brightly coloured but not always larger than the non-territorial ones.

Although such courtship sequence were observed more than 20 times, actual spawning was not seen. The gravid female often left the male's territory, at any phase of the courtship behaviour, and either returned to the same territory or visited another one repeatedly, before finally returning to the original school without spawning.

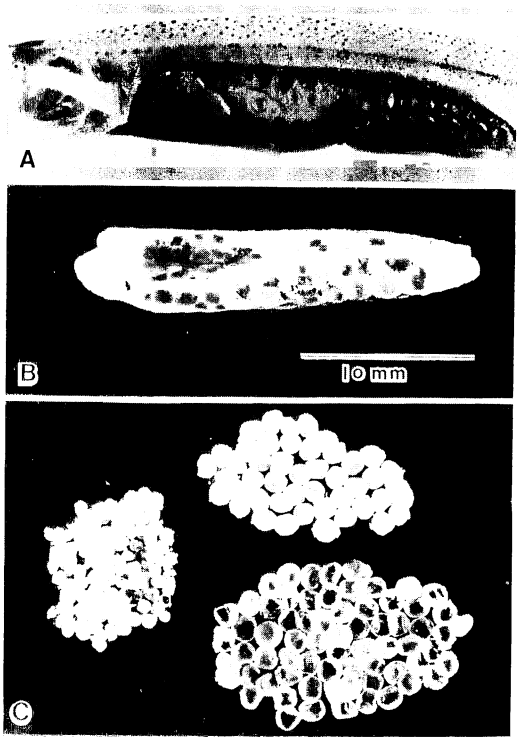

Fig. 1. Ovary of *Hypoptychus dybowskii*, 62.3 mm SL, collected on June 22, 1989 in Otsuchi Bay. A) Lateral view of female; B) lateral view of ovary removed from body cavity; C) three groups of eggs in size removed from ovary.

Reproductive behaviour in the aquarium

Establishment of territories.—For a few hours after being moved from the holding tank to the observation aquarium, all individuals schooled exhibiting similar, faintly yellow colouration. One of the males suddenly changed its body colour, simultaneously leaving the school to establish a territory around the planted sargasso. The territorial male changed to a bright yellow body colouration with deep black dorsal and anal fins, gill membranes, lower jaw tip and head. It swam very quickly and soon began attacking individuals passing nearby, by chasing and picking. During this excited condition, the male often spread its deep black gill membranes downward. Among 17 territorial males observed, the most intensively coloured male occupied about half

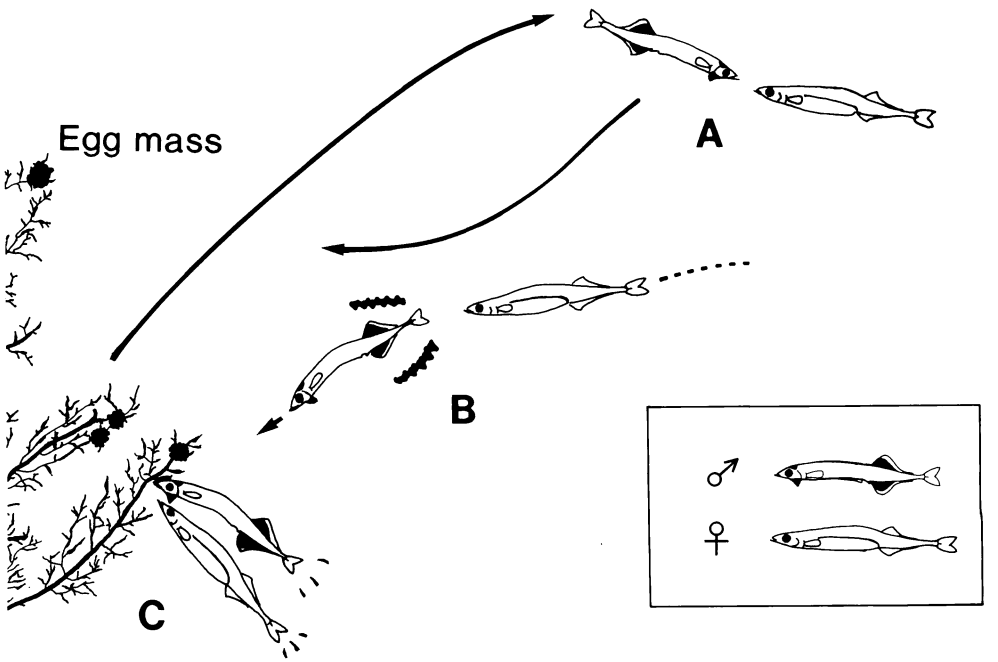

Fig. 2. Courtship behaviour in *Hypoptychus dybowskii.* A) Rush and return; B) quivering; C) pushing weeds.

of the aquarium (about 80cm in diameter at maximum), while less intensively coloured males had smaller territories. When the body colouration of the territorial male gradually faded, its territory became smaller, finally reaching about 30cm in diameter.

Prespawning behaviour.—Within a few minutes of the establishment of a territory by a male, one to several females approached it. These females never interfered with each other.

The territorial male immediately began to court the approaching gravid female, as observed in the field. When several females approached at the same time (more than 20 cases observed), the male repeated the courtship display almost equally toward each, suggesting no evidence of female selection by the male. The females did not leave the territory, even when the territorial male was courting another female.

When the gravid female(s) approached the territorial male, several (usually 3–5) non-territorial males also left the school to follow the former (more than 100 cases observed). They were often attacked by the territorial male and fled a short distance before quickly returned to follow the female again. Especially just before spawning, a greater number of non-territorial males gathered around the female. Accordingly, the territorial male was unable to defend the latter effectively against other males.

Spawning behaviour.—Spawning occured after careful examination, for up to one hour, of many branching points of the sargasso weed. The female oviposited by scraping her abdomen against the branching point or winding her body around it. The egg mass subsequently remained attached to the branching point. When several females were courted, it was not always the largest female that spawned, and on one occasion two females spawned in turn.

The territorial male and other gathering males (usually 5–20) rushed to the egg mass immediately after the female's departure. The territorial male, usually having been situated nearest to the female, was the first male to reach the egg mass. Fertilization might have occurred at that time, but was not confirmed. In each case of the 23 spawnings observed, several (usually 5–10) non-territorial males participated in addition to the territory owner.

Postspawning behaviour.—Females never returned to the egg mass after spawning. The territorial male, however, always remained with the egg mass, picking at it frequently with his snout for about half an hour. By such picking behaviour the egg mass gradually became tight and ball-shaped, which seemed to prevent it from becoming detached from the sargasso

weed. Some of the attendant, non-territorial males tried to approach the egg mass, but were driven away by the territorial male. Afterwards, paternal care such as fanning and guarding of eggs was not conducted by the territorial male, although occasional picking at the eggs occurred. It took more than seven days for eggs to hatch at 13–14°C.

Abandonment and take-over of the territory.—After several spawnings over a few hours or more, the territorial male abandoned the territory, its body colouration fading to that of the non-territorial males, with which the former then merged. The territory was abandoned before egg hatching.

Take-over of a territory was observed three times. When the body colouration of a schooling male suddenly intensified, more so than the initial territorial male, the former attacked the latter and took over the territory. The defeated male's colouration faded instantly, the fish fleeing into the school. The body size of the second male was a little larger or similar to that of the initial male (two of three cases) but smaller by more than 5 mm in the third instance.

Two territories were established concurrently in two cases when the second male's colouration was not so intense compared with the first territorial male. The body size of the two males differed by more than 3 mm.

Body size and GSI of males.—The standard length of males (55.2±3.0 mm, $n=157$) was significantly shorter than that of females (58.1±4.9 mm, $n=111$) ($t=5.92$, $p<0.01$) in those fishes used for aquarium observations, with the removal of territorial males (Fig. 3). Nine out of 157 males established territories. The territorial males (55.0±1.6 mm SL, 0.67±0.12 g BW, $n=9$) were not significantly larger than the remaining non-territorial males (55.2±3.1 mm SL, $n=148$ and 0.71±0.14 g BW, $n=89$) ($U=734$, $|z|=0.51$, $p>0.1$ for SL and $U=370$, $|z|=0.38$, $p>0.1$ for BW). GSI was also similer, mostly 1–2, in both the territorial (1.30±0.27, $n=9$) and non-territorial males (1.34±0.80, $n=89$) ($U=325$, $|z|=0.93$, $p>0.1$). No significant correlation was found between GSI and SL in males ($r=0.09$, $p>0.1$, $n=98$).

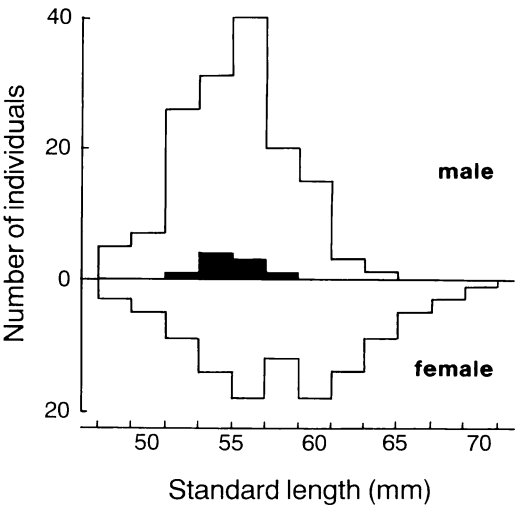

Fig. 3. Size-frequency distribution of *Hypoptychus dybowskii* used for aquarium observation. Number of individuals in each 2 mm size class is given for non-territorial males, territorial males (solid bars), and females.

Discussion

Courtship, paternal care and alternative male mating tactics.—The courtship behaviour of territorial males in *Hypoptychus dybowskii* consisted of three phases: "dash and return," "quivering" and "pushing weeds." The first phase may inform the gravid female of the existence of the territorial male and location of his territory. The second phase seems to tempt her to the spawning site in the centre of the territory and the third phase to recommend to her several branching points of the sargasso weed as potential spawning sites. The sequential pattern of courtship behaviour of the male corresponding to the reaction of the female was in keeping with the reaction chain model of Tinbergen (1961), though it was simpler than those of the gasterosteids (Wootton, 1976, 1984; McLennan et al., 1988).

After spawning, territorial males of *H. dybowskii* picked at the eggs so as to arrange them into a tight, ball-shaped mass, whitch was difficult to detach from the sargasso weed. Thus the picking behaviour can be regarded as paternal care, although it was conducted frequently for only about 30 min and only occasionally thereafter. The males never undertook additional parental care, such as guarding and fanning, which usually continues for several days until and post-hatching in gasterosteids (Wootton, 1976).

Non-territorial males from schools also participated in spawning by following the gravid female and rushing to the spawning site. They never undertook paternal care. Such alternative male mating tactics or strategies have been reported in many fishes, in most

of which territorial males were larger than non-territorial ones (Warner and Hoffman, 1980; Gross, 1984). In addition, non-territorial (sneaking or group spawning) males often have relatively larger testes than territorial males (Warner et al., 1975; Kazakov, 1981). In *H. dybowskii*, however, territorial and non-territorial males did not differ in body size and GSI, only in colouration. Non-territorial, schooling males suddenly became territorial by intensifying their colouration, such colour subsequently fading when the territory was departed for the school. This strongly suggests that a male can repeatedly alternate its mating tactics by changing its colouration, making it very unlikely that the two mating tactics correspond to two different life-history strategies or are adopted depending on age as a conditional strategy (Howard, 1978; Maynard Smith, 1982; Gross, 1984).

The costs and benefits of territorial mating, compared with non-territorial, in *H. dybowskii* were not measured in the present study, but several possibilities can be suggested. Territorial males seem to have fertilized more eggs than each of the non-territorial males participating in each spawning, since the former was situated nearest to the spawning site and was the first of all the males in the rush to fertilize the egg. Exhibition of parental care only by the territorial males may also suggest their higher probability of paternity. Although the difference in reproductive success per unit time between the two mating tactics was not measured, territorial males may have higher reproductive success, since females spawned only within the male territories and territorial males were in the minority in the male population. On the other hand, territorial males may suffer higher predation risk and energetic costs than non-territorial ones; one of the territorial males was attacked and eaten by a scorpaenid fish during the field observation, and territorial males swam more rapidly and showed higher aggressiveness than schooling males.

At present two possibilities can be suggested. If the two mating tactics have equal fitness, they may constitute a frequency-dependent mixed strategy (Brockmann et al., 1979; Maynard Smith, 1982; Gross 1984). Alternatively, if higher fitness results from territorial mating, males may adopt each of the two tactics depending on their physiological conditions, non-territorial mating being a subordinate tactic to make the best of a bad situation (BBS) (Maynard Smith, 1982; Gross, 1984).

Sexual differences in body size and nuptial colouration.—Female *H. dybowskii* grew larger than males. In most fishes large size is favored in male-male territorial competition (Warner and Hoffman, 1980; Gross, 1984). In *H. dybowskii*, however, territorial males were not always larger than other males. Even though large size is favoured in territorial defence, male *H. dybowskii*, irrespective of body size, may be unable to maintain territories for a long time because the costs involved seem to be very high, as already mentioned. On the other hand, larger females may be preferred by males if they have greater fecundity. However, the number of large, translucent eggs in the ovary was not correlated with female body size in *H. dybowskii*. When two or more gravid females approached territories, territorial males courted with them one after another, and no evidence of male choice of larger females was found.

The intensity of nuptial colouration is said to indicate the behavioural vigour of males (Rowland, 1984; McLennan and McPhail, 1989). Such association between colour and behaviour has been interpreted as an advertising mechanism (Kodric-Brown and Brown, 1984). In *H. dybowskii*, the yellow body and black nuptial colouration of territorial males are remarkably bright and intense in comparison with those of non-territorial males and females. More intensely coloured males had wider territories, and sometimes a more intensely coloured male took over the territory of one less intense. Thus the intense nuptial colouration of male *H. dybowskii* also seems to be associated with behavioural vigour, and appears to have developed as a signal to inform females and males of the male's condition, as well as to entice females to approach the territorial male for spawning. Female *H. dybowskii* visited several territorial males before spawning, but it was not confirmed in the present study whether or not they choose the more intensely coloured males.

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シワイカナゴ雄の代替繁殖戦術：なわばり行動，体長，婚姻色

赤川　泉・沖山宗雄

岩手県大槌湾での潜水調査及び水槽飼育で，シワイカナゴ（トゲウオ目）の繁殖行動を観察した．本種は雌雄ともに周年にわたり湾内で群をなすが，繁殖期の雄には，群を離れてホンダワラ類の周辺にテリトリーを形成する婚姻色の鮮明な雄（テリトリー雄）と，群に留まる色のうすい雄（群れ雄）の2タイプが観察された．腹部の膨満した雌が群を離れテリトリーに接近すると，3-5尾の群れ雄がこれを追尾し，テリトリー雄は，雌の接近に応じて3段階の求愛行動と，追尾する雄への攻撃を行なった．卵はテリトリー内のホンダワラ類の枝の分岐点に産みつけられ，一卵塊は，直径約2mmの卵を平均32個含んでいた．産卵直後，十尾程の雄が放精しようと卵に殺到したが，最も近い位置を占めたテリトリー雄が最も早かった．テリトリー雄は産卵後約30分ほど頻繁に吻で卵塊をつつき球状に固め，その後もときどき卵塊をつついたが，その他の卵保護行動は観察されなかった．テリトリーを形成したのは必ずしも大きな雄ではなかったことと，テリトリーの形成と放棄に際して，例外なく急激な体色変化が認められたことから，本種の雄は，その時々の生理的条件に応じて，あるいは，テリトリー雄の出現数の頻度に依存する混合戦略として，「テリトリー雄になるか」「群れ雄でいるか」の二つの繁殖戦術を使い分けていると推察された．

（〒164 東京都中野区南台 1-15-1 東京大学海洋研究所）