

Filial cannibalism in a paternal mouthbrooding fish in relation to mate availability

NOBORU OKUDA & YASUNOBU YANAGISAWA

Department of Biology, Ehime University

(Received 31 July 1995; initial acceptance 12 October 1995;
final acceptance 17 November 1995; MS. number: 4994)

Abstract. Cannibalism of the entire brood by mouthbrooding males was observed in the cardinal fish, *Apogon doederleini*, in warm temperate waters of southern Japan. This filial cannibalism always occurred within a day of spawning. Males preferentially ate broods produced by females smaller than themselves and by non-resident females, and always changed mates after cannibalism. Cannibalistic males re-mated more quickly than males whose broods were experimentally removed. These results indicate that cannibalistic males take advantage of multiple mate availability, by eating the first brood and rearing the second. It is suggested that filial cannibalism in this fish is associated with mating strategies of females that can shorten inter-spawning intervals by changing mates.

© 1996 The Association for the Study of Animal Behaviour

Filial cannibalism, the eating of offspring by parents, is well known in teleost fish, especially paternal species (reviewed by Dominey & Blumer 1984). In general, males make a large parental effort but a smaller gametic investment than females. They may parasitize the production of females by consuming their zygotes to offset the cost of parental care.

Filial cannibalism is categorized into partial and entire brood cannibalism. Rohwer (1978) suggested that partial brood cannibalism would give a parent the energy to care for the remaining brood and to keep in good physical condition. Theoretically, if partial brood cannibalism represents an investment in the remainder of the current brood, the incidence of partial brood cannibalism will increase with brood size (Sargent 1992). In contrast, entire brood cannibalism is more likely when broods are small (Ochi 1985; Petersen & Marchetti 1989; Petersen 1990). When the return from a small current brood does not exceed the cost of parental care, the parent will stop providing care and may even eat its entire brood (Rohwer 1978; Dominey & Blumer 1984). By cannibalizing the brood, the parent may

re-allocate its time and energy to the future brood cycle.

The reproductive loss entailed by entire brood cannibalism is compensated effectively if the parent re-mates quickly. The likelihood of entire brood cannibalism will increase as the opportunity for re-mating increases, and mate availability may be an important factor in determining whether to cannibalize the brood. However, no studies have examined the incidence of filial cannibalism in relation to mate availability; most reports on filial cannibalism are based on circumstantial evidence from the analysis of stomach contents (but see Hoelzer 1988; Petersen & Marchetti 1989).

The marine cardinal fish, *Apogon doederleini*, is a paternal mouthbrooder. Males fast during the mouthbrooding periods which can amount to 80% of the entire breeding season (May–October; Okuda & Yanagisawa 1996). They cannibalize entire broods more frequently in the late breeding season when their physical condition deteriorates. Deterioration of male physical condition may be an important factor in the incidence of filial cannibalism (Okuda & Yanagisawa 1996), as also suggested in some other fish species (Rohwer 1978; DeMartini 1987; Marconato & Bisazza 1988; Petersen & Marchetti 1989; Petersen 1990; Belles-Isles & FitzGerald 1991). However, in *A. doederleini* several males estimated to be in

Correspondence: Y. Yanagisawa, Department of Biology, Ehime University, 2-5 Bunkyo-cho, Matsuyama, Ehime 790, Japan. N. Okuda is now at the Center for Ecological Research, Kyoto University, Otsu 520-01, Japan.

good physical condition also cannibalized their entire brood (Okuda & Yanagisawa 1996). Multiple mate availability for a male may be a factor promoting entire brood cannibalism.

In this study, we confirmed the occurrence of cannibalism by extracting some of the stomach contents from live fish using a syringe. This non-destructive method enabled us to obtain information on their mating and cannibalistic experiences throughout the breeding season. We conducted field observations and experiments to investigate how filial cannibalism by male *A. doederleini* is related to mate availability.

METHODS

Subject Animal

Apogon doederleini inhabits shallow waters of the west Pacific. Both males and females use rock crevices, caves and nooks as sheltering and spawning sites (Kuwamura 1985). A pair forms a few days before spawning, and courtship consists of intermittent displays of parallel-circling. A cohesive egg mass 2–3 cm in diameter is pushed out from the female's cloaca when the fish take a parallel position after parallel-circling (Kuwamura 1985). Within a few seconds, the egg mass is taken into the male's mouth from the body of his mate. The male rears only one brood in each breeding cycle, and mouthbrooding continues for 5–17 days until hatching, depending on water temperature (Okuda & Yanagisawa 1996). During a breeding season, males and females spawn 5–10 and 4–9 broods, respectively.

Field Observation

We studied the fish on a quadrat of 10 × 20 m on the boulder slope at Murote Beach, Shikoku Island, Japan. At the beginning of the breeding season of 1992, we marked underwater all individuals in the quadrat, 53 males, 54 females and three individuals of unknown sex, by extracting two or three dorsal and/or anal fin rays. After measuring their standard length (SL), we released them at their capture sites. Prior to the breeding season of 1993, we re-measured 27 males and 37 females that had remained in the quadrat and marked and measured nine new residents (six males and three females).

We censused the fish on all but 5 days throughout the breeding season of 1993. In each census, which was usually made between 1100 and 1500 hours, we noted the brooding state of each male (mouthbrooding or non-brooding) and the degree of belly expansion of each female. The latter was classified into five categories by eye: stage I: belly deflated, just after spawning; stage II: belly flat as in the non-breeding season; stage III: belly in the incipient stage of inflation; stage IV: belly expanded and genital papilla not protruded; stage V: belly fully expanded and genital papillae protruded.

When we found a pair engaging in a courtship display (e.g. parallel-circling), we repeatedly visited them and noted the spawning and post-spawning behaviour. Post-spawning behaviour, consisting of frequent egg-churning by the male and parallel-circling in a pair (Kuwamura 1985), continued for up to 1 h, enabling us to identify the spawning pair. When we had observed only the courtship display of a pair but found the male mouthbrooding or potbellied (see below) next day, we judged that he had spawned with the paired female, provided her belly was deflated. If a male was mouthbrooding or potbellied but no marked female had a deflated belly, or if a female had a deflated belly but no marked male was mouthbrooding or potbellied, then we judged that he or she had spawned with an unmarked fish.

In 28 of 45 cases where the egg mass had disappeared from a male's oral cavity and he was potbellied, we captured the male with a hand net and examined his stomach contents by gently inserting a needle-less syringe through the oesophagus (see Okuda & Yanagisawa 1996). In all cases, stomach contents extracted included eggs of the same developmental stage as those the male had brooded. Therefore, we judged that such egg disappearance was due to filial cannibalism.

The sheltering site of each fish was defined as the site where we found it most frequently in daily censuses. The moving distance for each fish between the two breeding seasons was represented as the distance between its sheltering sites in September 1992 and in September 1993.

We did not census the fish over the entire breeding season in 1992, so in this paper, we use only the data from 1993 unless otherwise stated.

Field Brood Removal Experiment

For brood removal experiments, 24 males were captured and marked at a site about 10 m from the quadrat. To examine if the time interval from brood disappearance to the next spawning differs according to the causes of brood disappearance (brood cannibalism or hatching of eggs), we removed broods from these males at two different mouthbrooding phases: on the day after spawning, and 1–2 days before the expected day of hatching. Because entire brood cannibalism always occurred within a day of spawning (Okuda & Yanagisawa 1996), the former brood removal is equivalent to entire brood cannibalism in terms of timing. After the brood removal, we observed the time interval until the next spawning of these experimental males. This manipulation was performed one to six times for these males during the breeding season of 1993.

Six males were caught just after entire brood cannibalism. We compared the number of eggs in their stomachs with that of eggs in broods removed from males on the day after spawning.

RESULTS

Mating System and Spawning Cycle

Apogon doederleini showed strong site fidelity: males on average shifted only 2.1 m ($SD=2.0$, $N=19$) and females 2.6 m ($SD=4.7$, $N=28$) between the two breeding seasons. Courtship displays between marked fish usually took place near their sheltering sites ($\bar{X} \pm SD = 2.1 \pm 2.9$ m from male sheltering sites, 1.7 ± 2.0 m from female sheltering sites, $N=240$). Of 274 pairs that were observed in courtship displays, 71 broke up before spawning. The number of courtship partners per spawning was 1.35 ($SD=0.56$, $N=203$) for males and 1.28 ($SD=0.52$, $N=215$) for females. After spawning or courtship, the male and female in a pair separated to their respective sheltering sites, unless they had previously shared a single sheltering site.

Of 261 spawnings that involved marked fish, 167 occurred between two marked fish; about 70% of the pairs had their sheltering sites within 3 m (Fig. 1). Thirty-eight spawnings took place between marked males and unmarked females and 45 spawnings between marked females and unmarked males. For the remaining 11

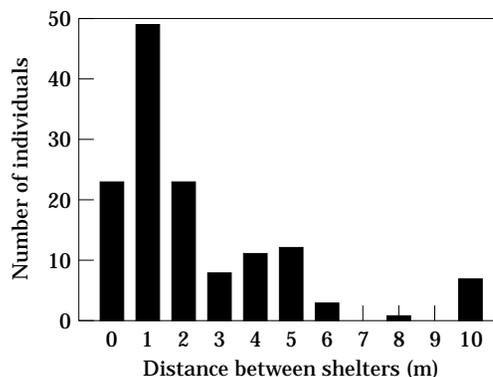


Figure 1. The distance between sheltering sites of a male and female in a spawning pair ($N=138$). Sheltering sites in March 1993 were used.

spawnings, we were unable to determine whether a marked fish mated with other marked fish or with an unmarked fish.

Spawnings between marked and unmarked fish were frequently preceded by a migration of females. We sometimes saw unmarked females whose bellies were expanded wandering about in the quadrat while courting with males in succession. Conversely, census data showed that marked females with expanded bellies occasionally left the quadrat. Their disappearance rate [(the total number of absences)/(the total number of censuses)] (285/3106) was significantly higher than that of marked males (178/2741; $\chi^2=14.4$, $df=1$, $P<0.001$). The absent females usually returned to their original sites after 1 (74.7%), 2 (10.8%) or 3 (5.7%) days. Some of these females (10.8%) had deflated bellies when they returned, indicating that they had spawned outside the quadrat.

During a breeding season, a male on average accepted 6.77 broods ($SD=1.31$, $N=30$) and mated with 3.50 different females ($SD=0.92$) and a female produced 6.29 broods ($SD=1.16$, $N=31$) and mated with 3.42 different males ($SD=1.35$). The mate change rate per spawning did not differ between the sexes (68.2% for males and 69.1% for females, $\chi^2=0.03$, $df=1$, $P>0.8$). The inter-spawning interval of females was shorter when they had changed their mates, but that of males was not (Table I).

When only male spawnings that resulted in hatching of eggs were considered, the inter-spawning interval of males was 15.2 days

Table I. The inter-spawning interval of males and females that did or did not change mates

Sex	Inter-spawning interval (days)				<i>t</i>	<i>df</i>	<i>P</i>
	Mate change		No mate change				
	<i>N</i>	$\bar{X} \pm \text{SD}$	<i>N</i>	$\bar{X} \pm \text{SD}$			
Female	112	14.1 ± 4.19	50	16.2 ± 3.41	-3.17	160	0.002
Male	84	15.5 ± 3.27	49	15.7 ± 3.00	-0.36	131	0.72

Spawnings that were followed by entire brood cannibalism are excluded from the data of males.

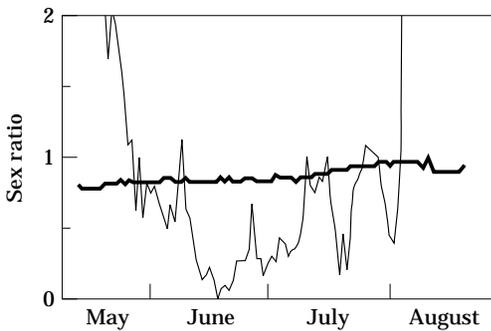


Figure 2. Fluctuation of the adult sex ratio (thick line; males:females) and the operational sex ratio (thin line; receptive males:receptive females) in the quadrat in the breeding season.

($\text{SD}=3.03$, $N=141$), and that of females was 14.8 days ($\text{SD}=4.06$, $N=178$). The frequency distribution of inter-spawning intervals throughout the breeding season did not differ between the sexes (Kolmogorov-Smirnov two-sample test: $P>0.2$). However, in the middle of the breeding season when the operational sex ratio was most female-biased (see Fig. 2), the interval was more variable in females (Table II). Since the inter-spawning interval of males includes the mouthbrooding period of 5–17 days, very short intervals were recorded only in females: the shortest interval for males was 9 days, whereas intervals of less than 9 days were recorded in 12 females.

The sex ratio (males:females) of the adult population was nearly constant throughout the breeding season, ranging from 0.78 to 1.00 (Fig. 2). Within the quadrat, females at stage III sometimes spawned by the next census (34 cases) but females at stage II never spawned. Therefore, to estimate the operational sex ratio (the ratio of receptive males to receptive females), we defined

receptive females as individuals whose belly expansion was at stages III–V, and sexually receptive males as individuals that were not mouthbrooding. In contrast to the sex ratio in the population, the operational sex ratio fluctuated greatly and it was usually female biased except at the beginning and end of the breeding season, when only some of the females had mature ovaries and most males were not mouthbrooding.

Filial Cannibalism and Re-spawning

Of 209 broods observed, 32 were cannibalized by the mouthbrooding males. Sixty per cent of males (18/30) practised filial cannibalism at least once during the breeding season: eight males once, six twice and four three times. Of 32 males that cannibalized broods, 30 re-spawned within the breeding season. In all cases where their mates could be identified ($N=28$), they re-mated with different females. This rate of mate change was significantly higher than that shown by males whose broods hatched ($57/100$; $\chi^2=16.3$, $df=1$, $P<0.0001$).

The cannibalistic males on average re-spawned 3.1 days after cannibalism (Table III). They re-spawned as quickly as males whose broods hatched (Mann-Whitney *U*-test: $z=-1.76$, $N_1=32$, $N_2=144$, $P>0.07$). When the broods were experimentally removed on the day after spawning, males on average took 7.6 days to re-spawn, longer than cannibalistic males ($z=-2.84$, $N_1=7$, $N_2=32$, $P<0.005$). When broods were removed 1–2 days before hatching, the time taken for males to re-spawn did not differ from that of males whose broods hatched ($z=-1.36$, $N_1=47$, $N_2=144$, $P>0.1$).

Cannibalistic males did not court more females before spawning ($\bar{X} \pm \text{SD}=1.23 \pm 0.43$, $N=30$)

Table II. Inter-spawning interval of males and females in three periods of the breeding season

Breeding season	Date	Mean water temperature (°C) (Min–Max)	Inter-spawning interval (days)					<i>z</i> *	<i>P</i>
			Male		Female				
			$\bar{X} \pm SD$ (Min–Max)	<i>N</i>	$\bar{X} \pm SD$ (Min–Max)	<i>N</i>			
Early	16 May–19 June	19.5 (18.3–21.3)	35	15.9 ± 1.82 (13–22)	37	17.0 ± 2.10 (11–21)	1.65	0.10	
Middle	20 June–24 July	19.6 (18.0–22.0)	58	16.8 ± 1.67 (12–22)	77	14.5 ± 3.34 (6–30)	3.09	0.002	
Late	25 July–28 August	24.3 (19.0–25.7)	48	12.7 ± 3.42 (9–24)	64	13.8 ± 5.13 (4–31)	0.98	0.33	

*Kolmogorov–Smirnov two-sample test.

Table III. The effect of different causes of brood disappearance on the time to re-spawn in males

Group	Cause of brood disappearance	<i>N</i>	Time to re-spawn after brood disappearance (days)	
			\bar{X}	SD
Natural	Cannibalism	32	3.13	2.99
	Hatching	144	3.53	2.53
Experimental	Removal on the day after spawning	7	7.57	5.26
	Removal 1–2 days before hatching	47	4.36	3.56

than non-cannibalistic males (1.36 ± 0.57 , $N=171$; $t = -1.13$, $df=199$, $P>0.2$). The time from the first courtship to spawning also did not differ between cannibalistic males ($\bar{X} \pm SD = 1.0 \pm 1.79$ days, $N=30$) and non-cannibalistic males (1.1 ± 1.62 days, $N=171$; $t = -0.41$, $df=199$, $P>0.6$).

Of 219 broods produced by marked females, 23 were cannibalized by their mates. Of these 23 broods, eight were the last ones produced by the females in the breeding season. The re-spawning rate of these females (15/23) was significantly lower than that of cannibalistic males (28/30; $\chi^2 = 7.32$, $df=1$, $P<0.007$). The inter-spawning interval of these females ($\bar{X} \pm SD = 15.7 \pm 5.01$ days, $N=15$) was as long as that of females whose broods hatched (14.7 ± 3.93 days, $N=159$; $t=0.86$, $df=172$, $P>0.3$).

Filial Cannibalism and Mate Choice

Females whose broods were cannibalized at least once ($\bar{X} \pm SD = 86.4 \pm 5.47$ mm SL, $N=18$) were as large as females whose broods were

never cannibalized (87.3 ± 2.99 mm, $N=20$; $t = -0.65$, $df=36$, $P>0.5$). Cannibalistic males (85.1 ± 4.88 mm, $N=18$) were as large as males who never cannibalized their broods (84.4 ± 2.68 mm, $N=12$; $t=0.48$, $df=28$, $P>0.6$). The size-difference ($SL_{\text{male}} - SL_{\text{female}}$) in spawning pairs was significantly greater where cannibalism occurred in 1992 but not in 1993 (Table IV). In 1993, females were usually larger than their mates owing to a higher mortality rate of adult males in the previous year (unpublished data).

The cannibalism rate of males was higher when they spawned with unmarked (10/38) than with marked females (21/167; $\chi^2 = 4.55$, $df=1$, $P<0.05$). In spawnings of females with unmarked males ($N=45$), few data are available on whether the males cannibalized their broods, because we were rarely able to locate them in successive censuses.

The number of eggs in a cannibalized brood ($\bar{X} \pm SD = 10\,464 \pm 1753$, $N=6$) did not differ from that of an early stage brood that was mouth-brooded ($10\,365 \pm 1641$, $N=12$; $t=0.12$, $df=16$, $P>0.9$).

Table IV. The size difference (mm; standard length of male minus female) within spawning pairs in which cannibalism did or did not occur

Year	Cannibalism		No cannibalism		<i>t</i>	<i>df</i>	<i>P</i>
	<i>N</i>	$\bar{X} \pm \text{SD}$	<i>N</i>	$\bar{X} \pm \text{SD}$			
1992	10	2.05 ± 2.76	112	-0.86 ± 3.80	2.36	120	0.02
1993	22	-0.57 ± 4.62	149	-2.04 ± 3.38	1.81	169	0.07

DISCUSSION

Filial Cannibalism and Mate Availability

In the present study, cannibalistic males re-spawned within a few days of cannibalism, whereas males whose broods were experimentally removed to coincide with the timing of brood cannibalism took longer to re-spawn. The delay of re-spawning in the latter cannot be attributed to the effects of brood removal, because males whose broods were removed just before hatching re-spawned as quickly as males whose broods hatched. Moreover, cannibalistic males always changed mates after cannibalism. From these results we suggest that males took advantage of multiple mate availability and ate the brood in expectation of quick re-spawning.

The opportunity for males to assess potential mate availability may occur during the pre-spawning phase, when they sometimes court with more than one female. Although the number of females courted before spawning did not differ between cannibalistic and non-cannibalistic males, this does not necessarily mean that actual mate availability did not differ between them. Because a bout of courtship behaviour is often short and intermittently repeated (Kuwamura 1985; personal observation), it is difficult to estimate accurately the number of available mates.

Males were more cannibalistic when they spawned with smaller females, but the absolute female size was not important in cannibalism. Several other studies on filial cannibalism have reported that cannibals preferentially eat small broods (Ochi 1985; Petersen & Marchetti 1989; Petersen 1990), and filial cannibalism has also been induced by experimentally reducing brood size (Mrowka 1987; Petersen & Marchetti 1989; Lavery & Keenleyside 1990). A parent may abandon the entire brood when its reproductive return does not offset the cost of providing care. In

A. doederleini, in contrast, the brood sizes of cannibalized and successfully mouthbrooded broods did not differ. Brood size relative to the male's buccal cavity, rather than absolute brood size, may be one criterion for cannibalism.

Males were also more cannibalistic when they spawned with unmarked females that visited from outside the quadrat. Although female counter-measures against cannibalism have not been investigated in detail, we occasionally observed females whose broods had been cannibalized attacking the cannibalistic males, suggesting that females can discern cannibalistic males and avoid re-mating with them. If this is so, it would be advantageous for males to eat broods produced by non-resident females, which return to their sites after spawning and are thus unaware of the subsequent cannibalism of their eggs.

Sexual Conflicts in Reproduction

Besides the family Apogonidae, nine teleost families have species in which the male alone orally broods or carries the eggs externally (Blumer 1979). This form of parental care apparently limits the bearing capacity and restricts the potential for polygamy. Thereby, a male may bear eggs from only one female at a time and a female may give her entire clutch to one male (but see Berglund et al. 1988). The majority of the apogonid fish for which data are available have such a monogamous mating pattern (Kuwamura 1983, 1985, 1986; personal observation; but see Fishelson 1970). This pattern is also shared by some species of pipefish and seahorses (Vincent et al. 1992). Nevertheless, a monogamous pair is rarely maintained throughout the breeding season, except for *Hippocampus* seahorses (Vincent & Sadler 1995) and *Corythoichthys* pipefish (Gronell 1984); more often, both sexes change mates during the breeding season if the

opportunities arise (Kuwamura 1985; Berglund et al. 1989).

The trend to polygamy may be due to a sexual difference in the potential rate of reproduction (the maximum number of offspring that each sex can produce per unit time; see Clutton-Brock & Vincent 1991). Because of a limited brooding capacity and lengthy care period, a female of a paternal caring species generally produces more eggs than a male can brood. For example, an average female pipefish, *Nerophis ophidion*, produces eggs to fill 1.8 males within the duration of one male pregnancy (Berglund et al. 1989). In *A. doederleini*, females shortened their inter-spawning intervals by changing mates, but males did not (Table I), suggesting a higher potential reproductive rate in the female. This means that females, but not males, could enjoy greater reproductive success through polygamous matings.

In pipefish, a higher potential reproductive rate of females is linked with a suite of reproductive features (Vincent et al. 1992): (1) the operational sex ratio is female biased; (2) females are the predominant competitors for mates; and (3) females are more modified by sexual selection. Animals with these features are traditionally regarded as sex-role reversed (Williams 1975; Vincent et al. 1992; Rosenqvist 1993). Our finding suggests that the former two features are shared by *A. doederleini*: the operational sex ratio was female biased almost throughout the breeding season, females more frequently moved to search for mates and agonistic encounters were more frequent between females (unpublished data). The third feature is unclear in *A. doederleini*: no clear sexual dimorphism or dichromatism can be detected.

If the operational sex ratio is biased towards females, males have an opportunity to be selective in mating (Berglund et al. 1986; Rosenqvist 1990). This situation must be a prerequisite to the occurrence of filial cannibalism by male *A. doederleini*. If two females are simultaneously available to a male, he profits more by eating the first brood and rearing the second than by merely choosing one of the two potential mates and rearing one brood. Thus filial cannibalism of this fish may be a consequence of sexual conflicts: females can benefit from polygamous matings, whereas males can compensate for the costs of brooding by exploiting multiple mate availability.

ACKNOWLEDGMENTS

We are grateful to A. Rossiter for helpful comments on the manuscript. This study was supported by Japanese Ministry of Education, Science and Culture Grant-in-Aid for Scientific Research on Priority Areas (319).

REFERENCES

- Belles-Isles, J.-C. & FitzGerald, G. J. 1991. Filial cannibalism in sticklebacks: a reproductive management strategy? *Ethol. Ecol. Evol.*, **3**, 49–62.
- Berglund, A., Rosenqvist, G. & Svensson, I. 1986. Mate choice, fecundity and sexual dimorphism in two pipefish species (Syngnathidae). *Behav. Ecol. Sociobiol.*, **19**, 301–307.
- Berglund, A., Rosenqvist, G. & Svensson, I. 1988. Multiple matings and paternal brood care in the pipefish *Syngnathus typhle*. *Oikos*, **51**, 184–188.
- Berglund, A., Rosenqvist, G. & Svensson, I. 1989. Reproductive success of females limited by males in two pipefish species. *Am. Nat.*, **133**, 506–516.
- Blumer, L. S. 1979. Male parental care in the bony fishes. *Q. Rev. Biol.*, **54**, 149–161.
- Clutton-Brock, T. H. & Vincent, A. C. J. 1991. Sexual selection and the potential reproductive rates of males and females. *Nature, Lond.*, **351**, 58–60.
- DeMartini, E. E. 1987. Paternal defence, cannibalism and polygamy: factors influencing the reproductive success of painted greenling (Pisces, Hexagrammidae). *Anim. Behav.*, **35**, 1145–1158.
- Dominey, W. J. & Blumer, L. S. 1984. Cannibalism of early life stages in fishes. In: *Infanticide: Comparative and Evolutionary Perspectives* (Ed. by G. Hausfater & S. B. Hrdy), pp. 43–64. New York: Aldine Press.
- Fishelson, L. 1970. Spawning behavior of the cardinal fish, *Cheilodipterus lineatus*, in Eilat (Gulf of Aqaba, Red Sea). *Copeia*, **2**, 370–371.
- Gronell, A. M. 1984. Courtship, spawning and social organization of the pipefish, *Corythoichthys intestinalis* (Pisces: Syngnathidae) with notes on two congeneric species. *Z. Tierpsychol.*, **65**, 1–24.
- Hoelzer, G. 1988. Filial cannibalism in a non-brood cycling marine fish. *Environ. Biol. Fish.*, **21**, 309–313.
- Kuwamura, T. 1983. Spawning behavior and timing of fertilization in the mouthbrooding cardinalfish *Apogon notatus*. *Jap. J. Ichthyol.*, **30**, 61–71.
- Kuwamura, T. 1985. Social and reproductive behavior of three mouthbrooding cardinalfishes, *Apogon doederleini*, *A. niger* and *A. notatus*. *Environ. Biol. Fish.*, **13**, 17–24.
- Kuwamura, T. 1986. Night spawning and paternal mouthbrooding of the cardinalfish *Cheilodipterus quinquelineatus*. *Jap. J. Ichthyol.*, **33**, 431–434.
- Lavery, R. J. & Keenleyside, M. H. A. 1990. Filial cannibalism in the biparental fish *Cichlasoma nigrofasciatum* (Pisces: Cichlidae) in response to early brood reductions. *Ethology*, **86**, 326–338.

- Marconato, A. & Bisazza, A. 1988. Mate choice, egg cannibalism and reproductive success in the river bullhead, *Cottus gobio* L. *J. Fish Biol.*, **33**, 905–916.
- Mrowka, W. 1987. Filial cannibalism and reproductive success in the maternal mouthbrooding cichlid fish *Pseudocrenilabrus multicolor*. *Behav. Ecol. Sociobiol.*, **21**, 257–265.
- Ochi, H. 1985. Termination of paternal care due to small clutch size in the temperate damselfish, *Chromis notata*. *Environ. Biol. Fish.*, **12**, 155–160.
- Okuda, N. & Yanagisawa, Y. 1996. Filial cannibalism by mouthbrooding males of the cardinal fish, *Apogon doederleini*, in relation to their physical condition. *Environ. Biol. Fish.* **45**, 397–404.
- Petersen, C. W. 1990. The occurrence and dynamics of clutch loss and filial cannibalism in two Caribbean damselfishes. *J. exp. mar. Biol. Ecol.*, **135**, 117–133.
- Petersen, C. W. & Marchetti, K. 1989. Filial cannibalism in the cortex damselfish *Stegastes rectifraenum*. *Evolution*, **43**, 158–168.
- Rohwer, S. 1978. Parent cannibalism of offspring and egg raiding as a courtship strategy. *Am. Nat.*, **112**, 429–440.
- Rosenqvist, G. 1990. Male mate choice and female–female competition for mates in the pipefish *Nerophis ophidion*. *Anim. Behav.*, **39**, 1110–1115.
- Rosenqvist, G. 1993. Sex role reversal in a pipefish. In: *Behavioural Ecology of Fishes* (Ed. by F. A. Huntingford & P. Torricelli), pp. 219–230. Chur, Switzerland: Harwood Academic Publishers.
- Sargent, R. C. 1992. Ecology of filial cannibalism in fish: theoretical perspectives. In: *Cannibalism: Ecology and Evolution among Diverse Taxa* (Ed. by M. A. Elgar & B. J. Crespi), pp. 38–62. Oxford: Oxford University Press.
- Vincent, A. C. J. & Sadler, L. M. 1995. Faithful pair bonds in wild seahorses, *Hippocampus whitei*. *Anim. Behav.*, **50**, 1557–1569.
- Vincent, A., Ahnesjö, I., Berglund, A. & Rosenqvist, G. 1992. Pipefishes and seahorses: are they all sex role reversed? *Trends Ecol. Evol.*, **7**, 237–241.
- Williams, G. C. 1975. *Sex and Evolution*. Princeton: Princeton University Press.