



Seasonal pattern of filial cannibalism by *Apogon doederleini* mouthbrooding males

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In temperate waters of southern Japan, mouthbrooding males of the cardinal fish *Apogon doederleini* sometimes ate their entire brood within a day of spawning. In spite of annual variation in age structure and length of the breeding season, however, the annual cannibalism rate (broods cannibalized to total broods spawned) was nearly constant, 12–16%. Fish 1 year old frequently cannibalized early broods of the season, especially the first brood, whereas the cannibalism rate by 2 year-old fish did not vary within the season. In contrast, the cannibalism by older males increased late in the season. This tendency was attributed to their different allocation patterns to growth and reproduction. For 1 year-old fish, which can enhance future reproductive success by growth and cannibalizing on early broods instead of mouthbrooding (at relatively low temperatures), this may be a tactic for investing energy in growth. For fish ≥ 3 years, which have more breeding cycles and grow little, cannibalizing late broods may be energetic compensation for their poor somatic condition. No seasonal variation of cannibalism by 2 year-old fish can be explained by their intermediate nature of growth and reproduction. Multiple mate availability is one factor facilitating the cannibalism by 2 and 3+ year-old fish whose operational sex ratio is female-biased.

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Key words: Apogonidae; paternal care; mouthbrooding; filial cannibalism; operational sex ratio.

INTRODUCTION

Brood care by males is widespread in fishes (Blumer, 1979; Sargent & Gross, 1993). Although the care may be effective in raising the survival rate of offspring, it inevitably imposes costs on the caring males, including deterioration of their physical condition and decrease in their growth and survival (van den Berghe, 1992; Marconato *et al.*, 1993; Smith & Wootton, 1995). Males of fishes generally make a smaller gametic investment than females, as in most other animal groups. They may 'parasitize' the production of females by consuming a part or the whole of their brood offsetting the care costs (Rohwer, 1978; DeMartini, 1987). Males which perform entire brood cannibalism may increase their future reproductive value by the caloric intake obtained by eating offspring and by re-allocating the time they would spend on parental care to feeding activities (Dominey & Blumer, 1984; Smith, 1992). If the benefit for future reproduction outweighs the loss of current reproduction entailed by filial cannibalism, this cannibalistic behaviour can be favoured by natural selection (Rohwer, 1978; Belles-Isles & FitzGerald, 1991; Sargent, 1992; Smith, 1992; Lindström, 2000).

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Brooding in the buccal cavity is an effective method of care in fishes to increase the reproductive success of parents (Oppenheimer, 1970). The physical condition of mouthbrooding males, however, may deteriorate more than that of males with other care behaviours, because they are precluded from feeding (Mrowka, 1984; Marconato & Bisazza, 1988). In addition, their broods are already in the buccal cavity. Consequently, mouthbrooding males may more often 'fall into a dilemma' as to whether to continue caring for the broods or to cannibalize them.

Cardinal fishes (Apogonidae) are a representative group of paternal mouthbrooders (Oppenheimer, 1970; Kuwamura, 1985). In these fishes, males alone rear the broods until hatching (Kuwamura, 1983, 1985; Okuda & Yanagisawa, 1996a, b). The life history and reproductive strategies of the cardinal fish *Apogon doederleini* Jordan & Snyder have been studied in detail in temperate waters of southern Japan (Okuda & Yanagisawa, 1996a, b; Okuda *et al.*, 1997, 1998). High site-fidelity of this fish enables mating of individual fish to be observed throughout the breeding season, and entire brood cannibalism can be detected from the male's swollen shape (Okuda & Yanagisawa, 1996a, b). Moreover, the age of individual fish is easily determined using a pattern of circuli on a scale removed underwater (Okuda & Yanagisawa, 1996a).

From field studies over two breeding seasons, Okuda *et al.* (1997) found that young males (1 and 2 years of age that were combined because of small sample size) of *A. doederleini* frequently cannibalized early broods of the season, whereas cannibalism by older males occurred mainly late in the breeding season. This age-related filial cannibalism was explained in terms of a trade-off between current and future reproduction. Young males, whose future reproductive success is enhanced by growth, can allocate more energy to growth by cannibalizing early broods. In contrast, cannibalism by older males which grow very little (Okuda *et al.*, 1998) can be a compensation for deterioration in their somatic condition that occurs as the breeding season progresses (Okuda & Yanagisawa, 1996b).

The data of two breeding seasons, however, were not enough to conclude that this age-related filial cannibalism is a regular male tactic, because reproductive ecology may vary according to annual variations in e.g. age structure and environmental conditions. Moreover, 1 and 2 year-old fish, which Okuda *et al.* (1997) categorized together as young males, may have different tactics because their growth differs (Okuda *et al.*, 1998). Consequently, a field study of the same population in two more seasons was carried out.

METHODS

Apogon doederleini is a middle-sized cardinal fish attaining up to 90 mm in standard length (L_S) and lives in shallow waters of the west Pacific. This fish is sexually monomorphic. In temperate waters of Japan, each adult has a shelter in a rock crevice or cave, staying there in the daytime (Kuwamura, 1983). After sunset it leaves the shelter to forage for benthic animals. Most fish mature 1 year after settlement. A mating pair is formed a few days before spawning. At spawning, the female of a mating pair pushes out a cohesive egg mass from her cloaca, while the pair take a parallel position and within a few seconds the male takes the whole egg mass into his mouth. The male keeps the egg

mass for 5–17 days until hatching, depending on water temperature (Okuda & Yanagisawa, 1996b). Both males and females repeat several spawnings in a breeding season (usually from May to August).

In 1996 and 1997, the same population as Okuda *et al.* (1997) studied in 1993 and 1995 at Murote Beach, Shikoku Island, Japan was investigated. The methods used were the same as in Okuda *et al.* (1997). Within a 10 × 20 m quadrat at depths of 5.8–9.0 m on the boulder slope, all *A. doederleini* were captured and given an individual mark by pulling out two or three dorsal and anal fin rays just before the onset of each breeding season. After measuring L_S (mm) and collecting a few scales for ageing, they were released at the capture sites. Throughout the breeding season, all individuals were censused in the quadrat between 1000–1400 hours, by recording the presence and absence of each fish, spawnings, egg-hatchings and entire clutch cannibalism by males (Okuda & Yanagisawa, 1996a, b; Okuda *et al.*, 1997). The degree of ‘belly expansion’ of each female was checked. This was classified into five stages by eye (Okuda & Yanagisawa, 1996a): I, belly deflated, just after spawning; II, belly flat as in the non-breeding season; III, belly in the incipient stage of inflation; IV, belly expanded and genital papilla not protruded; V, belly fully expanded and genital papillae protruded.

The fish were categorized into 1, 2 and 3+ (3–8) year-olds. The whole breeding period from the first spawning to the last hatching for each age-group was divided into three equal periods, designated as early, middle and late phases. The operational sex ratio (OSR) was represented by the ratio of cumulative number of receptive males to that of receptive females in each phase. Receptive males were all the non-mouthbrooders and receptive females were at stages III–V (Okuda & Yanagisawa, 1996a).

Just before the onset of the next breeding season, all marked fish were recaptured and L_S measured again. From the size data between two breeding seasons, the daily specific growth rate (G) was calculated for each individual as:

$$G = 100 (\ln L_{S2} - \ln L_{S1}) (t_2 - t_1)^{-1}$$

where L_{S1} and L_{S2} is standard length on the first capture date t_1 and the recapture date t_2 , respectively. Because of high site-fidelity, marked fish which disappeared from the quadrat and were not subsequently found were regarded as having died. The annual survival rate of each age-group was calculated from the number of marked fish which survived to recapture divided by all marked fish. The filial cannibalism rate was defined as the proportion of broods cannibalized to total broods spawned.

STATISTICAL ANALYSES

Normally only the data for males were analysed. Statistical tests were performed (StatView 5.0; SAS Institute Inc., 1998). Unpaired *t*-test or one-way ANOVA were used to compare the body size among years and among age-groups. *Post hoc* tests were performed with Scheffé’s *F* test. To evaluate the size relationship between spawning pairs, a simple regression was used. Kruskal–Wallis and Mann–Whitney *U* tests were used to compare growth rates, the first spawning date and the numbers of spawning among years and among age-groups. A Bonferroni adjustment was employed in the multiple comparisons by the Mann–Whitney *U*-test (Rice, 1989). Spearman’s rank correlation was used to evaluate the relationship between L_S and growth rate. Analysis of proportional difference among groups was determined by χ^2 or Fisher’s exact test. Statistical significance was set at $P < 0.05$.

RESULTS

AGE STRUCTURE, GROWTH AND SURVIVAL

The proportion of age-groups greatly varied among the 4 years (Fig. 1). A specific group was numerically dominant each year, 3+ year-olds in 1993, 1 year-olds in 1995 and 2 year-olds in 1996. The sex could not be identified for

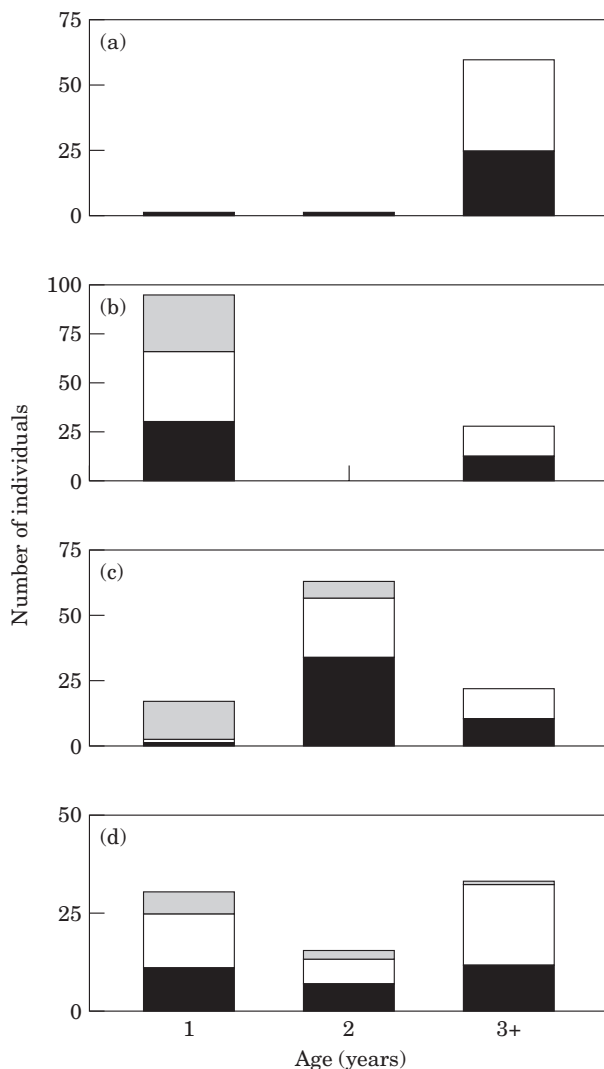


FIG. 1. Age structure of *Apogon doederleini* consisting of males (■), females (□) and unknown sex (▒) in (a) 1993, (b) 1995, (c) 1996 and (d) 1997.

37.2% of 1, 11.0% of 2 and 0.7% of 3+ year-olds because of no participation in breeding or early disappearance from the quadrat after marking. The population sex ratio of three age-groups did not significantly deviate from 1 : 1 each year ($P > 0.05$).

Body size of each male age-group usually differed between years (Table I), i.e. 1 year-olds between 1995 and 1997 ($t = 2.36$, d.f. = 38, $P < 0.05$) and 3+ year-olds (ANOVA; $F_{3,60} = 56.43$, $P < 0.0001$) between 1993 and 1995 (Scheffé's test, $P < 0.0001$), between 1993 and 1996 ($P < 0.0001$) and between 1993 and 1997 ($P < 0.0001$). When the data of 4 years were combined for each age-group, size difference was significant between 1 and 2 year-old fish (Scheffé's test, $P < 0.0001$), between 1 and 3+ year-old fish ($P < 0.0001$) and between 2 and 3+ year-old fish ($P < 0.0001$).

TABLE I. Standard length (mean \pm S.D., mm) of male *Apogon doederleini* at the beginning of each breeding season

Year	Age (years)					
	1	<i>n</i>	2	<i>n</i>	3+	<i>n</i>
1993	69	1	87	1	85 \pm 3	28
1995	69 \pm 5	27	—		90 \pm 2	13
1996	57	1	83 \pm 3	23	92 \pm 3	8
1997	63 \pm 5	13	84 \pm 2	5	91 \pm 4	16

TABLE II. Daily specific growth (mean \pm S.D.) and annual survival rates of male *Apogon doederleini*

Age (years)	1	<i>n</i>	2	<i>n</i>	3+	<i>n</i>
<i>G</i> ($\times 10^{-2}$)	5.3 \pm 1.5	21	2.0 \pm 0.5	8	0.2 \pm 0.5	25
Survival (%)	70.97	31	44.44	27	57.14	49

TABLE III. The first spawning date (mean \pm S.D., day 1=1 May) of male *Apogon doederleini*

Year	Age (years)					
	1	<i>n</i>	2	<i>n</i>	3+	<i>n</i>
1993	32	1	28	1	23 \pm 5	28
1995	38 \pm 12	27	—		21 \pm 3	12
1996	51	1	28 \pm 2	14	26 \pm 3	7
1997	27 \pm 6	11	9 \pm 3	5	6 \pm 5	14

Kruskal–Wallis test, in 1997, d.f.=2, $H=21.03$, $P<0.0001$.

The growth rate of 1 year-old fish was significantly greater than that of 2 year-old fish (Mann–Whitney *U*-test, $P<0.05$) and 3+ year-old fish ($P<0.05$), and the growth rate of 2 year-old fish greater than that of 3+ year-old fish ($P<0.05$; Table II). Among 1 year-old fish, the growth rate was correlated inversely with body size (Spearman's correlation coefficient, $r_s = -0.90$, $P<0.0001$), whereas the size-growth correlation was not significant in other age-groups. The annual survival rate did not differ among age-groups ($P>0.05$; Table II).

REPRODUCTION

The length of the breeding season varied annually, 107 days in 1993, 83 days in 1995, 81 days in 1996 and 102 days in 1997. The date of the first spawning differed significantly among age-groups in 1995 and 1997 (Table III); 1 year-old fish spawned later than other age-groups (Mann–Whitney *U*-test, in 1995:

TABLE IV. Age relationship of spawning pairs of *Apogon doederleini*

Year	Female age (years)	Male age (years)		
		1	2	3+
1993	1	2	—	0
	2	0	—	2
	3+	0	3	124
1995	1	69	—	3
	2	—	—	—
	3+	0	—	44
1996	1	1	2	2
	2	0	39	6
	3+	0	7	15
1997	1	24	0	0
	2	7	7	6
	3+	0	13	57

1 v. 3+ year-olds, $z = -4.87$, $P < 0.0001$; in 1997: 1 v. 2 year-olds, $P < 0.05$, 1 v. 3+ year-olds, $P < 0.05$). Among 1 year-old fish, the first spawning date was correlated inversely with body size (Spearman's correlation coefficient, in 1995, $r_s = -0.55$, $P < 0.05$; in 1997, $r_s = -0.69$, $P < 0.05$). One year-old males and females mated nearly exclusively with each other (Table IV), and matings of 2 and 3+ year-olds were also age-specific both in 1996 ($\chi^2 = 18.22$, d.f. = 1, $P < 0.0001$) and in 1997 ($\chi^2 = 5.68$, d.f. = 1, $P < 0.05$).

Males of 3+ years completed more breeding cycles in 1993 than in other years (Mann-Whitney U -test, 1993 v. 1995, $P < 0.05$; 1993 v. 1996, $P < 0.05$, 1993 v. 1997, $P < 0.05$; Table V), corresponding to the longer breeding season. In 1 and 2 year-old fish, breeding cycles did not differ between years ($P > 0.05$). One year-old fish had fewer cycles than older age-groups (Mann-Whitney U -test, in 1995: 1 v. 3+ year-olds, $z = -4.05$, $P < 0.0001$; in 1997, 1 v. 2 year-olds, $P < 0.05$, 1 v. 3+ year-olds, $P < 0.05$). Between 2 and 3+ year-old fish, no difference was seen in breeding cycles (1996 and 1997, $P > 0.05$).

Since each age-group mated assortatively, the operational sex ratio (OSR) was calculated for each (Fig. 2). The OSR of all age-groups was strongly male-biased late in the breeding season when most of the males were at the non-mouthbrooding stage. In the early and middle phases, the OSR of 1 year-old fish was usually male-biased, whereas that of 2 and 3+ year-old fish was female-biased or did not deviate from equality.

FILIAL CANNIBALISM

Entire brood cannibalism always occurred within a day of spawning ($n = 92$). The filial cannibalism rate of the population did not differ among years [15.8% (32 : 203), 16.3% (23 : 141), 12.1% (12 : 99) and 13.6% (25 : 184) in 1993, 1995, 1996 and 1997 respectively, $P > 0.05$]. When the data of 4 years were combined, the cannibalism rate did not differ among age-groups ($P > 0.05$). The seasonal pattern of cannibalism, however, differed among age-groups (Fig. 3). The

TABLE V. The number of spawnings (mean \pm s.d.) in a breeding season by male *Apogon doederleini* of each age-group

Year	Age (years)					
	1	<i>n</i>	2	<i>n</i>	3+	<i>n</i>
1993	5	1	6	1	7.0 \pm 1.3	26
1995	3.0 \pm 1.2	24	—	—	5.4 \pm 1.2	12
1996	1	1	5.2 \pm 0.9	14	5.2 \pm 0.8	5
1997	3.3 \pm 1.2	12	4.5 \pm 1.1	7	5.2 \pm 1.1	21

cannibalism by 1 year-old fish occurred more frequently in the early phase than in the middle phase (Fisher's exact test, $P < 0.05$); 27% (10 : 37) of them cannibalized the first brood of their lives. In the cannibalism rate of 2 year-old fish, there was no significant difference among the phases ($P > 0.05$). The cannibalism rate of 3+ year-old fish was higher in the late phase than in the early and middle phases ($\chi^2 = 12.63$, d.f. = 2, $P < 0.05$).

After cannibalism, 88.5% (77 : 87) of males re-spawned within the season. In all cases where their mates could be identified ($n = 42$), they re-mated with different females. One year-old fish took significantly longer to re-spawn than 2 year-old fish (Mann-Whitney U -test, $P < 0.05$) and 3+ year-old fish ($P < 0.05$; Fig. 4). Only in 1 year-olds, those which had cannibalized their brood re-spawned significantly later than those which had hatched their brood (Mann-Whitney U -test, $z = -3.73$, $P < 0.001$; Fig. 4).

DISCUSSION

ANNUAL VARIATION IN AGE-STRUCTURE AND REPRODUCTION

The age structure of *A. doederleini* varied greatly from year to year. Clearly, this variation was due to annual differences in juvenile recruitment, which created a dominant age-group each year (Fig. 1). The length of the breeding season also varied among years, recording a maximum difference of 26 days. Corresponding to this variation, the mean number of spawnings by one male per season also varied.

In contrast to these variations, the occurrence of entire brood cannibalism showed regular patterns. First, entire brood cannibalism always occurred within a day of spawning every year, as already reported for this species (Okuda & Yanagisawa, 1996a). In most fishes in which brood cannibalism, either partial or entire, has been observed, parents eat early stage eggs (Salfert & Moodie, 1985; Petersen & Marchetti, 1989; Lavery & Keenleyside, 1990; Petersen, 1990; Sikkel, 1994). The parent's preference for young eggs may be due to a greater nutritive value and smaller reproductive value of these eggs (FitzGerald, 1991). Furthermore, in case of entire brood cannibalism, early egg consumption can minimize the parental effort (Okuda & Yanagisawa, 1996a). Second, the filial cannibalism rate was nearly constant over a 4 year period, 12–16%. In some fish species such as the mosquitofish *Gambusia affinis* (Baird & Girard), environmental conditions such as food availability affect the occurrence of cannibalism

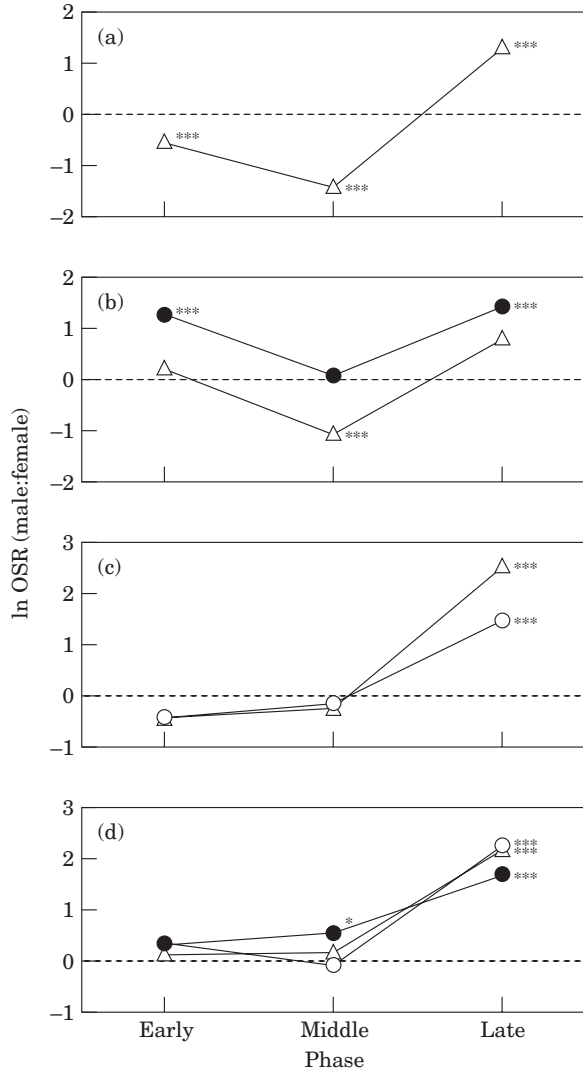


FIG. 2. The operational sex ratio of 1 (●), 2 (○) and 3+ (△) year-old *Apogon doederleini* in three phases of the breeding season in (a) 1993, (b) 1995, (c) 1996 and (d) 1997. The values are logarithmically transformed. Significant male and female bias * $P < 0.05$, *** $P < 0.001$.

(Dionne, 1985). In *A. doederleini*, the cannibalism rate did not differ significantly among age-groups but the seasonal pattern of cannibalism was age-specific. This suggests that the cannibalism of this fish would not be a simple populational response to environmental conditions. Filial cannibalism is widespread among apogonid fishes (Okuda, 1999a, b). The cannibalistic behaviour by male apogonids may be a regular reproductive tactic, although the cannibalism rate varies among species according to their ecology (Okuda, 1999b, 2000).

AGE-RELATED FILIAL CANNIBALISM

The seasonal pattern of entire brood cannibalism differed among age-groups. Cannibalism by 3+ year-old fish occurred most frequently late in the breeding

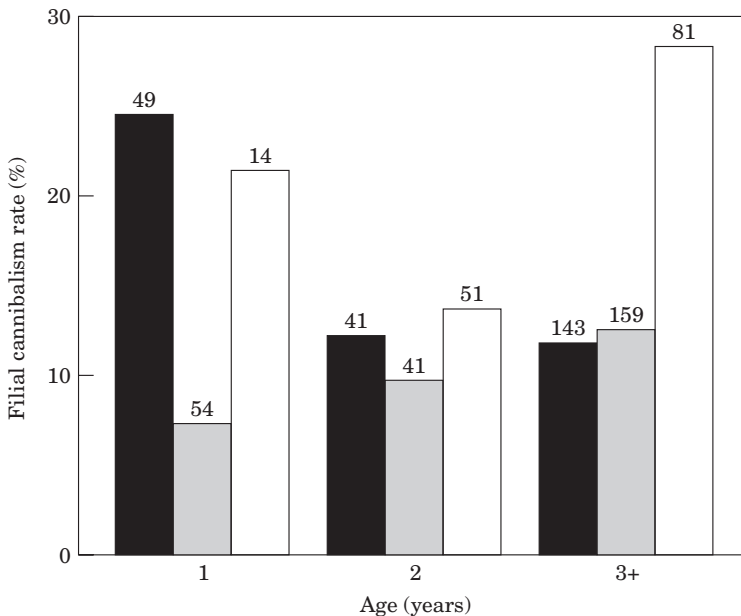


FIG. 3. The filial cannibalism rate of each age-group of *Apogon doederleini* in early (■), middle (▣) and late (□) phases of the breeding season. Numbers above bars are sample sizes.

season, whereas the cannibalism rate of 1 year-olds was greater early in the breeding season. In mouthbrooders, parents are precluded from eating ordinary food (Smith & Wootton, 1995; Yanagisawa & Sato 1990; Yanagisawa *et al.*, 1996). Because older males of *A. doederleini*, which complete several breeding cycles per season, fast for a large proportion of the breeding season (c. 80%; Okuda & Yanagisawa, 1996a), their somatic condition deteriorates dramatically as the breeding season progresses (Okuda & Yanagisawa, 1996b; Okuda *et al.*, 1997). Filial cannibalism that frequently occurred late in the breeding season in 3+-year-old fish seems to be caused by their poor physical condition (Okuda & Yanagisawa, 1996b).

Okuda *et al.* (1997) explained the frequent filial cannibalism of early broods by young males (1 and 2 year-olds combined) in terms of a trade-off between current and future reproduction. From the data of this study, it is obvious that their explanation cannot be applied to 2 year-olds, because filial cannibalism by these fish was not frequent early in the breeding season. Since reproductive success of male apogonids is limited by the buccal capacity that depends on their body size (Okuda *et al.*, 1998), 1 year-old fish, which have greater growth potential, may allocate more energy to growth than older males. Early in the breeding season when water temperature is relatively low, mouthbrooding will deprive males of feeding opportunities for a long period (up to 17 days; Okuda & Yanagisawa, 1996b). This will result in a serious decline of the energy reserves, especially in 1 year-old fish whose somatic condition is inferior to that of older males at the beginning of the breeding season (T. Takeyama, unpubl. data). For this reason, some 1 year-old fish may cannibalize the earliest broods. Interestingly,

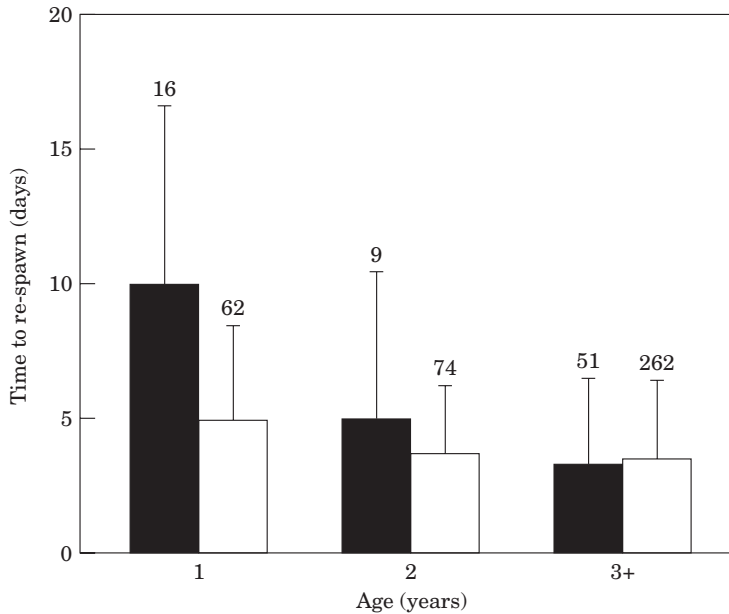


FIG. 4. Mean (+S.D.) time to re-spawn for male *Apogon doederleini* which cannibalized their broods (■) and males which hatched their broods (□). Numbers above bars are sample sizes.

2 year-olds whose growth rate was intermediate between 1 and 3+ year-olds had an intermediate cannibalism pattern, showing no clear seasonal trend (Fig. 3).

Multiple mate availability for male *A. doederleini* can be another factor facilitating filial cannibalism (Okuda & Yanagisawa, 1996a; Okuda *et al.*, 1997). In 2 and 3+ year-old fish, those which cannibalized the brood did not take more days to re-spawn than those which hatched the brood (Fig. 4). This suggests that cannibal males took advantage of multiple mate availability, eating the first brood and rearing the second (Okuda & Yanagisawa, 1996a). One year-old fish did not seem to take such advantage, because they took more days to re-spawn after cannibalism. The operational sex ratio affects which sex will have ready access to mates (Emlen & Oring, 1977; Kvarnemo & Ahnesjö, 1996). In a sympatric congener *Apogon notatus* (Houttuyn), the rate of filial cannibalism is low (6.0–10.7%; Okuda, 1999a) and it takes many days for males to re-mate after cannibalism (Okuda, 1999b, 2000). Cannibal males of *A. notatus* will encounter difficulty in searching for new mates because of the male-biased OSR (Okuda, 2000). In the present study, the OSR of *A. doederleini* was strongly male-biased late in the breeding season when most males were at the non-mouthbrooding stage (Fig. 2). Although all non-mouthbrooding males were regarded as sexually receptive in the estimation of OSR, some of them in fact may have been incapable of mating. It is therefore likely that the OSR was overestimated. In the early and middle breeding season, the OSR of 2 and 3+ year-old fish was female-biased or did not deviate from equality. Under this situation, some males may find opportunity to acquire multiple females simultaneously. By contrast, in 1 year-olds, whose OSR was not biased toward females, males probably have little opportunity for taking such advantage.

In conclusion, male *A. doederleini* of different ages probably have different tactics in performing filial cannibalism according to their allocation of energy to growth and reproduction and mate availability.

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