ORIGINAL ARTICLES

Noboru Okuda · Tomohiro Takeyama
Yasunobu Yanagisawa

Age-specific filial cannibalism in a paternal mouthbrooding fish

Abstract Entire-brood cannibalism by mouthbrooding males of the cardinal fish *Apogon doederleini* was investigated in temperate waters of southern Japan during two breeding seasons. The rate of cannibalism was 17–18% in each season and did not differ among age-groups. However, the seasonal pattern of cannibalism differed markedly among age-groups: young (1- and 2-year-old) males frequently cannibalized early broods, especially the first brood, of the season, whereas cannibalism by middle-aged (3- and 4-year-old) and old (5- and 6-year-old) males mainly occurred late in the breeding season. We explain this difference in terms of trade-offs between current and future reproduction. Young males, whose future reproductive success is enhanced by the growth increment, may allocate more time and energy to growth by cannibalizing early broods. In contrast, for older males who have had more breeding cycles and grow little, cannibalism could be a way to reverse the deterioration in their somatic condition that occurs as the breeding season progresses. It is also likely that the current reproductive loss entailed by the cannibalism is effectively compensated by quick re-mating with another female.

Key words Apogonidae · Entire brood cannibalism · Mate availability · Reproductive cost · Trade-offs

Introduction

Hetero-cannibalism, the killing and consumption of non-related conspecifics, occurs in a variety of taxa from lower eukaryotes to higher primates, whereas filial cannibalism, consumption of offspring by the parent, is restricted to some taxonomic groups (Hausfater and Hrdy 1984; Elgar and Crespi 1992). Filial cannibalism is more common in species with paternal care (Dominey and Blumer 1984; FitzGerald and Whoriskey 1992; Sargent 1992, 1997). The reason is associated with sexual conflicts of interest: males make a large parental effort but a smaller gametic investment than females, so that eating their zygotes without providing care can be advantageous to the males (FitzGerald 1992).

Filial cannibalism is of evolutionary interest because it appears to contradict the rule that organisms maximize their reproductive success. For an evolutionary explanation of this behavior, Rohwer (1978) argues that when the loss of current reproduction entailed by filial cannibalism is outweighed by the benefit from the future reproduction, this parental strategy can be favored by natural selection. A cannibalistic parent may increase its future reproductive value by: (1) increasing somatic growth directly by the caloric intake obtained by eating offspring and/or indirectly by re-allocating the time it would spend on parental care to feeding activities; (2) improving survival probabilities by allocating the energy gained from cannibalism to the maintenance of its somatic condition, and (3) increasing future opportunities for reproduction.

As predicted by life-history theory, individuals under different conditions will sustain a variety of costs in reproduction and allocate energy in different ways (Roff 1992). For example, an individual with a high growth potential may allocate more energy to growth than to reproduction, and an individual who is in good physical condition may invest more in reproduction than in the maintenance of somatic condition. Similarly, a decision to commit filial cannibalism by a parent will be affected by its life history, and physical and social conditions.

Males of the cardinal fish *Apogon doederleini* (Apogonidae) are known to eat their entire brood occasionally during the mouthbrooding period (Okuda and Yanagi-

T. Takeyama · Y. Yanagisawa
Department of Biology, Ehime University, 2-5 Bunkyo-cho,
Matsuyama, Ehime 790-8577, Japan

N. Okuda (✉)
Center for Ecological Research, Kyoto University,
Otsu 520-01, Japan
Fax: +81 (0)775 79 8457; e-mail: okuda@ecology.kyoto-u.ac.jp

sawa 1996a,b). In this study, we examined how the rate of filial cannibalism of this fish varies with time and with parental age, and estimated in which ways the cannibalistic males make trade-offs between current and future reproduction.

Methods

Reproductive biology and filial cannibalism

A. doederleini is a common fish in shallow waters of the west Pacific (Sale and Douglas 1984; Kuwamura 1987; Sakai et al. 1994). Its reproductive behavior, growth and life history have been investigated in detail (Kuwamura 1985; Okuda and Yanagisawa 1996a, b; Okuda et al. in press).

Spawning occurs in pairs, and the male mouthbroods a cohesive egg mass consisting of about 10,000 eggs from one female. The brooding period lasts for 5–17 days (depending on water temperature) until the eggs hatch. Males complete several breeding cycles in a breeding season (May-August in temperate waters of Japan). They fast during the mouthbrooding periods unless they eat their own broods (Okuda and Yanagisawa 1996b). Many males cannibalize a portion of the brood early in the brooding period, which possibly functions as a way to adjust eggs number to the buccal capacity (Okuda et al. in press). However, males sometimes cannibalize the entire broods within a day of spawning (Okuda and Yanagisawa 1996b). In this study, our attention was focused on the latter type of brood cannibalism.

Field study

We studied reproductive ecology of *A. doederleini* at Murote Beach, Shikoku Island, Japan, in 1993 and 1995. We set a 10 m × 20 m quadrat on the boulder slope. At the beginning of each breeding season, we captured all individuals inhabiting the quadrat with a hand net and quinaldine anesthetic, and gave them an individual mark underwater by pulling out two or three dorsal and/or anal fin rays. At the same time, we measured their standard length (SL) to the nearest 0.5 mm with a pair of calipers and gently removed at least three scales from the lateral body near the pectoral fin. The scales, on which a pattern of circuli is formed once a year (Okuda et al. in press), were used to age the fish in the laboratory. After releasing fish at the capture site, we observed the incidence of mating of individual males by daily censuses throughout the breeding season. We judged that entire brood cannibalism occurred if a male was potbellied when the brood disappearance was noticed: stomach contents of such a male, which were checked underwater with a needle-less syringe of 1 ml plunged through the esophagus, always included eggs of the same developmental stage as those which he had brooded (see Okuda and Yanagisawa 1996b). Within 2 weeks of the end of the breeding season and at the beginning of the next breeding season, we recaptured all marked fish that remained in the quadrat and remeasured their SL. Their growth rate was calculated as follows:

$$G = (\ln L_{t_2} - \ln L_{t_1})/(t_2 - t_1) \times 100$$

where G represents the daily specific growth rate, and L_{t_1} and L_{t_2} their SL (mm) on the first capture date t_1 and the recapture date t_2, respectively. The survival rate during the breeding season and the following non-breeding season were calculated from the number of marked fish which survived to recapture divided by all marked fish at capture. Since adults of this species showed strong site fidelity (Okuda and Yanagisawa 1996a), marked fish which had disappeared from the quadrat and were not subsequently found nearby were regarded as having died.

Estimation of operational sex ratio

The operational sex ratio (OSR), the ratio of males to females ready to mate, was estimated. The OSR can be influenced by three factors: the adult sex ratio, distribution of males and females in time and space, and sexual difference in the potential reproductive rate (PRR) (Clutton-Brock and Parker 1992). The PRR is defined as the maximum number of offspring that each parent can produce per unit time (Clutton-Brock and Vincent 1991). The OSR at a given time is calculated as follows:

$$\text{OSR}(t) = \frac{\mathrm{d}_m(t)}{\mathrm{d}_f(t)} \times \frac{M(t)}{F(t)} \times \frac{\text{PRR}_m(t)}{\text{PRR}_f(t)}$$

where $\mathrm{d}(t)$ is the proportion of individuals at the breeding site to the adult population at time t, and $\frac{M(t)}{F(t)}$ the adult sex ratio. Subscripts m and f are for the male and female, respectively. Because site fidelity was very high in adult *A. doederleini* of both sexes (Okuda and Yanagisawa 1996a), the effect of spatio-temporal fluctuation on the sex ratio was negligible $\left(\frac{\mathrm{d}_m(t)}{\mathrm{d}_f(t)} \cong 1\right)$. Since a male received the brood from one female and a female gave her entire clutch to one male (Okuda and Yanagisawa 1996a), the PRR ratio was approximated by the ratio of an inverse of the shortest inter-spawning intervals observed among males and females.

Data analysis

The examination of scales showed that this study population consisted of 1- to 6-year-old fish (Table 1). Males were divided into three age-groups: young (1- and 2-year-old), middle-aged (3- and 4-year-old), and old (5- and 6-year-old) fish. In 1993 young and old fish were extremely scarce, whereas in 1995 the middle-aged fish were scarce (this difference was due mainly to fluctuations of juvenile recruitment between the years). Therefore, to facilitate a statistical comparison among these groups, we pooled the data of 1993 and 1995. For the seasonal pattern of reproduction, however, we did not combine the data, since the breeding season of 1995 terminated about one month earlier than that of 1993. In each year, the breeding season was divided into three phases according to reproductive experience of each male: phase I includes the first and second breeding attempts, phase II the third and fourth attempts, and phase III the fifth to seventh attempts.

Body size was significantly greater in older age-groups (young: $\bar{x} \pm \text{SD} = 69.8 \pm 5.3$ mm, $n = 29$, middle-aged: 85.2 ± 2.9 mm, $n = 27$, old: 90.1 ± 1.7 mm, $n = 13$; ANOVA, $df = 2$, $F = 161.2$, $P < 0.001$). The size difference between the young and middle-aged (Scheffé F-test, $P < 0.0001$) was much greater than that between the middle-aged and old (Scheffé F-test, $P < 0.003$).

Table 1 The age structure of *Apogon doederleini* at the beginning of the breeding season in 1993 and 1995

Year	Sex	Age						Total
		1	2	3	4	5	6	
1993	Male	1	1	17	9	2	0	30
	Female	1	1	22	6	5	2	37
1995	Male	27	0	0	1	9	2	39
	Female	30	0	2	2	11	1	46

Results

Occurrence of filial cannibalism

The cannibalism rate, the proportion of broods canni-balized to the total broods spawned, was 16.5% ($n = 90$), 16.8% ($n = 185$) and 14.1% ($n = 71$) for young, middle-aged, and old males, respectively, which was not significantly different among the groups ($\chi^2 = 0.29$, $df = 2$, $P > 0.8$). Cannibals, defined as males that practiced entire brood cannibalism at least once in the breeding season, accounted for 35.7% ($n = 28$), 59.3% ($n = 27$) and 38.5% ($n = 13$) of all males in the respective groups, which also did not differ among the groups ($\chi^2 = 3.40$, $df = 2$, $P > 0.1$). How-ever, the seasonal pattern of filial cannibalism was markedly different among the groups (Table 2). The cannibalism rate by middle-aged and old males was higher in the later phases. Cannibalism by young males of 1995 all occurred in phase I, mostly in the first breeding cycle (cannibalism rate: 34.5% in the first cycle and 13.6% in the second cycle).

All of entire brood cannibalism occurred by the day following spawning. Of 55 males who cannibalized broods, 48 re-spawned within the breeding season. All but one of these males mated with a different female after cannibalism, which contrasted with a relatively low rate of mate change by males who hatched their broods (60.4%, $n = 187$). Within a few days of cannibalism, middle-aged and old males re-spawned, whereas young males took much longer to re-spawn (Fig. 1; ANOVA, $df = 2$, $F = 16.6$, $P < 0.001$; Scheffé F-test, young vs. middle-aged: $P < 0.001$, young vs. old: $P < 0.001$, but middle-aged vs. old: $P > 0.7$). Among young males, those who hatched broods re-spawned significantly sooner than those who cannibalized broods ($t = 3.69$, $P < 0.001$).

Operational sex ratio

The shortest inter-spawning interval was shorter each month in the female than in the male (Table 3). The adult sex ratio did not significantly deviate from equality
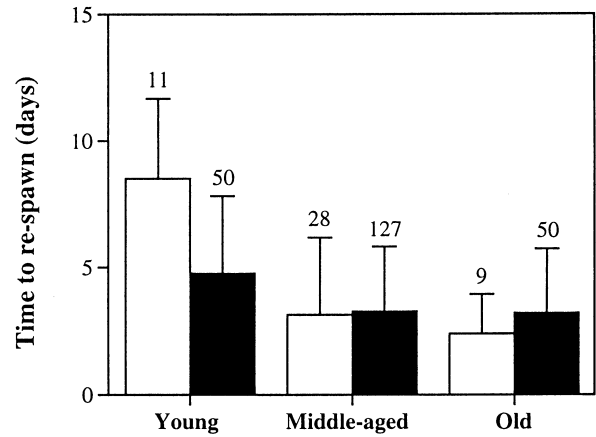

Fig. 1 The time taken to re-spawn for males who cannibalized their broods (*white*) and males who hatched their broods (*black*). *Vertical lines* and *numerals* indicate the standard deviation and sample size, respectively

($\chi^2 = 0.37$, $df = 1$, $P > 0.5$ in 1993 and $\chi^2 = 0.29$, $df = 1$, $P > 0.5$ in 1995). As a result of higher PRR in the female, OSR was female-biased throughout the breeding season.

Reproduction and growth

Young males tended to start the first breeding later than older males (Fig. 2). There was a negative correlation between male body size and the date of the first breeding across age-groups ($r = -0.85$, $P < 0.001$ in 1995, but $r = -0.33$, $P = 0.07$ in 1993). This trend was also seen within young and middle-aged males (young: $r = -0.59$, $P < 0.003$ in 1995, middle-aged: $r = -0.38$, $P = 0.05$ in 1993, old: $r = -0.52$, $P > 0.1$ in 1995).

Males completed fewer breeding cycles in 1995 (Ta-ble 4; $\bar{x} \pm SD = 3.29 \pm 1.36$, $n = 34$) than in 1993 (5.70 ± 0.91, $n = 27$; $t = -7.90$, $P < 0.001$). This differ-ence was not only due to a shorter breeding period in 1995 but also to the numerical dominance of young males in 1995. Middle-aged and old males completed more breeding cycles than young males (Table 4; AN-OVA, $df = 2$, $F = 54.6$, $P < 0.001$; Scheffé F-test, young vs. middle-aged: $P < 0.001$, young vs. old:

Table 2 The rate of filial cannibalism in three phases of the breeding season. Phases I-III include the 1st–2nd, the 3rd–4th and the 5th–7th breeding attempts for each individual, respectively. Sample sizes are in parentheses

Year	Age-group	Cannibalism rate (%)			I vs. II	I vs. III	II vs. III
		I	II	III			
1993	Young	0.0 (4)	25.0 (4)	0.0 (2)		Not applicable	
	Middle-aged	5.8 (52)	19.2 (52)	27.5 (51)	*	**	NS
	Old	25.0 (4)	25.0 (4)	100.0 (2)		Not applicable	
1995	Young	25.5 (51)	0.0 (21)	– (0)	**	–	–
	Middle-aged	50.0 (2)	100.0 (3)	– (0)		Not applicable	
	Old	0.0 (22)	18.2 (22)	11.1 (9)	a	NS	NS

Fisher's exact probability test: [a]$0.05 < P < 0.1$, *$P < 0.05$, **$P < 0.01$, NS not significant

Table 3 The shortest inter-spawning interval for the male and female, the adult sex ratio (SR, male:female) and the operational sex ratio (OSR) in each month of the breeding season

Year	Month	Inter-spawning interval (days)		SR	OSR
		Male	Female		
1993	May	–	–	0.82	–
	June	13	6	0.84	0.39
	July	9	7	0.90	0.70
	August	9	4	0.93	0.41
1995	May	22	–	0.89	–
	June	11	8	1.05	0.76
	July	10	5	0.91	0.46

Table 4 The number of breeding cycles completed by a male in a breeding season. Sample sizes are in parentheses

Year	Young	Middle-aged	Old
1993	5.00 ± 1.41 SD (2)	5.79 ± 0.88 SD (24)	5.00 (1)
1995	2.67 ± 1.09 SD (24)	– (0)	4.80 ± 0.42 SD (10)
Total	2.85 ± 1.26 SD (24)	5.79 ± 0.88 SD (24)	4.82 ± 0.41 SD (11)

$P < 0.001$). Accordingly, they spent more time mouthbrooding (64.8 and 61.2% of the entire breeding season, respectively) than young males (33.5%).

During the breeding season, young males showed a much higher growth rate (G) $(\bar{x} \pm SD = 7.63 \pm 4.42 \times 10^{-2}, n = 24)$ than middle-aged and old males $(0.08 \pm 1.46 \times 10^{-2}, n = 24$ and $-0.38 \pm 0.60 \times 10^{-2}, n = 12$; ANOVA, $df = 2$, $F = 48.5$, $P < 0.001$; Scheffé F-test, young vs. middle-aged: $P < 0.001$, young vs. old: $P < 0.001$). Among young males, the growth rate was inversely correlated with the breeding frequency in a season $(r = -0.43, P < 0.05, n = 22)$ but not with the frequency of cannibalism $(r = 0.11, P > 0.6, n = 22)$.

Their growth rate was also correlated with the date of the first breeding $(r = 0.49, P < 0.03, n = 20)$: those who started the first breeding later grew more. In middle-aged and old males, neither the frequency of breeding nor the frequency of cannibalism had any effect on growth (for middle-aged of 1993, breeding: $r = 0.16, P > 0.4$, cannibalism: $r = 0.04, P > 0.8$, for old of 1995, breeding: $r = -0.00, P > 0.9$, cannibalism: $r = 0.00, P > 0.9$).

Reproductive success and survival in relation to cannibalism

Two fitness parameters, reproductive success and survival rate, were compared between cannibals and non-cannibals (Table 5). The number of broods which cannibals received in a season was greater than that of non-cannibals, but reproductive success, measured as the number of broods hatched, did not differ between them. Their survival rate did not differ during the breeding season nor during the non-breeding season.

Discussion

Cost of parental care

Life-history theory assumes that the current reproduction carries a cost in terms of future growth, survival and fecundity (Williams 1966). In fish, parental effort can reduce growth (Smith and Wootton 1995). In *A. doederleini*, middle-aged and old males who completed more breeding cycles nearly ceased growing (also see Okuda et al. in press). Among young males, there was a negative correlation between breeding frequency and growth. Since mouthbrooding forces the male to fast (Okuda and Yanagisawa 1996b), increased breeding frequency will reduce its feeding opportunities and consequently will decrease its growth rate. A decline in growth rate may lower the potential for future reproduction through (1) limitation on the buccal capacity and (2) female preference to larger male body size. This suggests that parental care imposes a fitness cost, in the form of growth retardation, on male *A. doederleini*. The cost may be especially great for young males who have a high growth potential.
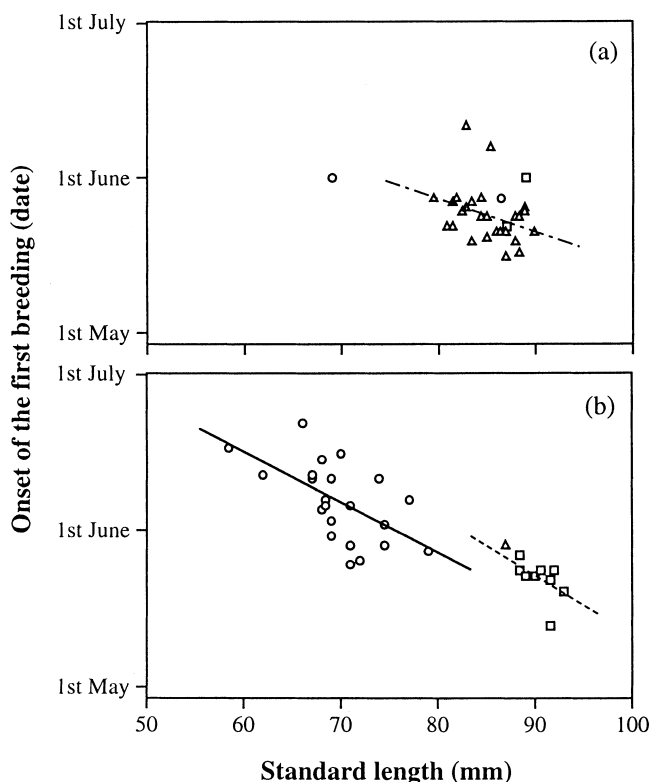

Fig. 2 Onset of first breeding in relation to male body size. *Solid, chain* and *dotted lines* indicate the regression lines for young (*circles*), middle-aged (*triangles*) and old (*squares*) males, respectively. Breedings that resulted in filial cannibalism were omitted

Table 5 Comparison of the reproductive success and survival rate between cannibal and non-cannibal males. Sample sizes are in parentheses

	1993			1995		
	Cannibals	Non-cannibals[a]	Statistical test	Cannibals	Non-cannibals[a]	Statistical test
Mating success (no. of spawnings)	7.27 ± 2.07 SD (15)	6.25 ± 0.75 SD (12)	$t = 2.15$ $P < 0.05$	4.55 ± 3.27 SD (11)	3.52 ± 1.35 SD (23)	$t = 2.00$ $0.05 < P < 0.1$
Reproductive success (no. of broods hatched)	5.40 ± 0.83 SD (15)	6.08 ± 0.63 SD (12)	$t = -2.05$ $0.05 < P < 0.1$	2.91 ± 2.69 SD (11)	3.48 ± 1.44 SD (23)	$t = -1.15$ $P > 0.2$
Survival rate (%)						
In breeding season	83.3 (18)	100 (12)	Fisher's $P > 0.2$	84.6 (13)	92.0 (25)	Fisher's $P > 0.5$
In non-breeding season	46.7 (15)	75.0 (12)	Fisher's $P > 0.2$	81.8 (11)	78.3 (23)	Fisher's $P > 0.9$

[a] Difference between the numbers of spawnings and breedings is due to the brood loss before mouthbrooding

An increase in mortality due to parental care is common in a variety of animals (Clutton-Brock 1991). In care-giving fish, restricted feeding opportunities during caring force the parent to exhaust its energy reserves and its somatic condition often deteriorates (Unger and Sargent 1988; Dufresne et al. 1990; Barbieri et al. 1992; van den Berghe 1992; Marconato et al. 1993). The depletion of the parent's energy reserves may increase its risk of death through disease, hyposthenia, and starvation (Smith and Wootton 1995). In *A. doederleini*, both males and females store fat in the liver prior to the breeding season. Males decrease their liver weight more drastically than females by the end of the breeding season, suggesting a greater overall energetic cost associated with parental care (Okuda and Yanagisawa 1996b). Correspondingly, male mortality was highest late in the breeding season (Okuda and Yanagisawa 1996b). Middle-aged and old males spent twice as much time as young males in mouthbrooding. For them, the cost of parental care in terms of decreased survival potential may be great.

Trade-offs in filial cannibalism

The occurrence of filial cannibalism differed seasonally across age-groups: young males practiced cannibalism early in the breeding season, mostly in the first breeding cycle, whereas middle-aged and old males mainly did so late in the breeding season. One obvious benefit from cannibalism is the caloric intake from the egg consumption. Young males, who can benefit by growth increment, may transfer the energy into growth, although the direct effect of egg consumption on their growth has not been investigated. For them, a delayed start of reproduction through cannibalism may be another way of increasing growth. In the early breeding season, when water temperature is relatively low, a lengthy brooding period will further reduce their feeding opportunities. Some young males may abandon the early broods for this reason. The fact that cannibalistic young took longer to re-mate than young who hatched their broods supports this possibility.

Okuda and Yanagisawa (1996b) found that in middle-aged and old males of *A. doederleini*, the frequent occurrence of cannibalism late in the breeding season coincided with the deterioration of their somatic condition, as also suggested in other paternal care fish (DeMartini 1987; Petersen and Marchetti 1989; Petersen 1990; Belles-Isles and FitzGerald 1991; Marconato et al. 1993). This is probably not the case in young males whose total fasting period due to mouthbrooding was much shorter than older males. It has been reported in some fish species that cannibalism has a significant effect on somatic weight increase and consequently enhances survival (Meffe and Crump 1987; Belles-Isles and FitzGerald 1993). In fact, cannibal males of *A. doederleini* did not show a higher survival rate than non-cannibals (Table 5). This, however, does not necessarily mean that brood cannibalism is

ineffective in improving somatic condition. Our preliminary analysis of body components of this fish (K. Omori, N. Okuda, Y. Yanagisawa and R. Manabe, unpublished work) showed that cannibals had a lower protein content than non-cannibals, though there was no difference in lipid content. This may indicate that cannibals were inferior to non-cannibals in somatic condition when they ate the brood. If this is true, the fact that there was no difference in survival between them means that filial cannibalism had a positive energetic effect. Clearly more detailed work needs to be done to understand the energetic bases of filial cannibalism of this fish.

For filial cannibalism to evolve, some compensation for the loss of current reproduction is necessary (Rohwer 1978). However, it was not clear if middle-aged and old males of *A. doederleini* can compensate completely for the current reproductive loss by enhancing survival through cannibalism. It is also unlikely that they disproportionately increase the reproductive success in the next season, because the number of breeding cycles is limited by the developmental time of embryos (Okuda et al. in press). For these males, another possible factor facilitating filial cannibalism may be multiple mate availability. The OSR in *A. doederleini* was female-biased throughout the breeding season, as is often the case in paternal egg-bearers (Bayer 1980; Vincent et al. 1994, but see Vincent 1994a, b). Where the OSR is female-biased, mate availability is potentially high for males. If two females ready to spawn are simultaneously available to a male, he can re-mate with the second female soon after cannibalizing the brood from the first one, and such a re-mating can effectively compensate for the reproductive loss entailed by cannibalism. Cannibalistic middle-aged and old males of *A. doederleini* actually re-mated more quickly than males whose broods were experimentally removed (Okuda and Yanagisawa 1996a). This contrasts with the pattern found for cannibalistic young, who re-mated later than young who hatched their broods. Okuda and Yanagisawa (1996a) suggested that cannibalistic middle-aged and old males took advantage of multiple mate availability. Their filial cannibalism may be a conditional tactic that is affected by social factors such as local mate availability as well as by their physical condition.

References

Barbieri LR, Santos RP dos, Andreata JV (1992) Reproductive biology of the marine catfish, *Genidens genidens* (Siluriformes, Ariidae), in the Jacarepaguá Lagoon system, Rio de Janeiro, Brazil. Environ Biol Fish 35:23–35

Bayer RD (1980) Size, seasonality, and sex ratios of the bay pipefish (*Syngnathus leptorhynchus*) in Oregon. Northwest Sci 54:161–167

Belles-Isles J-C, FitzGerald GJ (1991) Filial cannibalism in sticklebacks: a reproductive management strategy? Ethol Ecol Evol 3:49–62

Belles-Isles J-C, FitzGerald GJ (1993) A fitness advantage of cannibalism in female sticklebacks (*Gasterosteus aculeatus* L.). Ethol Ecol Evol 5:187–191

Berghe EP van den (1992) Parental care and the cost of reproduction in a Mediterranean fish. Behav Ecol Sociobiol 30:373–378

Clutton-Brock TH (1991) The evolution of parental care. Princeton University Press, Oxford

Clutton-Brock TH, Parker GA (1992) Potential reproductive rates and the operation of sexual selection. Q Rev Biol 67:437–456

Clutton-Brock TH, Vincent ACJ (1991) Sexual selection and the potential reproductive rates of males and females. Nature 351:58–60

DeMartini EE (1987) Paternal defence, cannibalism and polygamy: factors influencing the reproductive success of painted greenling (Pisces, Hexagrammidae). Anim Behav 35:1145–1158

Dominey WJ, Blumer LS (1984) Cannibalism of early life stages in fishes. In: Hausfater G, Hrdy SB (eds) Infanticide: comparative and evolutionary perspectives. Aldine, New York, pp 43–64

Dufresne F, FitzGerald GJ, Lachance S (1990) Age and size-related differences in reproductive success and reproductive costs in threespine sticklebacks (*Gasterosteus aculeatus*). Behav Ecol 1:140–147

Elgar MA, Crespi BJ (1992) Cannibalism: ecology and evolution among diverse taxa. Oxford University Press, Oxford

FitzGerald GJ (1992) Filial cannibalism in fishes: why do parents eat their offspring? Trends Ecol Evol 7:7–10

FitzGerald GJ, Whoriskey FG (1992) Empirical studies of cannibalism in fish. In: Elgar MA, Crespi BJ (eds) Cannibalism: ecology and evolution among diverse taxa. Oxford University Press, Oxford, pp 238–255

Hausfater G, Hrdy SB (1984) Infanticide: comparative and evolutionary perspectives. Aldine, New York

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 (1987) Coastal fish fauna at the mouth of Tanabe Bay: a comparison between 1974/75 and 1985/86 (in Japanese) Nankiseibutsu 29:113–120

Marconato A, Bisazza A, Fabris M (1993) The cost of parental care and egg cannibalism in the river bullhead, *Cottus gobio* L. (Pisces, Cottidae). Behav Ecol Sociobiol 32:229–237

Meffe GK, Crump ML (1987) Possible growth and reproductive benefits of cannibalism in the mosquitofish. Am Nat 129:203–212

Okuda N, Yanagisawa Y (1996a) Filial cannibalism in a paternal mouthbrooding fish in relation to mate availability. Anim Behav 52:307–314

Okuda N, Yanagisawa Y (1996b) Filial cannibalism by mouthbrooding males of the cardinal fish, *Apogon doederleini*, in relation to their physical condition. Environ Biol Fish 45:397–404

Okuda N, Tayasu I, Yanagisawa Y (in press) Determinate growth in a paternal mouthbrooding fish whose reproductive success is limited by the buccal capacity. Evol Ecol

Petersen CW (1990) The occurrence and dynamics of clutch loss and filial cannibalism in two Caribbean damselfishes. J Exp Mar Biol Ecol 135:117–133

Petersen CW, Marchetti K (1989) Filial cannibalism in the cortez damselfish *Stegastes rectifraenum*. Evolution 43:158–168

Roff DA (1992) The evolution of life histories. Chapman and Hall, New York

Rohwer S (1978) Parent cannibalism of offspring and egg raiding as a courtship strategy. Am Nat 112:429–440

Sakai Y, Ohnishi N, Okuda N, Kotani K, Miyauchi M, Matsumoto T, Maeda K, Dozaki M (1994) Fish fauna at coastal boulder sites of Uchiumi Bay, Shikoku Island, Japan (in Japanese). Jpn J Ichthyol 41:195–205

Sale PF, Douglas WA (1984) Temporal variability in the community structure of fish on coral patch reefs and the relation of community structure to reef structure. Ecology 65:409–422

Sargent RC (1992) Ecology of filial cannibalism in fish: theoretical perspectives. In: Elgar MA, Crespi BJ (eds) Cannibalism: ecology and evolution among diverse taxa. Oxford University Press, Oxford, pp 38–62

Sargent RC (1997) Parental care. In: Godin J-GJ (ed) Behavioural ecology of teleost fishes. Oxford University Press, Oxford, pp 292–315

Smith C, Wootton RJ (1995) The costs of parental care in teleost fishes. Rev Fish Biol Fish 5:7–22

Unger LM, Sargent RC (1988) Allopaternal care in the fathead minnow, *Pimephales promelas*: females prefer males with eggs. Behav Ecol Sociobiol 23:27–32

Vincent ACJ (1994a) Seahorses exhibit conventional sex roles in mating competition, despite male pregnancy. Behaviour 128:135–151

Vincent ACJ (1994b) Operational sex ratios in seahorses. Behaviour 128:153–167

Vincent A, Ahnesjö I, Berglund A (1994) Operational sex ratios and behavioural sex differences in a pipefish population. Behav Ecol Sociobiol 34:435–442

Williams GC (1966) Natural selection, the costs of reproduction, and a refinement of Lack's principle. Am Nat 100:687–690