学位申請論文

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DOCTORAL THESIS

Life History and Sexual Strategies of the Cardinal Fish (Pisces: Apogonidae) in the Temperate Sea

by

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要旨

京都大学大学院理学研究科生物科学専攻動物学系学位申請論文
「温帯海域に生息するテンジクダイ科魚類の生活史・性戦略」
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　南日本の温帯海域に生息する雄口内保育テンジクダイ科魚類3種の生活史・性戦略を比較研究した。転石域に生息するオオスジイシモチ、クロホシイシモチと砂地に生息するクロイシモチの間には明瞭な生活史戦略の相違が見られた。クロイシモチは転石生息種2種より顕著に高い死亡率を示した。これは砂地域で繁殖活動を営む際の高い捕食リスクによることが示唆された。クロイシモチは他2種と比べて小卵多産型で、その上、長い繁殖期間に多くの産卵・保護を行った。この戦略によって、砂地種は若成魚期に多くの孵化仔魚数を実現することができた。クロイシモチの例は成魚に対する死亡率が高い環境では若い時期に繁殖努力を大きくすべきである、という生活史理論の予測によく当てはまっていた。

　一方で、幾つかの生活史形質は生息域とは無関係に種間で類似していた。3種とも1歳で繁殖を開始し、極めて限定的な成長パターンを示した。雄が卵を口内保育するという繁殖様式のため、テンジクダイ科魚類の繁殖成功度は年齢に伴って飛躍的に増加することはなかった。かれらにとって、繁殖の早期開始は生涯繁殖成功度を大きくする1つの有効な手段であると考えられる。また、限定的な成長パターンも雄口内保育に伴う繁殖上の制約によってもたらされることが最適エネルギー分配モデルより示唆された。

　この特殊な繁殖様式のため、潜在的繁殖率（単位時間当り産出可能な子の数）は雌の方が高い値を示した。どの種においても、雌たちは多かれ少なかれ複婚的な番い戦略を採ることによって高い繁殖成功度を実現することが可能であった。一方、雄たちは口内保育のコストを補うためにしばしば自身の卵を食べる（フィリアル・カニバリズム）戦略を採用した。このように片方の性にとっての利益を増加する戦略はしばしば他方の性による損失のもとに成り立っている。この利害をめぐって対立する両性の戦略（すなわち性戦略）は種間で異なっていた。オオスジイシモチでは雌の複婚的戦略によって実効性比が雌に偏り、これが結果的に雄のカニバリズム戦略を促進していた。砂地種クロイシモチで上述の性戦略は主に2つの生態的要因すなわち異性の疎らな分布と高い捕食リスクによって抑制されていた。オオスジイシモチと同じ転石種でも、個体群密度の高いクロホシイシモチのペア雌は近接する同種他個体を排除する行動に多くを費やし、雄より有意に高い死亡率を示した。この死亡率の性差は個体群性比を雄に著しく偏らせた。この状況下で、雄たちは自身の卵よりライバル雄の卵を食べる（ヘテロ・カニバリズム）戦略を頻繁に採用した。この種間比較研究は、雌雄の利害をめぐる対立関係が生態的・社会的環境によって影響されることを明らかにした。

Summary

Life history and sexual strategies were compared among three paternal mouthbrooding cardinal fishes, *Apogon doederleini*, *A. notatus* and *A. niger* in the temperate waters of southern Japan. The former two species live in the boulder area, while the latter lives in the sandy area. The sandy dwelling *A. niger* had a higher adult mortality, suggesting that it was due mainly to predation. Some aspects of the life history strategy were markedly different between the boulder and sandy species. The sandy species produced a large number of smaller eggs per brood and more broods during the lengthy breeding season. These traits enabled this fish to have more hatched larvae at young age compared to the boulder species. This case agrees with the general theory of life history, that is, organism in the environment with a high adult mortality should make a greater reproductive effort early in life.

Among the three species, some other life history traits were unvaried, irrespective of their habitats. All these species attained maturity at age 1 and grew determinately. The early maturity may be effective in increasing the lifetime reproductive success for cardinal fishes whose reproductive success do not disproportionately increase with age. An optimal energy allocation model and higher taxonomic comparison suggest that their determinate growth can be attributed to reproductive constraints linked with a paternal mouthbrooding.

Because of their care form, the potential rate of reproduction was usually higher in females. In any species, more or less, females practiced polygamous matings to enjoy greater reproductive success, while males practiced filial cannibalism to compensate for the cost of parental care. Such sexual strategies varied species to species. In *A. doederleini*, female polygamous trend caused the female-biased operational sex ratio and consequently facilitated filial cannibalism by males. In *A. niger*, these sexual strategies were restrained by two ecological factors, a sparse distribution of adult fish and high predation risk. In *A. notatus* in which a population density is very high, increased reproductive role of females caused their higher mortality, resulting in the male-biased operational sex ratio. In this situation, males more often practiced hetero cannibalism. Male cannibalism strategy, whether it is filial or hetero, inflicts a cost on females. This comparative study showed that the sexual strategy of either sex was mutually affected by that of the other sex and that the balance of sexual conflicts varied depending on ecological and social factors.

Acknowledgements

Noboru Okuda

Contents

Chapter 1

Introduction

The cardinal fish (family: Apogonidae) is the common member of reef fish communities in the temperate sea (Kuwamura 1976, Sakai et al. 1994, Hirata et al. 1996). This family is characterized by two habits. One is that they are nocturnal (Livingston 1971, Collette and Talbot 1972). The other is that they are paternal mouthbrooders (Breder and Rosen 1966, Blumer 1982). These two habits may reduce interspecific competition for food with diurnal fishes and for space, such as spawning sites, with demersal egg spawners.

The cardinal fish is also one of the most species-rich families (Thresher 1991), for example, the number of species recorded in Japan is more than 80 (Nakabo 1993). Some remarkably diversified fish groups have developed a wide variety of morphology associated with their food utilization (e.g. cyprinid fishes (Howes 1991) and cichlid fishes (Liem 1991, Yamaoka 1997)). Such diversification is often viewed as a consequence of food resource partitioning. In contrast, the pattern of food utilization by cardinal fishes is not much diversified: they are usually opportunistic carnivores on planctonic and benthic small invertebrates (Allen 1975, Chave 1978, Finn and Kingsford 1996). Instead, their habitat pattern are greatly different among sympatric species, for example, in terms of substratum, depth, time and so on (Strasburg 1966, Chave 1978, Luckhurst and Luckhurst 1978, Kuwamura 1983a). It is evident that organisms living in different environments are put under different selection pressure, and this may be therefore a possible driving force of divergence in the cardinal fishes.

In this thesis, the main purpose is to know how environmental factors could affect diversification of cardinal fishes by comparing strategies among species. Here, a term *strategy* is defined as a set of traits, such as behavior, morphology, physiology and lifetime schedule developed by an organism or group of organisms to meet a particular set of environmental conditions (Lincoln et al. 1982). It is thus predicted that there are some differences in the strategy among species which live in the different environments.

The strategy of cardinal fishes is viewed in some aspects, especially linked with their care

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form. I first describe the reproductive biology and life history of a species, *Apogon doederleini* (fig. 1a) (**Chapter 2**). In this chapter, a special attention is focused on the cost of reproduction. As predicted by life history theory, the current reproduction carries a cost in terms of future growth, survival and fecundity (Williams 1966). I quantify a cost of parental care provided by males using some indices of somatic condition and compare with a female reproductive cost. In the next chapter, I discuss life historical consequences of paternal mouthbrooding, focussing on its growth pattern (**Chapter 3**).

In *A. doederleini*, males often eat their own eggs during the mouthbrooding period. To understand this phenomenon, I take three approaches. First, I examine relevance of the parental somatic condition to filial cannibalism (**Chapter 4-1**). If mouthbrooding carries a great energetic cost, then males should devise a means to compensate for the care cost. These males may benefit from eating their own eggs. In contrast, females whose eggs are eaten suffer a cost. Thus, filial cannibalism can be viewed as conflict of interests between the sexes (**Chapter 4-2**). Filial cannibalism is also of evolutionary interest because it appears to contradict the rule that organisms maximize their reproductive success. The cannibalistic males may offset the current reproductive loss by the future benefit through filial cannibalism. I treat filial cannibalism as a life historical problem of trade-offs between the current and future reproduction (**Chapter 4-3**).

The strategy of *A. doederleini* is compared with that of closely related species *A. notatus* and *A. niger* (Fig. 1b, c). These three species are sympatric but their habitats are different (Kuwamura 1983a). The interspecific comparison in strategies is made from two points of view: life history strategy (**Chapter 5-1**) and sexual strategy (**Chapter 5-2**). I describe similarities and differences in both strategies among these species and discuss what kind of environmental factors could cause interspecific variations as evolutionary consequences.
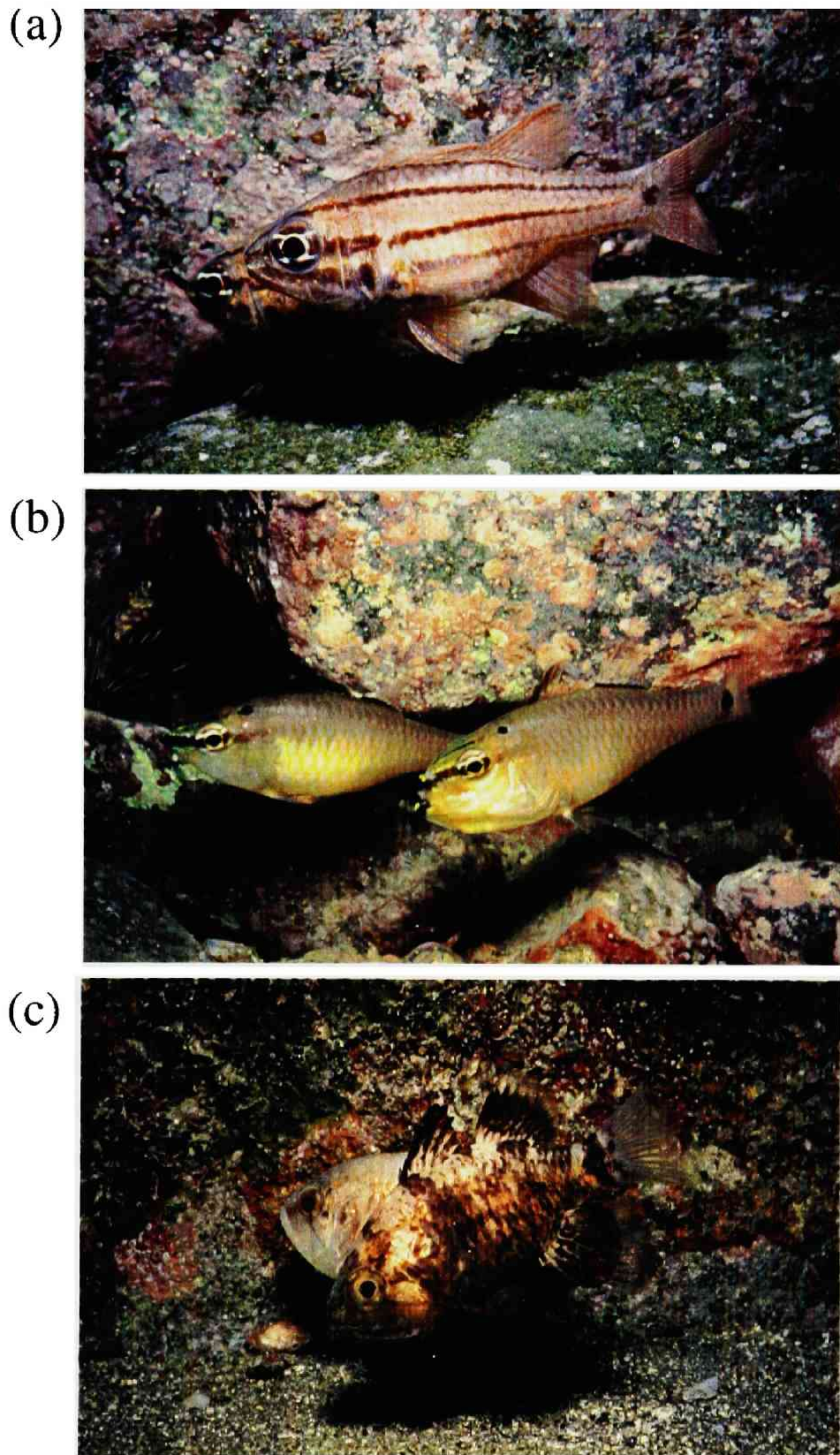
Fig. 1.1   Underwater photographs of three cardinal fishes. A
courtship pair of a male (backward) and female (forward) in *A.
doederleini* (a). A post-spawning pair of a mouthbrooding male
(right) and female (left) in *A. notatus* (b). A courtship pair of a

Chapter 2

Life history and reproductive biology

I. Introduction

Mouthbrooding is an effective care style under high predation pressure on offspring (Keenleyside 1991). However, it often prevents the parents from feeding because the buccal cavity during the mouthbrooding period is insufficient for food intake (Oppenheimer 1970, but see Yanagisawa and Sato 1990, Yanagisawa and Ochi 1991). Smith and Wootton (1994) and Balshine-Earn (1995) reported that mouthbrooding cichlid fishes decreased somatic weight during the parental phase, and concluded that this weight loss was due to the reduced feeding opportunities during the mouthbrooding period. In such way, the mouthbrooding carries a large energetic cost with the care-giving sex.

The cardinal fish *Apogon doederleini*, the subject species of this study, is a paternal mouthbrooder. In this chapter, I first measure the frequency and time which males spend in the parental care during the entire breeding season. Then I estimate a cost of mouthbrooding using some indices of somatic condition. The care cost for males is compared with a reproductive cost for females, who provide no parental care but make a great effort for egg production.

I also investigate life history of *A. doederleini*. The collection of fish is useful in analyzing the life history and demography. By this method, however, the data of individual experiences throughout the lifetime is unavailable. If it is possible to estimate the age of fish without killing them, then such a non-destructive method will give us information on their following experiences and hence the life histories of individuals. In some cardinal fishes, the scales are used to estimate the age (Suzuki and Ueno 1983, Suzuki and Ueno 1987, Ueno et al. 1987). I examine whether the scales of *A. doederleini* have the age character, and if so, I estimate the age of live fish by removing the scales from them underwater.

II. Materials and Methods

Study sites

I conducted the field study at Uchiumi Bay,
Shikoku Island, southern Japan (Fig. 2.1a). This
bay is located in the temperate region and is
subjected to the influence of Kuroshio Current,
which transports a large number of sub-tropical
fish through Bungo Channel. Because of this
current, the fish fauna constitutes an
intermediate feature between the temperate and
tropical reef fish communities (Sakai et al.
1994). The field observation was made at
Murote Beach and the collection of fishes at
Funakoshi Beach (Fig. 2.1b). Both sites are
abundant in *Apogon doederleini*. Fish
community structure and physical environment
were not much different between the two sites
(Sakai et al. 1994).
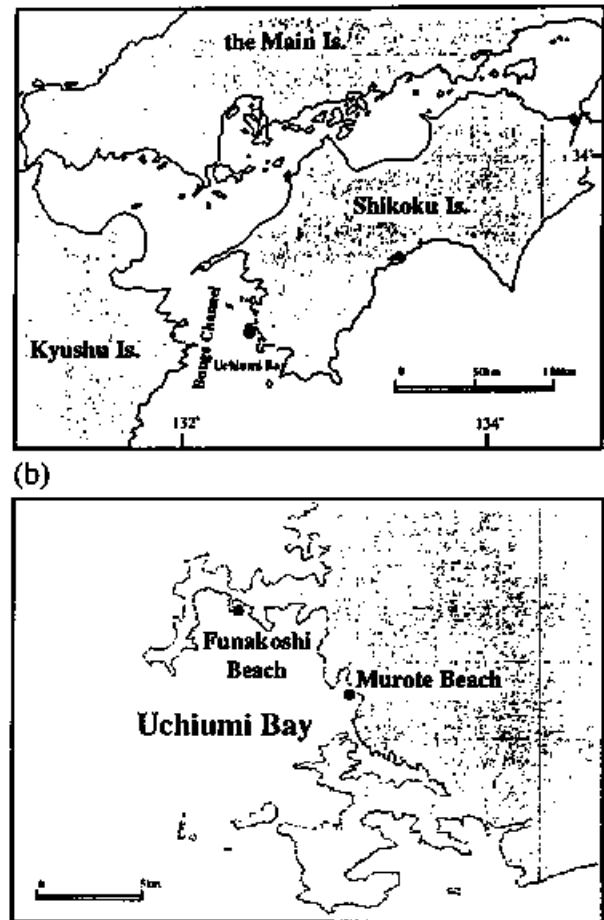
Fig. 2.1 Map of Shikoku Island (a) and Uchiumi Bay
(b).

Study species

The subject fish *A. doederleini* has been investigated in detail about its reproductive behavior
(Kuwamura 1985), diurnal activities (Okuda 1994) and habitat utilization (Kuwamura 1983a). This
fish use rock crevices and caves as sheltering and spawning sites. Reproductive activity is high in
the daytime, especially between 1100 and 1400. One male and female form a pair a few days before
spawning, intermittently displaying courtship behavior such as parallel-circling. A cohesive egg
mass 2-3cm in diameter is pushed out from the female's cloaka when they take parallel position

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after parallel-circling. Within a few seconds, the egg mass is taken into the males' mouth. Post-spawning behavior, consisting of frequent egg-churning by the male and parallel-circling in a pair, continues for up to 1 h and thereafter they separate to their respective sheltering sites. Mouthbrooding ends at the time of egg-hatch.

Field observation

I made field observations with the aid of SCUBA from 1992 to 1994. I set a 10×20m quadrat on the boulder slope at a depth of 5.8-9.0m (Okuda 1994). At the beginning of the breeding season of 1992, I marked underwater all individuals of *A. doederleini* inhabiting the quadrat, 53 males, 54 females and three individuals of unknown sex, by extracting two or three dorsal and/or anal fin rays. After removing a few scales from the marked fish, I released them at their capture sites. I removed scales again from these fish soon after the breeding season. The scales were preserved in 10% formalin to estimate the age in the laboratory. Prior to the breeding season of 1993 and 1994, these procedures were repeated for all surviving marked individuals and new residents.

I censused the fish throughout the entire breeding season of 1993. In each census, which was usually made between 1100 and 1500 hours, I noted the brooding state of each male (mouthbrooding or non-brooding) and the degree of belly expansion of each female. The latter was used as an index of gonad maturation. When I found a pair engaging in a courtship display (e.g. parallel-circling), I repeatedly visited them and noted the spawning and post-spawning behavior. The post-spawning behavior, which continues for a while, enabled me to identify the spawning pair. When I had observed only the courtship display of a pair but found the male mouthbrooding next day, I judged that he had spawned with the paired female, provided her belly was deflated.

In each month, I noted the presence of each marked fish in the quadrat on more than six successive days. The monthly disappearance rate (%) was calculated by the equation, 100 × (marked fish that disappeared in a month) / (all marked fish that were present in the last census of the previous month).

Monthly collection

From May 1992 to April 1993, I monthly captured about 30 fish of *A. doederleini* at Funakoshi Beach. The fish were preserved in 10% formalin and were used for analysis in the laboratory. I dissected the fish and extracted their liver, gonad and gut. I weighed the gut contents in wet condition and sorted only the stomach contents. The fish body and its extracted organs were dried and weighed. The condition factor (K = $100 \times$ total dry body weight (mg) / SL (mm)^3) and the hepatosomatic index (HSI = $100 \times$ dry liver weight (mg) / total dry body weight (mg)) were used as indices of somatic condition. The gonadosomatic index (GSI = $100 \times$ dry gonad weight (mg) / total dry body weight (mg)) was used as an index of gonad maturation and the gut fullness index (GFI = $100 \times$ wet weight of gut contents (mg) / total wet body weight (mg)) as an index of feeding intensity.

Ageing

For ageing the fish from scales, I followed the methods of Suzuki and Ueno (1983, 1987) and Ueno et al. (1987). An application of this method to *A. doederleini* was validated in two ways: monthly collection of fish specimens and examination of scales from the same individuals in two different times, prior to and soon after the breeding season. Both methods showed that the annulus was formed during the breeding season.

The annual survival rate was calculated as the probability of a t-year-old fish surviving to age t+1. If a marked fish disappeared from the quadrat and was not subsequently seen nearby, it was recorded as having died because adults of this fish showed strong site fidelity (also see **Chapter 4-2**).

III. Results

Life history

The first recruitment of juveniles took place early June, a half month after the onset of reproduction. Their minimum size was 9.0mmSL. At this stage, they appeared in small shoals behind the rocks but became solitary as they grew. One-year-old fish, which survived from the

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juvenile stage to the next season, established their sheltering sites and all of those that were observed throughout the breeding season attained maturation (also see **Chapter 3**). Fish that survived to age 1 were very few in both 1993 and 1994 (Fig. 2.2), although a substantial recruitment of juveniles occurred in each year. The survival rate for juveniles could not be estimated because their recruitment and disappearance concomitantly occurred during June-September.

The annual survival rate for adult fish did not significantly differ among age-groups (χ^2=6.86, df=4, P>0.1, 5- and 6-year-old fish combined; Table 2.1). The oldest males and females were 5 and 7 years old, respectively (Fig. 2.2). The survival rate of males (50.9% in 1992 and 53.1% in 1993) was lower than that of females (70.8% in 1992 and 70.7% in 1993; χ^2=3.38, df=1, P>0.06 in 1992; χ^2=1.70, df=1, P>0.1 in 1993; χ^2=6.64, df=1, P=0.01 when data of both years are combined).
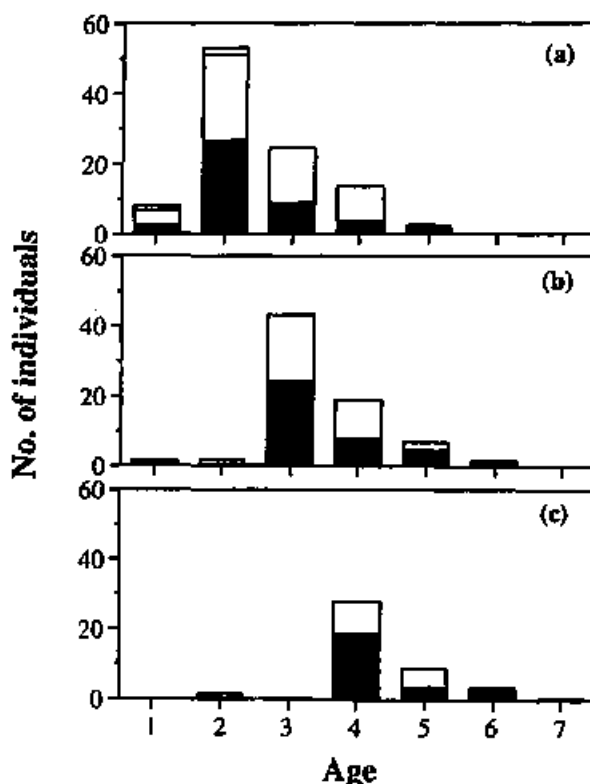
Fig. 2.2 The age structure of *A. doederleini* in 1992 (a), 1993 (b) and 1994 (c). Solid, shaded and open bars indicate female, male and individual of unknown sex, respectively.

Seasonal pattern of reproduction

I observed 261 spawnings by marked individuals (including spawnings with non-

Table 2.1. Annual survival rate (%) for adult fish. The data from 1992 to 1994 are pooled. Sample size in parentheses

		Age				
1	2	3	4	5	6	total
30.0	69.1	63.2	51.6	60.0	50.0	60.8
(10)	(55)	(68)	(31)	(10)	(2)	(176)

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marked fish) in 1993 (Fig. 2.3). The first spawning was observed on 16 May and the last spawning on 28 August. The mouthbrooding period varied from 5 to 17 days depending on water temperature (y(days)=104-69.1×log$x$(°C), r^2=0.92, P<0.0001; also see Fig. 5-1.6, **Chapter 5-1**). Although there were several small spawning peaks, these peaks did not coincide with any particular phase of the lunar cycle.

Individual males spawned 5-10 times in one breeding season ($\bar{x}$±SE=6.8±0.2, N=30). The number of spawns which one male brooded until hatching was 4-7 (5.6±0.2, N=30). Males on
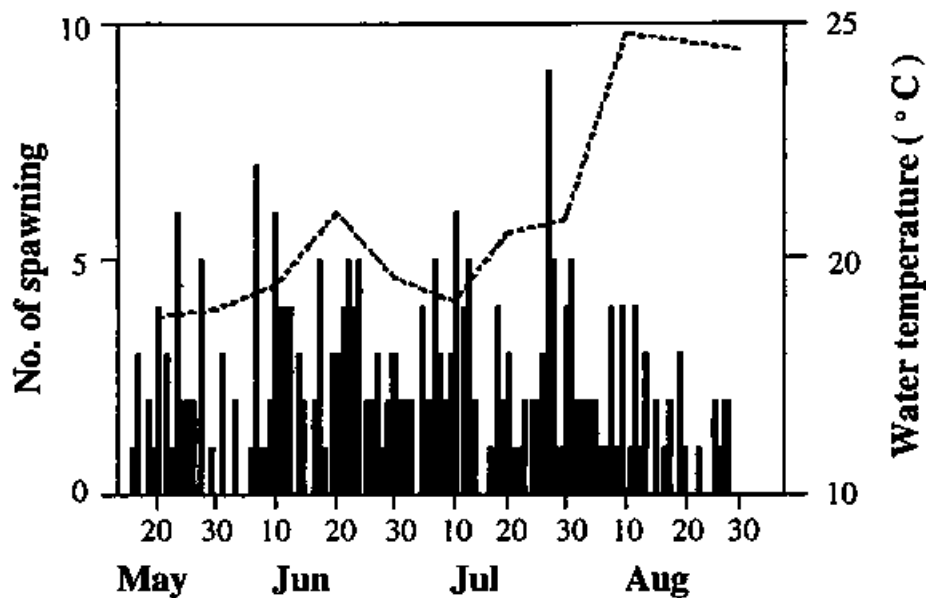
Fig. 2.3 Daily spawning occurrences in the 10×20m quadrat. A broken line shows water temperature.

average spent 78.1% (±1.1SE, N=30) of their time mouthbrooding during the breeding season. On the other hand, females spawned 4-9 times per season (6.3±0.2, N=31). Their inter-spawning interval was 14.8 days (±0.3SE, N=178) on average and did not correlate with water temperature (r=-0.11, P>0.1, N=166).

Male disappearance rate was highest in August both in 1992 and 1993, and female disappearance rate peaked in August in 1992 and July in 1993 (Fig. 2.4). In the breeding season, males usually disappeared during the non-brooding period and it was rare for them to disappear during the mouthbrooding period (3 cases in 1992 and no case in 1993). Most of these disappearances may be attributed to their death because adults of this fish showed strong site fidelity.
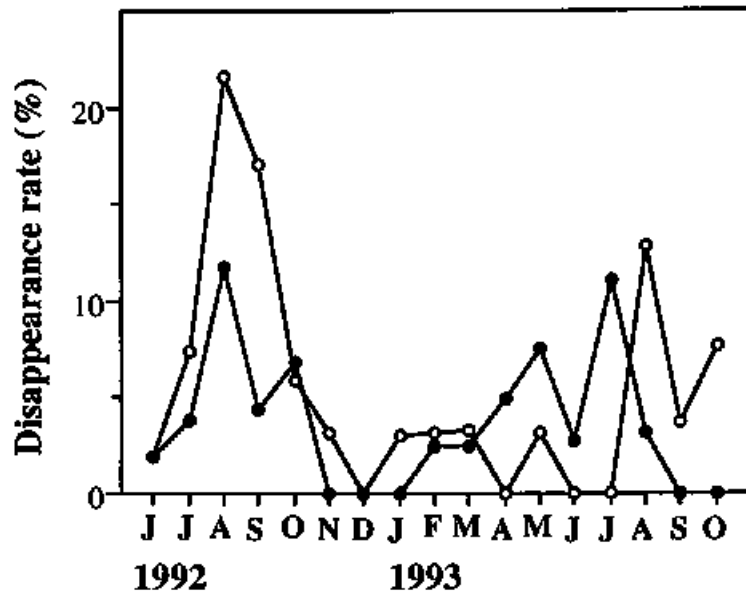
Fig. 2.4 Monthly changes of the disappearance rate in males (open circles) and females (closed circles).

Somatic condition

The gonadosomatic index (GSI) for both males and females was high in the breeding season, but declined by late August, when no males were mouthbrooding at the collection site (Fig. 2.5). Seasonal patterns of the condition factor (K) were similar for the two sexes, except that the K for females peaked in June when their gonad weight greatly increased (Fig. 2.6a). The decreased rate in K during the breeding season was 12.2% for males and 9.0% for females. The K recovered slightly soon after the breeding season but remained low during the winter. The hepatosomatic index (HSI) for both sexes was highest early in the breeding season but lowered drastically late in the season (Fig. 2.6b). The HSI decreased by 59.0% for males and by 54.8% for females during the breeding
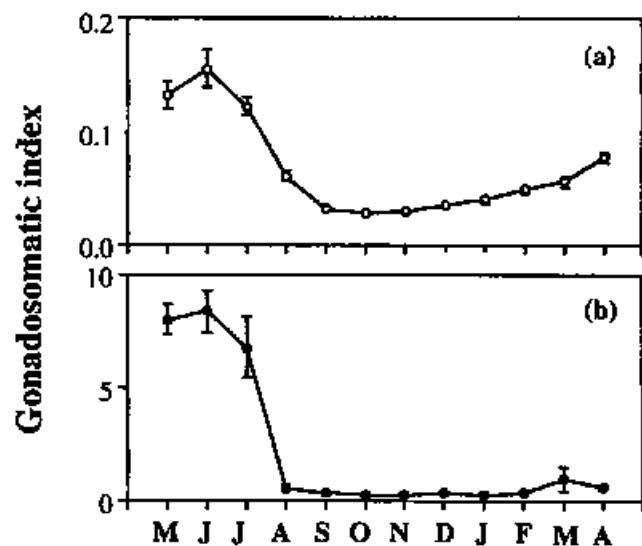
Fig. 2.5 Monthly changes of the gonadosomatic index for males (a) and females (b). Vertical lines indicate the standard error.

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season; the daily specific decrease rate was $1.46 \times 10^{-2} \% \cdot day^{-1}$ for males and $1.30 \times 10^{-2} \% \cdot day^{-1}$ for females. Thereafter, the HSI gradually recovered until the next breeding season though it stagnated in winter.

Stomach contents

Both males and females collected at Funakoshi mainly fed on small benthic crustaceans such as gammalids, mysids, shrimps and crabs, and minor food items were small fish and annelids. The gut fullness index (GFI) for females was high just before and during the breeding season, while the GFI for males showed no clear seasonal pattern (Fig 2.6c). The GFI for females was significantly higher than that for males in the breeding season (t=2.93, P<0.005, N=43, 45), but not in the non-breeding season (t=1.40, P>0.1, N=129, 115).

Out of 23 mouthbrooding males, 21 did not have any food items other than some eggs in the stomach (also see Table 4-1.1, **Chapter 4-1**). In the remaining two cases, stomachs contained unidentified matter, which were almost digested: these may have been eaten before mouthbrooding began.

IV. Discussion
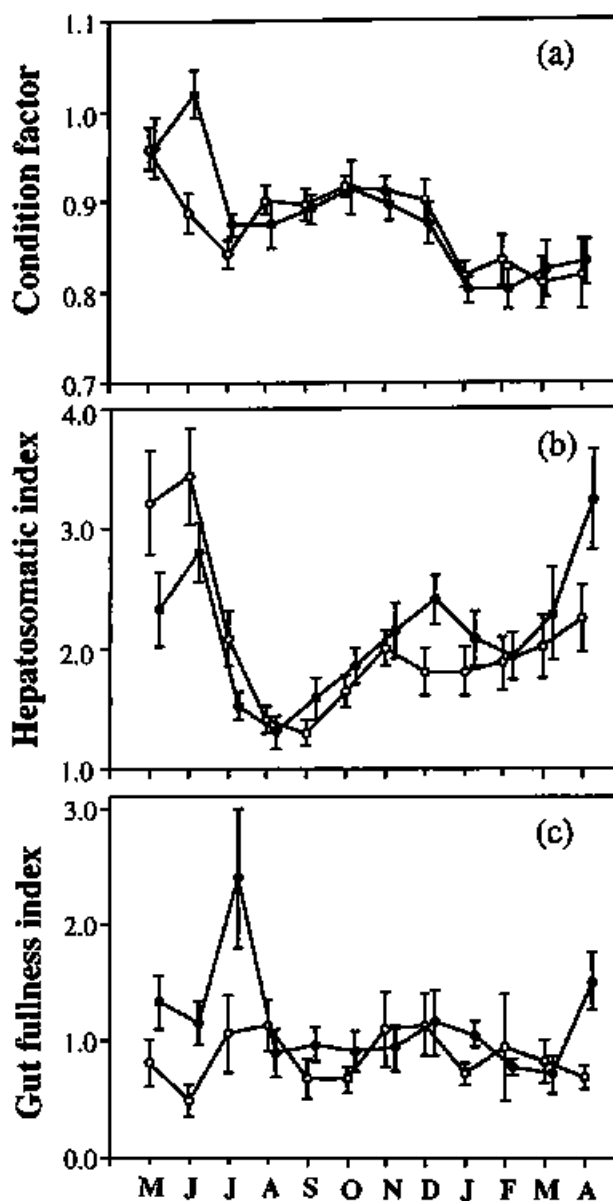
Fig. 2.6 Monthly changes of the condition factor (a), hepatosomatic index (b), and gut fullness index (c) for males (open circles) and females (closed circles). Vertical lines indicate the standard error.

Somatic condition and reproductive costs

The HSI of male *Apogon doederleini* declined rapidly during the breeding season. This species has no intestinal fat in the mesentery, namely, a nonfatty fish. It is well known that nonfatty fishes store a large quantity of lipid in the liver to prepare for reproduction and their liver weight decreases through the breeding season (Jangaard et al. 1967, Medford and Mackay 1978, Diana and Mackay 1979). The decrease of HSI is generally greater in females than in males because of the great effort required of females for egg production (e.g. pike *Esox lucius* (Lenhardt 1992), cod *Gadus morhua* (Jangaard et al. 1967) and *G. macrocephalus*, (Smith et al. 1990) and burbot *Lota lota*, (Pulliainen and Korhonen 1990)). In *A. doederleini*, in contrast, the decrease of HSI was greater in males than in females. Parallel to the decrease of HSI, the males also decreased K during the breeding season. The somatic weight loss of males during the breeding season is commonly known in paternal fishes (e.g. minnow *Pimephales promelas* (Unger 1983), threespine stickleback *Gasterosteus aculeatus* (Dufresne et al. 1990), cat fish *Genidens genidens* (Barbieri et al. 1992) and river bullhead *Cottus gobio* (Marconato et al. 1993)).

In the breeding season, males of *A. doederleini* spent 78% of their time mouthbrooding eggs. During the mouthbrooding period, they did not take any food items other than a few eggs. The decrease in HSI and K during the breeding season may be primarily due to their limited food intake. Under a fasting treatment, the rainbow trout *Salmo irideus* decreased HSI by 49.6% in 85 days (Takashima et al. 1971). The daily specific decrease rate of male *A. doederleini* ($1.46 \times 10^{-2}\%\cdot\text{day}^{-1}$) is greater than that of this fish ($0.81 \times 10^{-2}\%\cdot\text{day}^{-1}$). It is likely that males of *A. doederleini* are under very poor ration conditions throughout the breeding season and therefore their somatic condition severely deteriorates as the season progresses.

Male mortality was high late in the breeding season. Reproduction carries a survival cost in some ways (Roff 1992): conspicuous reproductive action puts reproducing organisms at risk from predators, intense intra-sexual combat for mates does them a fatal injury and/or the deterioration of somatic condition during reproduction increases the risk of death through disease, hyposthenia and starvation. In external egg bearers such as pipefishes, reproduction may increase a likelihood that parents are preyed upon because they often more visible and less mobile (Svensson 1988). However, males of *A. doederleini* rarely disappeared during the mouthbrooding period. This result

suggests that the predation risk involved by mouthbrooding action is less important in the mortality of this species. The competition for mates may not also account for male high mortality because it is less intense among the males (Okuda and Yanagisawa 1996b; also see **Chapter 4-2**). The males begin to metabolize their own muscle tissue in the late breeding season, when they have already exhausted the fat reserve (Omori et al., unpublished data). This nutritive condition is very severe for fish (Templeman and Andrews 1956) and may cause an increase in the mortality. The annual mortality was slightly higher in males. Therefore, the cost of male parental care may be greater than the reproductive cost of females.

V. Summary

The paternal mouthbrooding cardinal fish *Apogon doederleini* reproduced from May to August in temperate waters of southern Japan. Juveniles appeared early in June and reached maturity in the next season. After spawning in pairs, males mouthbrooded eggs for 5-17 days, depending on water temperature. During this period, they took almost no food items. Males raised 4-7 broods in a season and females produced 4-9 broods. The males spent 78% of the time mouthbrooding during the breeding season and their somatic condition more greatly lowered in the late breeding season than that of females. Male mortality in this season was among the highest through the year. The observed life span was 5 and 7 years for males and females, respectively. These results suggests that males suffer a greater overall energetic cost associated with parental care.

Chapter 3

Life history strategy:
A trade-off between growth and reproduction

I. Introduction

Ectothermic vertebrates (i.e. fishes, amphibians and reptiles) generally show indeterminate growth, continuing their growth after maturation. This pattern is explicable in terms of fecundity advantage. As the internal space to accommodate eggs or embryos increases with the body size, their clutch size will increase in proportion to their body size (Tilley 1968, Wootton 1979, Lemen and Voris 1981, Gibbons et al. 1982, Ford and Seigel 1989). This advantage of large clutch size will not be impaired by the breeding ability of the parents, because their post-laying care is generally either lacking or non-depreciable, where costs do not increase proportionally with clutch size (Blumer 1979, Gross and Shine 1981, Shine 1988).

In contrast, in homeotherms (i.e. birds and mammals), litter or clutch size correlates less positively with maternal size, although the offspring body size may depend on maternal size (Blueweiss et al. 1978). This obscure size-fecundity relationship is due partly to the narrow size range of mature adults resulting from their determinate growth. A crucial constraint on offspring number is the rearing of hatched or live-birth young until fledgeling or weaning, irrespective of parental size. For example, avian clutch size is restricted strongly by the ability of parents to feed young (Lack 1954) and mammalian litter size by lactation ability (Clutton-Brock 1991). An increase in offspring number often results in a high offspring mortality and lowers parental survivorship and future fecundity (Dijkstra et al. 1990, Roff 1992).

Determinate growth is generally linked with reproductive constraints in homeotherms, but this rule may also be applicable to ectothermic vertebrates if they have a particular set of brooding constraints. Here I focus on the fishes, which have a great variety of reproductive styles, from no parental care through paternal to maternal care in external fertilizers, and from oviparity to viviparity in internal fertilizers (Gross and Sargent 1985), and with which interspecific variation in

the size-fecundity relationship is great (Wootton 1979). First, I describe a case study of the cardinal fish *Apogon doederleini*, focussing on its growth pattern and size- and age-fecundity relationships. Second, using a modified model of Kozlowski and Uchmanski (1987), I discuss if determinate growth is linked with brooding constraints in *A. doederleini*.

II. Methods

Measurement of life history parameters

Life history of *Apogon doederleini* was investigated at Murote Beach, from 1992 to 1994 (**Chapter 2**). At the beginning of the breeding season of 1992, I captured and marked underwater all individuals of this fish inhabiting a 10×20m quadrat on the boulder slope. I removed a few scales from the body with a pair of tweezers and preserved them in 10% formalin to age the fish in the laboratory. The fish were released at the capture sites after measurement of their standard length (SL). Prior to the breeding season of 1993 and 1994, these procedures were repeated for all surviving marked individuals and new residents.

From three years mark-recapture data, the annual individual growth rate was calculated. The growth rate (G_t) at age t is given as follows,

$$G_t = (\ln L_{t+1} - \ln L_t) \times 100 \tag{1}$$

where L_t represents SL (mm) at age t. The growth pattern is fitted to the von Bertalanffy growth equation,

$$L_t = L_\infty (1 - \exp(-K(t-t_0))) \tag{2}$$

where L_t is the length at age t, L_∞ the asymptotic length, K the growth coefficient, and t_0 the hypothetical time at which the length is zero. K determines the shape of the growth curve: the greater is K, the more steeply the growth curve ascends and the more sharply it bends. To fit the von Bertalanffy model to the data set of annual individual growth increments, a Walford plot was

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used: when L_{t+1} of each fish is plotted against its L_t, the linear regression gives values of K and L_∞ (Ricker 1979). Here, the length of newly-hatched larvae (3.15mmTL; Kuwamura 1983a) was substituted for L_0.

To estimate a potential growth rate of *A. doederleini*, I made monthly correction of juveniles at Funakoshi Beach, from May 1992 to April 1993. Below an inflection point of juvenile growth curve, all energy is considered to be allocated to growth (Kozlowski and Uchmanski 1987).

Measurement of reproductive success

Daily observations enabled me to obtain data on the number of broods which each female produced and each male received during the entire breeding season of 1993 (**Chapter 2**). To count the number of eggs per brood, I captured a total of 62 males outside the quadrat at two different mouthbrooding phases: within a day of spawning (N=11) and one or two days before the expected day of hatching (N=51). After anaesthetizing them with quinaldine, I removed the broods and measured SL of the males. In 47 cases where their mates could be identified, I also measured SL of these females.

III. Results

Growth

Body size differed significantly among age-groups (ANOVA, df=6, F=51.0, P<0.0001; Table 3.1). When the body size was compared between two successive age-groups, however, the difference was significant only between 1- and 2-year-old fish (Scheffe F-test, F=18.1, P<0.0001) and between 2- and 3-year-old fish (F=5.79, P<0.0001). No sexual size dimorphism was seen in the same age-groups (two-way factorial ANOVA, P>0.8). The minimum size at maturity was 69.0mm in the male and 73.0mm in the female.

One-year-old fish grew at a high rate but the growth of more than 1-year-old fish decreased drastically (Table 3.1); the growth rate of 1-year-old fish was significantly higher than that of fish in any other age-class (Scheffe F-test, P<0.05 for each). No sexual difference was seen in the

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growth rate in the same age-groups (two-way factorial ANOVA, P>0.2).

Table 3.1. Body size and growth rate in each age-group of *A. doederleini*.

Age	N	Standard length (mm)	N	Annual growth rate (%)
1	9	71.0 ± 3.32SD	4	17.5 ± 5.59SD
2	55	82.8 ± 3.43SD	40	3.33 ± 2.65SD
3	69	86.2 ± 3.31SD	43	2.03 ± 2.18SD
4	59	87.9 ± 2.93SD	16	0.36 ± 2.07SD
5	19	89.1 ± 2.71SD	6	0.20 ± 1.76SD
6	6	90.8 ± 1.78SD	1	-5.07
7	1	85.5	0	—

Data from 1992 to 1994 are pooled. Body size in each age-group did not differ between the years (two-way factorial ANOVA).

From the linear regression of L_{t+1} against L_t, the three parameters of the von Bertalanffy equation were obtained as follows: K=1.56, L_∞=86.5, t_0=-0.02 for the male (r^2=0.86, N=48, P<0.0001) and K=1.62, L_∞=88.6, t_0=-0.02 for the female (r^2=0.71, N=71, P<0.0001). Growth curves were similar between the sexes (Fig. 3.1).

No juveniles were captured at Funakoshi Beach in May and June. Their growth exponentially increased from July to October and thereafter retarded gradually (Fig. 3.2). The potential growth rate was estimated to be $79.3L^{0.0476}$ from their growth within four months of settlement.

Reproductive success
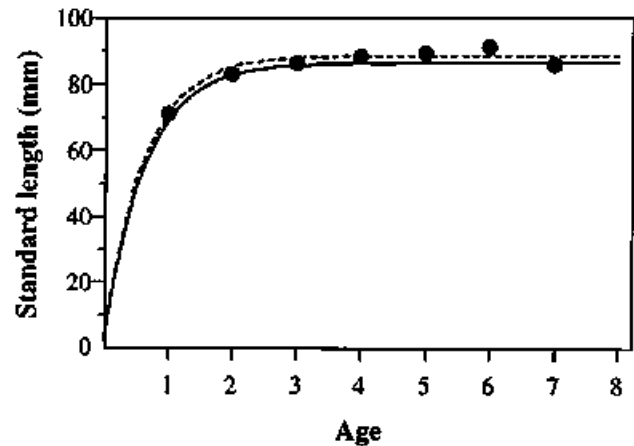
Fig. 3.1 Hypothetical growth curves drawn from the von Bertalanffy growth equation. Solid and dotted lines are for the male and female, respectively. Each plot presents the mean body length in Table 3.1.
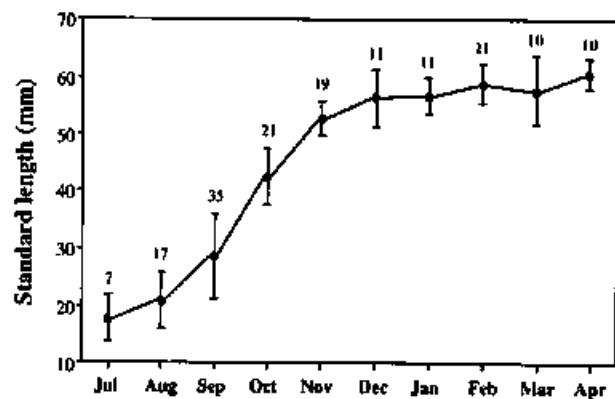
Fig. 3.2 Monthly changes of the body size of juvenile *A. doederleini*. Vertical lines and numerals indicate the standard deviation and sample size, respectively.

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The size of broods removed just before hatching ($\bar{x}\pm$SD=8567±1641, N=51) was significantly smaller than that removed on the day following spawning (10177±1580, N=11; t=2.97, P<0.005), although there was no significant difference in body size of the parents between the two groups (t=-1.48, P>0.1 for the male; t=-0.37, P>0.7, N=8, 39 for the female). Spawning pairs were size-assortative (r^2=0.71, P<0.0001, N=39), and brood size just before hatching positively correlated with body size of the male (r^2=0.44, P<0.0001, N=51) and of the female (r^2=0.29, P<0.0005, N=39). Stepwise multiple regression analysis, however, showed that this brood size correlated with male size (R^2=0.42, F=27.2, P<0.0001) but not with female size. The relationship between brood size (y) and male size (x mmSL) is expressed by an allometric equation, y=1.44$x^{1.96}$.

Brood size near hatching increased with male age (Table 3.2). However, the stepwise multiple regression analysis showed that most of the variance in brood size was explained by variance in male size (R^2=0.39, F=30.0, P<0.0001) but not in male age. Brood size also did not correlate with female age (r^2=0.05, P>0.1, N=39).

The number of broods that a male received in one breeding season positively correlated with his body size (r^2=0.22, N=30, P<0.01) but not with his age (r^2=0.01, N=30, P>0.5). As a result

Table 3.2. A life table of *A. doederleini* showing survival rate ($l(x)$) and annual reproductive success ($m(x)$). Sample size in parentheses.

Age	$l(x)$ [a]	Male Brood size	Male No. of hatched broods	$m(x)$	Female Brood size of mate [b]	Female No. of hatched broods	$m(x)$
1	1.00	4577±717SD (3)	4 (1)	9154	5788	3 (1)	8682
2	0.30	8469±899SD (6)	6 (1)	25407	8493	4 (1)	16986
3	0.21	8720±1322SD (36)	5.82±1.02SD (17)	25375	8748	5.74±1.20SD (19)	25107
4	0.13	9679±1682SD (5)	5.56±0.73SD (9)	26908	8166	5.20±1.64SD (5)	21232
5	0.07	9014 [c]	5.00±0.00SD (2)	22943	8991	5.75±2.22SD (4)	25849
6	0.04	—	—	—	9375	6 (1)	28125
7	0.02	—	—	—	—	—	—

[a] Relative values calculated from the annual survival rate in Table 2.1, Chapter 2.

[b] Brood size estimated from the mean length of mates with which females spawned.

[c] Brood size estimated from the length back-calculated from the von Bertalanffy equation.

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of occasional brood cannibalism by mouthbrooding males (Okuda and Yanagisawa 1996a, b; also see **Chapter 4-1**), variance in the number of broods that a male hatched in one breeding season (s^2=0.86, Min=4, Max=7) was smaller than that of broods that he received (s^2=1.70, Min=5, Max=10), and the number of broods hatched correlated weakly with male size (r^2=0.15, N=30, P<0.04). The number of broods that a female produced in one breeding season correlated weakly with her body size (r^2=0.12, N=31, P=0.05) but not with her age (r^2=0.11, N=31, P>0.07). The number of broods that her mates successfully hatched did not correlate with her body size (r^2=0.10, N=31, P>0.09).

From the above data, annual reproductive success at age x (m_x) was obtained for each sex. The m_x is expressed as half of the average brood size near hatching multiplied by the average number of broods hatched in a breeding season (Table 3.2). The annual reproductive success increases until age 2 in the male and until age 3 in the female and thereafter it remains nearly constant (Fig. 3.3). The reproductive expectancy ($l_x m_x$), which is here defined as the expectancy of reproduction at age x, is greatest at age 1 for both sexes, and contribution to the lifetime reproductive success decreases with age (Fig. 3.3).
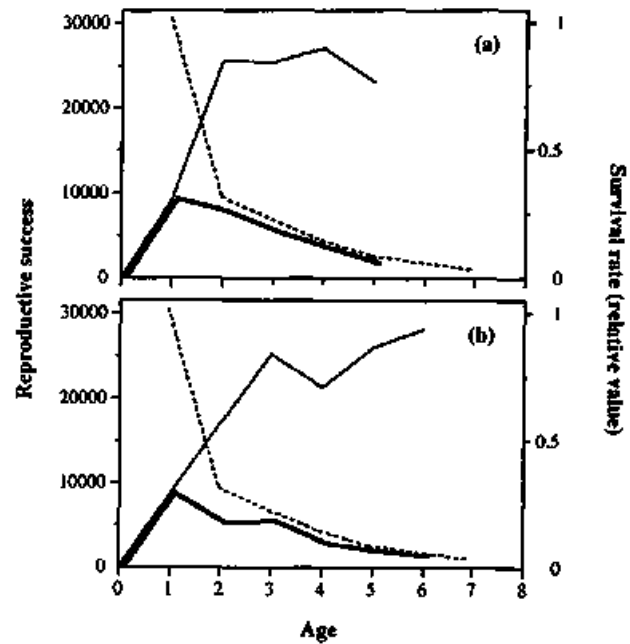
Fig. 3.3 The reproductive expectancy $l(x)m(x)$ (thick lines) calculated from $l(x)$ (dotted lines) and $m(x)$ (thin lines) in Table 3.2 for the male (a) and female (b), respectively.

IV. Discussion

Growth pattern

Growth of *Apogon doederleini* showed a marked decrease at age 2 and became nearly asymptotic at age 3. The relative size at maturity to asymptotic size (L_α/L_∞), which is an index of determinate growth, was 0.80 for the male and 0.82 for the female. The value of L_α/L_∞ varies greatly among

fish species from 0.22 to 0.87 (Appendix I), with the mean value of 0.61 (Beverton and Holt 1959). The value of L_α/L_∞ for *A. doederleini* is among the highest of fish species (Fig. 3.4), and higher than the mean values of snakes (0.68, Shine and Charnov 1992) and lizards (0.74, Shine and Charnov 1992), though not as high as the mean value of birds (0.96, Ricklefs 1968).

The von Bertalanffy growth coefficient K for male and female *A. doederleini* is 1.56 and 1.62, respectively. These values are the highest known for fishes (mean=0.33, Fig. 3.5). A high
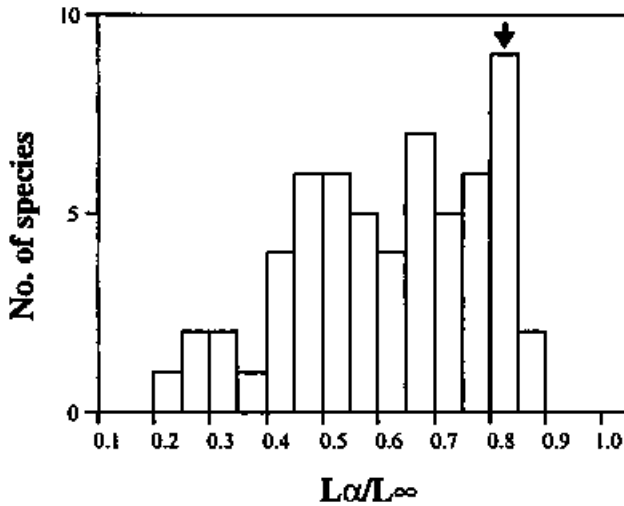
Fig. 3.4 Frequency distribution of L_α/L_∞ among fish species. An arrow indicates the value of *A. doederleini*. Full details given in Appendix I.
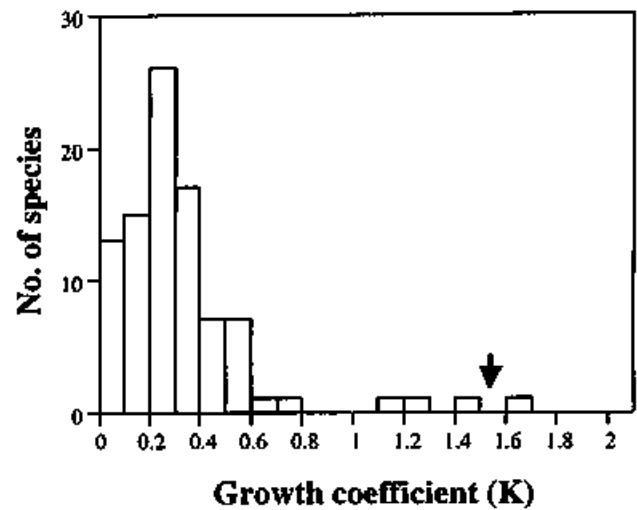
Fig. 3.5 Frequency distribution of the growth coefficient K among fish species. An arrow indicates the value of *A. doederleini*. Full details given in Appendix I.

value of K also indicates effectively determinate growth.

K varies considerably even among populations of a fish species (Appendix I). The growth pattern of fishes is much affected by biotic and abiotic factors (Wootton 1991), of which food availability and predation pressure have been accepted as the most influential factors in natural populations (Mann 1973, Nakashima and Leggett 1975, DeMartini and Anderson 1980, Schmitt and Hubert 1983, Noltie 1988, Chisnall 1989). It is reported in some species that populations under low food availability or high predation pressure depress the growth increment. In *A. doederleini*, different populations attain a similar adult size and show a similar determinate growth pattern (Okuda 1994). In this study site, gammalids, the staple prey of *A. doederleini*, are abundant (Satoh et al. 1993) and potential predators are few. There seems little reason to believe that low food availability or high predation pressure caused the effectively determinate growth in this fish. The

determinate growth of *A. doederleini* may be a species-specific life history trait.

Optimal allocation to growth and reproduction

I here examine how the determinate growth of *A. doederleini* is related to brooding constraints, applying the model of Kozlowski and Uchmanski (1987). This model predicts the optimal lifetime energy allocation to growth and reproduction in a perennial species with indeterminate growth. It assumes that the species lives in a seasonal environment with a stable population, adult mortality is independent of body size, and the switch from growth to reproduction is complete but reversible and occurs at most once per year. On these assumptions, a set of optimal switching time $t1,...,t\omega$ that maximizes the lifetime reproductive success (R_0) is calculated,

$$R_0 = \sum_{k=1}^{\omega} R_k(t_1,...,t_k)$$

where w is the life span and Rk and tk are the number of offspring and the switching time at age k, respectively.

Now, let me consider a model species for *A. doederleini*, which has annual survivability *q* and lives to age 7 (**Chapter 2**). This species has the somatic growth rate $f(L)$ and reproductive rate $H(L)$ with respect to body length L, and produces offspring which are uniform in size and quality and whose survival rate is independent of population density. Individuals are under the same physiological constraints and their food availability is not limited.

I estimated $f(L)$ to be $79.3L^{0.0476}$ (Fig. 3.2). The reproductive rate $H(L)$ was estimated to be $10.1L^{1.96}$, which is equal to the reproductive rate of a male which raised seven broods per season. I here assume that the reproductive rate becomes constant above the critical size L^* due to constraints that repress the reproductive size-advantage: $H(L)=10.1L^{1.96}$ if $L< L^*$ and $H(L)=H(L^*)$ if
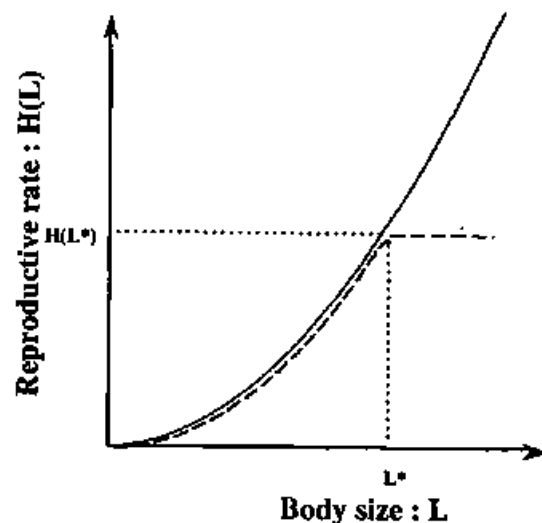
Fig. 3.6 The reproductive rate ($H(L)$)with respect to body size (L)in a species with no reproductive constraints (solid line) and with reproductive constraints (broken line), in which it is assumed that the reproductive rate becomes constant at a critical size L^*.

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$L \geq L^*$ (Fig. 3.6). I consider three stages of limitation: $H1(L)$ is without limitation, $H2(L)$ with an upper limitation at $L^*=176.0$mm and $H3(L)$ with an upper limitation at $L^*=88.0$mm, which is equal to the asymptotic length of *A. doederleini*. The annual survival q is represented as 0.3 and 0.7 from Table 2.1 (**Chapter 2**).

I calculate the optimal fraction of energy allocation to growth with respect to each $H(L)$ with an initial condition of $L_0=3.15$mm. Under high survival (q=0.7; Fig. 3.7a), stronger limitation makes the model species mature at a younger age (3.67, 1.86 and 0.95y for $H1(L)$, $H2(L)$ and $H3(L)$, respectively) and at smaller size (324, 159 and 78.5mm). In any case, it shows an extremely determinate growth ($L\alpha/L_\infty=0.93$, 0.90 and 0.89). In contrast, under low survival (q=0.3; Fig. 3.7b), age and size at maturity are similar among $H1(L)$, $H2(L)$ and $H3(L)$ (0.93, 0.93 and 0.81y and 76.7, 76.7 and 66.4mm). As the limitation becomes stronger, the model species shows a more
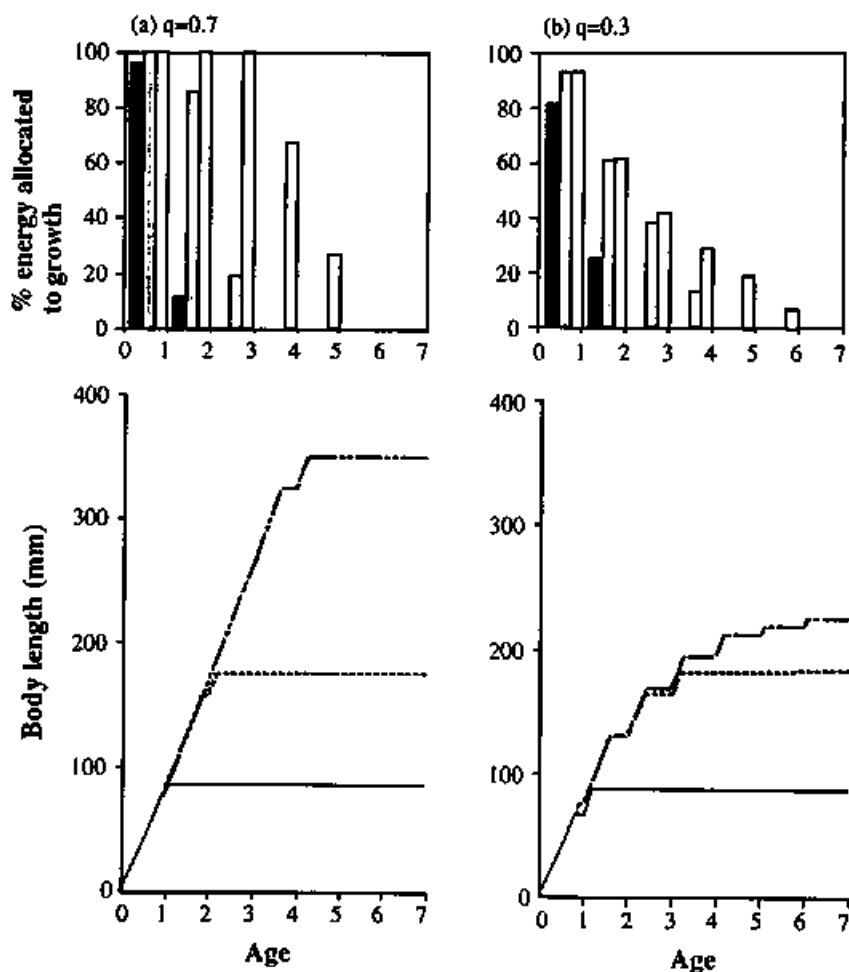
Fig. 3.7 Optimal energy allocation to growth at each age under the condition of q=0.7 (a) and q=0.3 (b) (upper) and the individual growth curve resulting from the optimal allocation (lower). Open, shaded and solid bars and chain, dotted and solid lines show cases of no reproductive limitation, an upper limitation at $L^*=176$mm and $L^*=88$mm, respectively.

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determinate growth ($L\alpha/L_\infty$=0.35, 0.44 and 0.75).

Kozlowski and Uchmanski (1987) demonstrated that in Arctic charr *Salvelinus alpinus*, the predicted growth pattern fitted well with field data, assuming that its fecundity increases indeterminately with growth. In *A. doederleini*, however, the growth curve and reproductive schedule of the model species without a reproductive limitation greatly differ from field data within the range of their possible survival rate. On the other hand, the model species with a reproductive limitation shows similar features to *A. doederleini*. This suggests that there exist some constraints that repress the reproductive size-advantage in *A. doederleini*.

Reproductive constraints

Brood size just before hatching was smaller than that at an early brooding phase, suggesting that a part of the brood had disappeared during the mouthbrooding period. This brood reduction is due to frequent occurrence of partial brood cannibalism (Okuda and Yanagisawa 1996a; also see **Chapter 4-1**). A possible function of partial brood cannibalism for parental males is to adjust the number of offspring to their buccal capacity, rather than to get a nutritive profit. Since mouthbrooding males aerate the brood continuously by churning, overcrowding may cause a deficiency of air supply and lower the probability of the embryos surviving to hatching. Actually, brood size closely correlates with the volume of the male buccal cavity (M. Miyazaki, unpublished data). Thus male reproductive success may be limited primarily by his buccal capacity.

The male reproductive rate is also restricted by the developmental time of embryos, which varies greatly according to water temperature but is not affected by male size. Since individual males spend about 80% of the time mouthbrooding in the breeding season (**Chapter 2**), there would be little scope left them for increasing the number of broods.

The fact that brood size just before hatching correlates with male size but not with female size indicates that female reproductive success is also limited by the buccal capacity of her mate. If females mate with males much larger than themselves, their mates would be able to brood all eggs that they produce. However, such mating facilitates entire brood cannibalism by these males (Okuda and Yanagisawa 1996b; also see **Chapter 4-2**). Small brood size relative to male brooding capacity will increase the per egg cost of parental care, and the males may abandon the entire brood

when its reproductive return does not offset the care cost (Petersen and Marchetti 1989). In female *A. doederleini*, disproportionate pairing results in decreased reproductive success.

Another limiting factor of female reproductive success is mate availability. Because of a higher potential reproductive rate in the female, receptive males (=non-brooding males) are usually in short supply (Okuda and Yanagisawa 1996b; also see **Chapter 4-2**). Females are the predominant competitors for mates, as in other cardinal fishes (Kuwamura 1985; also see **Chapter 5-2**). However, monopolization of multiple mates does not occur among females because females deliver their single brood to only one male. What females actually do to increase their reproductive rate is to change mates between spawnings (Okuda and Yanagisawa 1996b; also see **Chapter 4-2, 5-2**). The fact that the number of broods produced by one female in a breeding season only weakly correlated with her size suggests that female size has little influence on her mating chances. Thus reproductive success of female *A. doederleini* is not a direct measure of their fecundity but greatly depends on brooding characteristics of males, especially their buccal capacity.

In fish species where males alone orally brood or carry the eggs externally, such as cardinal fishes, pipefishes and seahorses (Blumer 1979, Blumer 1982), the bearing capacity of males is commonly limited. In most of these species, males have a lower potential reproductive rate and limit reproductive success of females (Kuwamura 1985, Berglund et al. 1989, Ahnesjö 1992, Okuda and Yanagisawa 1996b; also see Clutton-Brock and Vincent 1991 for review). Although a larger male has the larger bearing capacity, his reproductive success can also be limited by the fecundity of his mate if she is much smaller than he, as in the case of *A. doederleini*. This is a primary reproductive constraint for paternal bearing species. In this model, the assumption that reproductive success becomes constant above the critical size is based on such a constraint. Both sexes of the paternal bearer could be prevented from indeterminate growth because they limit reproductive success of each other (see **Chapter 5-1**). However, there will be cases for both sexes to grow indeterminately when body size has genetic variance and there is a strong size-assortative mating. It is a theoretical problem to be solved under what conditions the determinate growth by mutual sexual limitation is realized.

V. Summary

Both males and females of *A. doederleini* almost ceased to grow at age 3, though some of them lived to age 7. Their growth pattern, represented by the relative size at sexual maturity to the asymptotic size and the von Bertalanffy growth coefficient, was among the most determinate in ectothermic vertebrates. Brood size just before hatching increased in proportion to the second power of the body size of the brooding male, and correlated more positively with the male's than the female's body size, suggesting that it was limited by the male buccal capacity. The estimated total number of broods hatched in a breeding season showed a weak or no correlation with the body size or age in either sex. Using life history parameters from data of *A. doederleini*, a simulation model of energy allocation without considering sexual interaction revealed that the optimal growth pattern shows an indeterminate growth which greatly differs from actual growth pattern of *A. doederleini*. This suggests that there exist some brooding constraints to size-advantage of reproductive success in this species. The primary constraint to reproduction in *A. doederleini* is that reproductive success of both sexes are limited by each other.

Chapter 4

Filial cannibalism as sexual strategy

4-1. Physiological aspect:
Energetic cost of parental care

I. Introduction

Paternal care is the prevalent care style in fishes (Blumer 1979, Blumer 1982). In many paternal fishes, filial cannibalism, that is, eating of offspring by the parents, has been reported (reviewed by Dominey and 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, thereby remaining in good physical condition for re-mating (Rohwer 1978). Some studies have suggested that deterioration of somatic condition in brooding males is the primary factor in the incidence of filial cannibalism (Rohwer 1978, DeMartini 1987, Petersen and Marchetti 1989, Petersen 1990, Belles-Isles and FitzGerald 1991, Marconato et al. 1993). However, few studies have examined parental somatic condition quantitatively in connection with filial cannibalism (but see Marconato et al. 1993).

Mouthbrooding is an effective care style under high predation pressure on offspring (Keenleyside 1991). However, it usually forces the parents to fast throughout the mouthbrooding period (Oppenheimer 1970; but see Yanagisawa and Sato 1990, Yanagisawa and Ochi 1991). The cost of mouthbrooding may be higher than that of guarding on the substrate and may greatly lower the somatic condition of the brooders. Species in which males mouthbrood the young may be particularly likely candidates for filial cannibalism. Filial cannibalism in mouthbrooders has been observed when brood size was experimentally varied in aquaria (Mrowka 1987). In nature, however, there are no unambiguous reports that mouthbrooding fish have actually eaten their own eggs, except for Kuwamura (1983) reporting that eggs were found in the stomachs of mouthbrooding cardinal fish *Apogon notatus*.

The cardinal fish *Apogon doederleini*, the subject animal of this chapter, is also a paternal mouthbrooder. In **Chapter 2**, I showed that male somatic condition deteriorated due to the limited feeding opportunities during the mouthbrooding period. Thus, males of this species are most likely to eat their own eggs while mouthbrooding. In this chapter, I examine how the occurrence of filial cannibalism is correlated with the parental somatic condition.

II. Methods

Confirmation of filial cannibalism

Study was conducted at Murote Beach in 1992 and 1993. I investigated reproductive experiences for marked males of *Apogon doederleini* inhabiting a 10×20m quadrat (**Chapter 2**). I sometimes found broods disappearing from males' mouths before the expected day of hatching. In such cases, I captured the males and anesthetized them underwater with quinaldine. Then I extracted a small part of their stomach contents by plunging a needle-less syringe of 1 ml through the esophagus. If the extracted stomach contents included eggs of the same developmental stage as those which he had brooded, I judged that the egg disappearance was due to filial cannibalism. Once recovered from the anesthesia, the males were released at the capture sites. By this method, I confirmed filial cannibalism without killing fish.

Stomach contents analysis

I captured 23 brooding and 20 non-brooding males of *A. doederleini* at Funakoshi Beach in the breeding season (**Chapter 2**). The fish were preserved in 10% formalin and were used for analysis in the laboratory. I dissected the fish and extracted their gut. I weighed the gut contents in wet condition and noted whether the stomach contained conspecific eggs. The fish body and other organs were dried and weighed. The gut fullness index (GFI = 100 × wet weight of gut contents / total wet body weight) was calculated.

III. Results

Occurrence of filial cannibalism

In daily censuses in 1992 and 1993, 47 of 361 broods disappeared from the males' mouths before the expected day of hatching. These broods all disappeared within a day of spawning. In two cases, males had lost their broods and their bellies were not inflated when I visited them to observe their post-spawning behavior. I conjectured that these two broods had disappeared due to predation before or after the males took them into their mouths, because post-spawning males were often chased by fishes such as labrids and apogonids (also see Kuwamura 1983b). All other males were potbellied when the brood disappearance was noticed. For 28 such males whose stomach contents were checked with a needle-less syringe, early developmental eggs were found in all stomachs.

In a few cases, a male had an inflated belly soon after post-spawning behavior while some part of the egg mass was still in his mouth. The remaining egg mass was frequently turned round in the mouth. Within a few hours, his belly became more inflated. However, in most cases, a male retained the egg mass in his mouth until the evening but in the census of next day (at about 1100 hours), he had an inflated belly and the egg mass had disappeared from his mouth.

The occurrence rate of filial cannibalism, the proportion of broods cannibalized to total broods spawned, was 8.6% (13/152) in 1992 and 15.5% (32/207) in 1993. The rate was low in the early breeding season but increased as the season progressed (χ^2=9.61, df=3, p<0.03; Fig. 4-1.1).
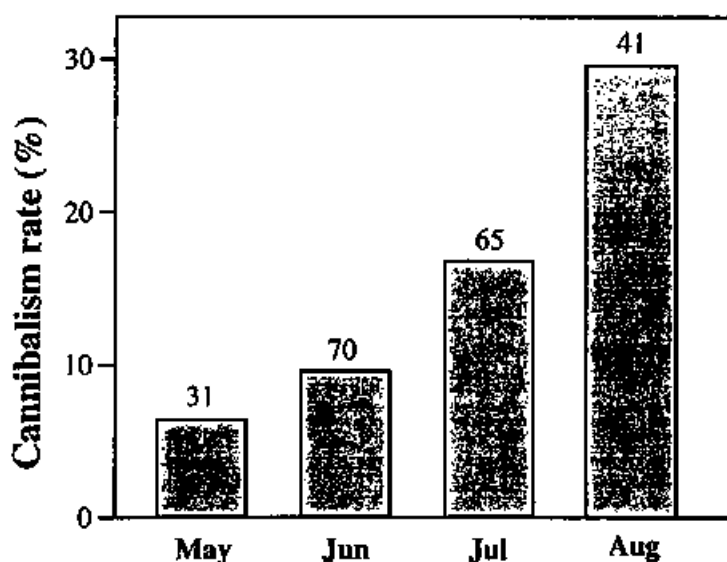
Fig. 4-1.1   Monthly changes in the rate of filial cannibalism in 1993. Sample sizes above bars.

Stomach contents

The stomachs of mouthbrooding males did not contain any ordinary food items (Table 4-1.1), except for two males whose stomach contents were almost digested; these may have been eaten before mouthbrooding began. In contrast, most males brooding young eggs had some eggs in their stomachs, while most males brooding late-stage eggs had empty stomachs (Fisher's exact probability test, early vs. middle: $P>0.3$, early vs. late: $P<0.05$, middle vs. late: $P>0.3$). Except for two males whose stomachs contained only a few unfertilized eggs, eggs in their stomachs were at the same developmental stage as those they were brooding. This suggests that they ate their own eggs. The proportion of eggs eaten to the entire brood ranged from 0.02 to 19.4% ($\bar{x}$ $\pm SD=8.06\pm9.66$, N=4); most of eggs in the stomachs were semi-digested and were not countable. The stomach of one mouthbrooding male contained an egg mass as large as the entire brood, suggesting that he had re-spawned with other female soon after filial cannibalism of the previous brood. The GFI for the males brooding young eggs was not significantly different from that for non-brooding males in the breeding season ($\bar{x}\pm SD=0.76\pm0.60$, N=20; Mann-Whitney U-test, $p>0.05$). The GFI for the mouthbrooding males decreased remarkably as the developmental stage of their broods advanced (ANOVA, F=3.66, df=2, $p<0.05$; Table 4-1.1).

Table 4-1.1. Stomach contents and GFI of males at various mouthbrooding phases. The mouthbrooding phase was divided into three by egg coloration.

Mouthbrooding phase	N	Stomach contents			GFI
		Empty	Eggs	Unidentified matter	Mean±SD
Early	9	0	7	2	1.66±1.80
Middle	7	4	3	0	0.44±0.42
Late	7	6	1	0	0.22±0.13
Total	23	10	11	2	0.85±1.29

IV. Discussion

Filial cannibalism

Filial cannibalism is categorized into partial and entire brood cannibalism (Smith 1992). This study demonstrated that both types of filial cannibalism frequently occurred: at least 48% of mouthbrooding males practiced partial brood cannibalism (Table 4-1.1), while 8.6% (1992) and 15.5% (1993) performed entire brood cannibalism in a breeding cycle.

Both types of filial cannibalism occurred during the early mouthbrooding phase: all cases of entire brood cannibalism occurred within a day of spawning. Some studies on filial cannibalism in fishes report that parents preferentially eat young eggs (Salfert and Moodie 1985, Petersen and Marchetti 1989, Petersen 1990). FitzGerald (1991) suggested that the preference for young eggs is due to the greater nutritive value and less reproductive value of these eggs. In addition, in the case of entire brood cannibalism, early egg consumption can minimize the parental effort that yields no reproductive return.

Rohwer (1978) proposed that partial brood cannibalism would give a parent the energy to care for the present brood and keep it in good condition until the subsequent brood cycle. However, Smith (1992) demonstrated in the stickleback *Gasterosteus aculeatus* that energy gain by partial brood cannibalism does not exceed the loss by parental care. For *A. doederleini* males which consume only a small portion of the brood (less than 20% of the entire brood), energy gain also may be insufficient for maintaining good somatic condition. As stated in **Chapter 3**, brood size of males was limited primarily by their buccal capacity. Since mouthbrooding males aerate an egg mass continuously by churning, overcrowding may cause a deficiency of air supply and lower the probability of the embryos surviving to hatching. A possible function of partial brood cannibalism for male *A. doederleini* is to adjust the number of offspring to their buccal capacity, rather than to get a nutritive profit.

When a parental male cannibalizes the entire brood, he may re-allocate its energy to future breeding cycles (Rohwer 1978, Dominey & Blumer 1984). Rohwer (1978) hypothesized that, in species with several breeding cycles per season, parents should be more cannibalistic in the early breeding season because they have less chance of re-mating in the late breeding season. On the

contrary, Petersen (1990) and Belles-Isles & FitzGerald (1991) reported that filial cannibalism in a damselfish and a stickleback occurred in the late breeding season, respectively. Even in a species with a single breeding cycle per season, of which duration is very long, parents tend to eat their own eggs at the end of this cycle (e.g. river bullhead *Cottus gobio* (Marconato et al. 1993)). Also in *A. doederleini*, I found that entire brood cannibalism occurred frequently in the late breeding season, when the somatic condition of males lowered. These cases suggest that the parental males practice filial cannibalism to reverse the deterioration in their somatic condition, consequently improving their survival.

In this species, it is obvious that the parental somatic condition is an important factor in the occurrence of entire brood cannibalism. Then, why did not more males practice entire brood cannibalism in the late breeding season? And, why did some males do so in the early breeding season? In the following chapter, I will discuss another factor facilitating filial cannibalism by male *A. doederleini*.

V. Summary

Entire broods sometimes disappeared from mouthbrooding males *Apogon doederleini* within a day of spawning. A stomach check with a syringe ascertained that these brood disappearances were due to filial cannibalism. The incidence of this cannibalism was higher late in the breeding season. It is suggested that the parental males practiced entire brood cannibalism to improve their somatic condition that lowered as the breeding season progressed. The males also frequently ate the small portion of their own broods at the early mouthbrooding phase. Its possible function for parental males is to adjust the number of offspring to their buccal capacity, rather than to get a nutritive profit.

4-2. Sociobiological aspect:
Conflict of interests between sexes

I. Introduction

Filial cannibalism is categorized into partial and entire brood cannibalism (Smith 1992). Rohwer (1978) suggested that partial brood cannibalism would give a parent the energy to care for the remaining brood. Theoretically, if partial brood cannibalism represents an investment in the remainder of the current brood, the incidence of this cannibalism will increase with brood size (Sargent 1992). In contrast, entire brood cannibalism is more likely when broods are small (Ochi 1985, Petersen and 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 and Blumer 1984). By cannibalizing the brood, the parent may re-allocate its time and energy to the future brood cycle.

The reproductive loss 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. In **Chapter 4-1**, I described that male *Apogon doederleini* cannibalized entire broods and concluded that this cannibalism was facilitated by deterioration of male somatic condition. However, several males cannibalized the entire broods in the early breeding season, when they are estimated to be in good physical condition. I propose a possibility of male mate availability as another factor facilitating entire brood cannibalism in *A. doederleini.*

So far, no studies have related filial cannibalism to mate availability for cannibals; most reports on filial cannibalism are based on circumstantial evidence from the analysis of stomach contents (but see Hoelzer 1988, Petersen and Marchetti 1989). In the previous chapter, I confirmed the occurrence of filial cannibalism by extracting some of the stomach contents from live fish using a syringe. This non-destructive method enabled me to obtain information on their mating and cannibalistic experiences throughout the breeding season. In this chapter, I explore how filial cannibalism by male *A. doederleini* is related to mate availability.

II. Methods

Field observation

I observed reproductive behavior of *Apogon doederleini* inhabiting a 10×20m quadrat at Murote Beach in 1992 and 1993 (**Chapter 4-1**). I made daily censuses throughout the breeding season of 1993. In each census, I recorded 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; stage V: belly fully expanded and genital papillae protruded.

To identify spawning pairs of marked fish, I followed the methods in **Chapter 2**. When I had observed only the courtship display of a pair but found the male mouthbrooding or potbellied next day, I 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 I judged that he or she had spawned with an unmarked fish.

The sheltering site of each fish was defined as the site where I 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.

I did not census the fish over the entire breeding season in 1992, so I 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), I removed broods from these males at two different mouthbrooding phases: on the day after spawning, and 1-2

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days before the expected day of hatching. Because entire brood cannibalism always occurred within a day of spawning (**Chapter 4-1**), the former brood removal is equivalent to entire brood cannibalism in terms of timing. After the brood removal, I observed the time interval until the next spawning of these experimental males. This manipulation was performed one to six times for each male during the breeding season of 1993.

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

III. Results

Mating system and spawning cycle

Apogon doederleini showed strong site fidelity: males on average shifted only 2.1 m (±2.0SD, N=19) and females 2.6 m (±4.7SD, N=28) between the two breeding seasons. Courtship displays between marked fish usually took place near their sheltering sites ($\bar{x}$±SD=2.1±2.9m from male sheltering sites, 1.7±2.0m 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 (±0.56SD, N=203) for males and 1.28 (±0.52SD, N=215) for females. After spawning or courtship, the male and female in a pair separated to their respective sheltering site, 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 3m (Fig. 4-2.1). Thirty-eight spawnings took place between marked males and unmarked females and 45 spawnings between marked females and unmarked males. For the remaining 11 spawnings, I was
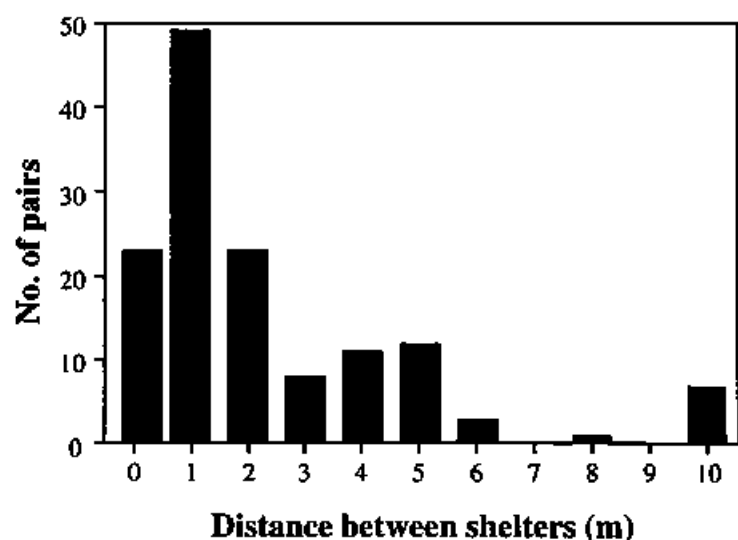
Fig. 4-2.1   The distance between sheltering sites of a male and female in a spawning pair (N=138). Sheltering sites in March 1993 were used except for new residents.

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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. I 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 absence rate [(the total number of absences) / (the total number of censuses)] (285/3106) was significantly higher than that of marked males (178/2741; χ^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 6.8 broods (±1.3SD, N=30) and mated with 3.5 different females (±0.9SD) and a female produced 6.3 broods (±1.2SD, N=31) and mated with 3.4 different males (±1.4SD). The mate change rate per spawning did not differ between the sexes (68.2%, N=154 for males and 69.1%, N=162 for females, χ^2=0.03, df=1, P>0.8). The inter-spawning interval of females was shorten when they had changed their mates, but that of males was not (Table 4-2.1).

When only male spawnings that resulted in hatching of eggs were considered, the inter-spawning interval of males was 15.2 days (±3.0SD, N=141), and that of females was 14.8 days (±4.1SD, 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 females-biased (see Fig. 4-2.2), the interval was more variable in females (Table 4-2.2). 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

Table 4-2.1. Inter-spawning interval of males and females that did or did not change mates.

| Sex | Inter-spawning interval (days) | | | | | |
| | Change | | No change | | | |
	N	Mean±SD	N	Mean±SD	t	P
Female	112	14.1±4.2	50	16.2±3.4	-3.17	0.002
Male	84	15.5±3.3	49	15.7±3.0	-0.36	0.72

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

Table 4-2.2. 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)				z*	p
			Male		Females			
			N	Mean±SD (Min-Max)	N	Mean±SD (Min-Max)		
Early	16 May - 19 June	19.5 (18.3-21.3)	35	15.9±1.8 (13-22)	37	17.0±2.1 (11-21)	1.65	0.10
Middle	20 June - 24 July	19.6 (18.0-22.0)	58	16.8±1.7 (12-22)	77	14.5±3.3 (6-30)	3.09	0.002
Late	25 July - 28 August	24.3 (19.0-25.7)	48	12.7±3.4 (9-24)	64	13.8±5.1 (4-31)	0.98	0.33

* Kolmogorov-Smirnov two-sample test

days were recorded in 12 females (6.7%).

The sex ratio (males : females) of the adult population was nearly constant throughout the breeding season, ranging from 0.78 to 1.00 (Fig. 4-2.2). 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), I defined receptive females as individuals whose belly expansion was at stage 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
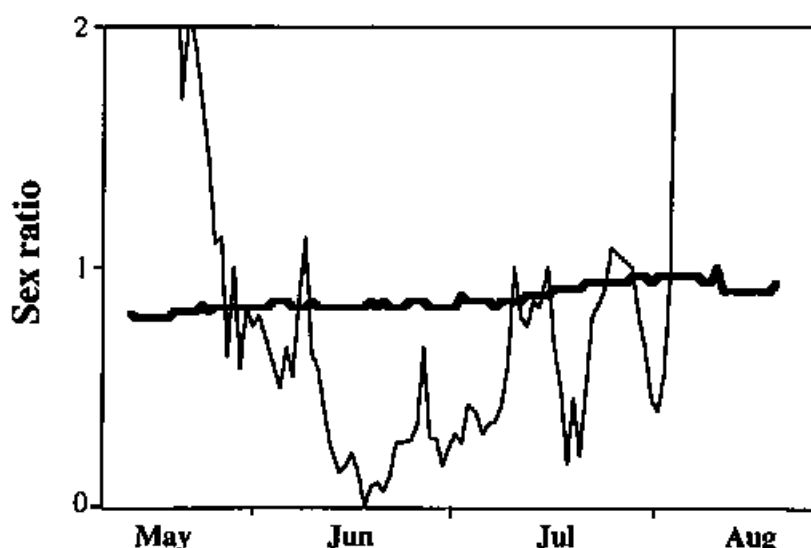
Fig. 4-2.2   Seasonal changes of the adult sex ratio (thick line) and the operational sex ratio (thin line).

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) practiced 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, χ^2=16.3, df=1, P<0.0001).

The cannibalistic males on average re-spawned 3.1 days after cannibalism (Table 4-2.3). They re-spawned as quickly as males whose broods hatched (Mann-Whitney U-test, z=-1.76, N=32, 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=7, 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=47, 144, P>0.1).

Cannibalistic males did not court more females before spawning ($\bar{x}$±SD=1.2±0.4, N=30) than non-cannibalistic males (1.4±0.6, 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 ($\bar{x}$±SD=1.0±1.8 days, N=30)

Table 4-2.3. The effect of different causes of brood disappearance on the time to re-spawn in males.

Group	Cause of brood disappearance	Time to re-spawn after brood disappearance(days)		
		N	Mean	SD
Natural	Cannibalism	32	3.1	3.0
	Hatching	144	3.5	2.5
Experimental	Removal on the day after spawning	7	7.6	5.3
	Removal 1-2 days before hatching	47	4.4	3.6

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and non-cannibal males (1.1±1.6 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 cannibal males (28/30; χ^2=7.32, df=1, P<0.007). The inter-spawning interval of these females ($\bar{x}$±SD=15.7±5.0 days, N=15) was as long as that of females whose broods hatched (14.7±3.9 days, N=159; t=0.86, df=172, P>0.3).

Filial cannibalism and mate choice

Females whose broods were cannibalized at least once ($\bar{x}$±SD=86.4±5.5mm SL, N=18) were as large as females whose broods were never cannibalized (87.3±3.0mm, N=20; t=-0.65, df=36, P>0.5). Cannibalistic males (85.1±4.9mm, N=18) were as large as males who never cannibalized their broods (84.4±2.7 mm, N=12; t=0.48, df=28, P>0.6). The size difference ($SL_{male} - SL_{female}$) in spawning pairs was significantly greater where cannibalism occurred in 1992 but not in 1993 (Table 4-2.4). In the spawning pairs of 1993, females were as large as their mates or slightly larger.

The cannibalism rate of males was higher when they spawned with unmarked (10/38) than with marked females (21/167; χ^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 I was rarely able to locate them in successive censuses.

The number of eggs in a cannibalized brood ($\bar{x}$±SD=10464±1753, N=6) did not differ from that of an early stage brood that was mouthbrooded (10365±1641, N=12; t=0.12, df=16, P>0.9).

Table 4-2.4. 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		t	P
	N	Mean±SD	N	Mean±SD		
1992	10	2.05±2.76	112	-0.86±3.80	-2.36	0.02
1993	22	-0.57±4.62	149	-2.04±3.38	-1.81	0.07

IV. Discussion

Filial cannibalism and mate availability

In this 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 I 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 behavior is often short and intermittently repeated (Kuwamura 1985, Okuda, 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 and Marchetti 1989, Petersen 1990), and filial cannibalism has also been induced by experimentally reducing brood size (Mrowka 1987, Petersen and Marchetti 1989, Lavery and 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, size of broods cannibalized and successfully mouthbrooded 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 countermeasures against cannibalism have not been investigated in detail, I 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 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 cardinal fishes for which data are available have such a monogamous mating pattern (Kuwamura 1983b, Kuwamura 1985, Kuwamura 1987; **Chapter 5-2**; 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 and 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 and Vincent 1991, Clutton-Brock and Parker 1992). Because of a limited brooding capacity and lengthy care period, a female of paternal caring species generally produce 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 4-2.1), 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 (Vincent et al.

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1992, Kvarnemo and Ahnesjö 1996). 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 (T. Takeyama, unpublished data). The third feature is not clear 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

V. Summary

Males of *Apogon doederleini* preferentially ate entire broods produced by smaller females than themselves and by non-resident females, and usually 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, effectively compensating for a parental care cost by eating the first brood and rearing the second. It is suggested that filial cannibalism by the males is associated with mating strategies of females that can shorten inter-spawning intervals by changing mates.

4-3. Evolutionary aspect:
Trade-offs between current and future reproduction

I. 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). 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 of 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: (I) 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, (II) improving survival probabilities by allocating the energy gained from cannibalism to the maintenance of its somatic condition, and (III) 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 *Apogon doederleini* eat their entire brood occasionally during the mouthbrooding

period (**Chapter 4-1**). In the present chapter, I examine how the rate of filial cannibalism of this fish varies with time and with parental age, and estimate in which ways the cannibalistic males make trade-offs between current and future reproduction.

II. Methods

Field study

Study was conducted with the assistance of my colleague at Murote Beach, from 1993 to 1996. Methods are the same as the previous study (**Chapter 4-1, 4-2**). In 1993 and 1995, we measured the standard length (SL) of marked fish *Apogon doederleini* inhabiting a 10×20m quadrat and estimated fish age from their scales. We recorded individual mating experience and the occurrence of entire brood cannibalism throughout the two breeding season. Soon after the finish 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.

We calculated the growth rate and survival rate. The individual growth rate was calculated as follows,

$$G=(\ln L_{t2}-\ln L_{t1})/(t_2-t_1) \times 100$$

where G represents the daily specific growth rate, and L_{t1} and L_{t2} 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 at recapture divided by all marked fish at capture. Since adults of this fish showed strong site fidelity, marked fish which had disappeared from the quadrat and were not subsequently found nearby were regarded as having died (**Chapter 2**).

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,

$$OSR(t) = \frac{dm(t)}{df(t)} \times \frac{M(t)}{F(t)} \times \frac{PRRm(t)}{PRRf(t)}$$

where $d(t)$ is the proportion of individuals at the breeding site to the adult population at time t, and $M(t)/F(t)$ 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 (**Chapter 4-2**), the effect of spatio-temporal fluctuation on the sex ratio was negligible $(dm(t)/df(t) \equiv 1)$. Since a male received the brood from one female and a female gave her entire clutch to one male, 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 4-3.1). In this paper, the data of reproductive experience was used only for males. 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: $\bar{x} \pm SD = 69.8 \pm 5.3$mm, N=29, middle-aged: 85.2 ± 2.9mm, N=27, old: 90.1 ± 1.7mm, N=13; ANOVA, df=2, F=161.2,

Table 4-3.1. The age structure of *A. doederleini* at the beginning of the breeding season in 1993 and 1995.

Year	Sex	Age 1	2	3	4	5	6	Total
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

$P<0.001$). The size difference between the young and middle-aged (Scheff F-test, $P<0.0001$) was much greater than that between the middle-aged and old (Scheff F-test, $P<0.003$).

Results

Occurrence of filial cannibalism

The cannibalism rate, the proportion of broods cannibalized 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 (χ^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 (χ^2=3.40, df=2, P>0.1). However, the seasonal pattern of filial cannibalism was markedly different among the groups (Table 4-3.2). The cannibalism rate by middle-aged and old males was higher in the later phases. Cannibalism by young males of 1995 all occurred in the 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,

Table 4-3.2. 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)	†	NS	NS

Fisher's exact probability test: † $0.05<P<0.1$, * $P<0.05$, ** $P<0.01$ and NS not significant

middle-aged and old males re-spawned, whereas young males took much longer to re-spawn (Fig. 4-3.1; ANOVA, df=2, F=16.6, P<0.001; Scheffe F-test, young vs. middle-aged: P<0.0001, young vs. old: P<0.0001, 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).
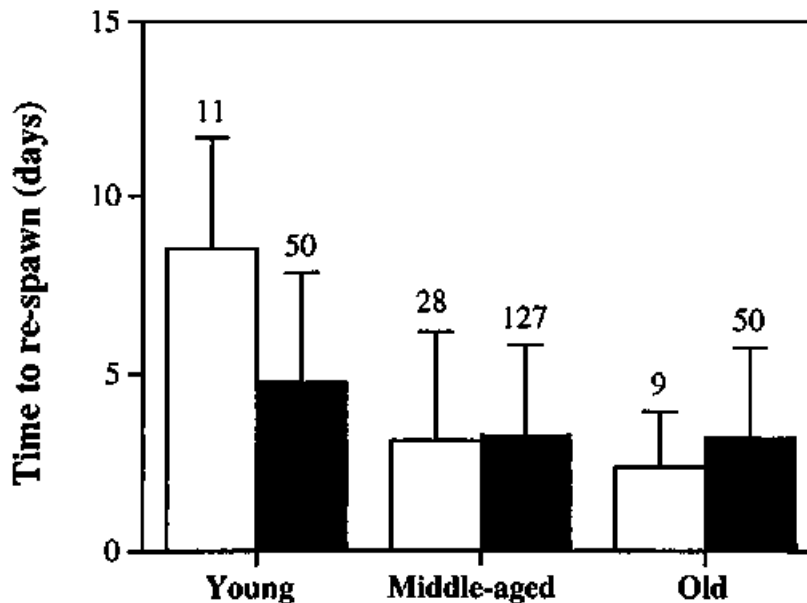
Fig. 4-3.1   The time taken to re-spawn for males who cannibalized their broods (white) and males who hatched their broods (black). Vertical lines and numerals indicate the standard deviation and sample size, respectively.

Operational sex ratio

The shortest inter-spawning interval was shorter each month in the female than in the male (Table 4-3.3). The adult sex ratio did not significantly deviate from equality ($\chi^2=0.37$, df=1, P>0.5 in 1993 and $\chi^2=0.29$, df=1, P>0.5 in 1995). As a result of higher potential reproductive rate in the female, OSR was female-biased throughout the breeding season.

Table 4-3.3. 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) Male	Female	SR	OSR
1993	May	—	—	0.82	—
	June	13	6	0.84	0.39
	July	9	7	0.9	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

Reproduction and growth

Young males tended to start the first breeding later than older males (Fig. 4-3.2). 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 (Table 4-3.4; $\bar{x}$ ±SD=3.3±1.4, N=34) than in 1993 (5.7±0.9,

Fig. 4-3.2   Onset of first breeding in 1993 (a) and 1995 (b) 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.

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Table 4-3.4. The number of breeding cycles completed by a male in a breeding season. Sample sizes are in parentheses.

Year	Young	Middle-aged	Old
1993	5.0±1.4SD	5.8±0.9SD	5.0
	(2)	(24)	(1)
1995	2.7±1.1SD	—	4.8±0.4SD
	(24)	(0)	(10)
Total	2.9±1.3SD	5.8±0.9SD	4.8±0.4SD
	(24)	(24)	(11)

N=27; t=-7.90, P<0.0001). This difference 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 4-3.4; ANOVA, df=2, F=54.6, P<0.0001; Scheffe F-test, young vs. middle-aged: P<0.0001, young vs. old: P<0.0001). 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) ($\bar{x}$ ±SD=7.63±4.42×10^{-2}, N=24) than middle-aged and old males (0.08±1.46×10^{-2}, N=24 and 0.38±0.60×10^{-2}, N=12; ANOVA, df=2, F=48.5, P<0.0001; Scheffe F-test, young vs. middle-aged: P<0.0001, young vs. old: P<0.0001). 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 4-3.5). The number of broods which cannibals received in a season was

Table 4-3.5. Comparison of the reproductive success and survival rate between cannibal and non-cannibal males. Sample sizes are in parentheses.

	1993			1995		
	Cannibals	Non-cannibals*	Statistical test (P value)	Cannibals	Non-cannibals*	Statistical test (P value)
Mating success	7.3±2.1SD	6.3±0.8SD	0.04[a]	4.6±3.3SD	3.5±1.4SD	0.051[a]
(no. of spawnings)	(15)	(12)		(11)	(23)	
Reproductive success	5.4±0.8SD	6.1±0.6SD	0.054[a]	2.9±2.7SD	3.5±1.4SD	0.26[a]
(no. of broods hatched)	(15)	(12)		(11)	(23)	
Survival rate (%)						
In breeding season	83.3	100	0.26[b]	84.6	92.0	0.59[b]
	(18)	(12)		(13)	(25)	
In non-breeding season	46.7	75.0	0.24[b]	81.8	78.3	0.99[b]
	(15)	(12)		(11)	(23)	

* Difference between the numbers of spawnings and breedings is due to the brood loss before mouthbrooding.

[a] t-test; [b] Fisher's exact probability test

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

Age-specific cost of mouthbrooding

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 **Chapter 3**). Among young males, there was a negative correlation between breeding frequency and growth. Since mouthbrooding forces the male to fast (**Chapter 2**), the 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 (I) limitation on the buccal capacity and (II) 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.

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 forces 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 (**Chapter 2**). Correspondingly, male mortality was highest late in the breeding season (**Chapter 2**). 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.

In **Chapter 4-1**, it has been 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 4-3.5). This, however, does not necessarily mean that brood cannibalism is ineffective in improving somatic condition. A preliminary analysis of body components of this fish (K. Omori et al., unpublished data) showed that cannibals had 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 (**Chapter 3**). For these males, another possible factor facilitating filial cannibalism may be multiple mate availability. The OSR in this fish 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, Vincent 1994b). 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 thus 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 within a few days of entire brood cannibalism (**Chapter 4-2**). This contrasts with the pattern found for cannibalistic young, who took a longer time to re-mate. Brood removal experiment suggested that cannibalistic middle-aged and old males could re-mate quickly by taking advantage of multiple mate availability (**Chapter 4-2**). 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.

V. Summary

The rate of entire brood cannibalism by male *Apogon doederleini* 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. I explained 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.

Chapter 5

Interspecific variation in strategies

5-1. Life history strategy

I. Introduction

In the previous chapters, I viewed the ecology of *Apogon doederleini*, mainly in evolutionary aspects. As stated in **Chapter 1**, a strategy is defined as a set of traits developed by an individual or a group of organisms to meet a particular set of conditions. If species are exposed to the different environmental conditions, then they will have some differences in the strategy. Using comparative methods, we can know that a diversity of strategies across related species result from the present and/or past adaptation to the different environments (Harvey and Pagel 1991). In this chapter, I describe differences in a life history strategy among three sympatric cardinal fishes, *A. doederleini*, *A. notatus* and *A. niger*, whose habitats are different from each other, and discuss what kind of environmental factors could cause the differences in the strategies.

More often, we will see similarlities between related species even if their surroundings are much different. The more closely related, the better they resemble each other in physiological, behavioral and morphological traits. We can know that these similarities are due to a phylogenetic constraint through comparison among higher taxonomic groups. In **Chapter 3**, I treated the problem of lifetime energy allocation to growth and reproduction in *A. doederleini*. A theoretical model suggested that its determinate growth could be ultimately attributed to the reproductive constraint connected with paternal mouthbrooding. If that is true, other cardinal fishes with paternal mouthbrooding will also show the determinate growth. To test this prediction, I investigate the growth pattern of two cardinal fishes *A. notatus* and *A. niger*.

The main purpose of this chapter is to provide an evolutionary explanation of similarities and differences in the life history strategy among three cardinal fishes through comparative methods.

II. Materials and Methods

Measurement of life history parameters

I studied reproductive biology and life history of *Apogon notatus* and *A. niger* to compare with those of *A. doederleini*. Studies were conducted from 1994 to 1996 for *A. notatus* and from 1992 to 1994 for *A. niger*. The former species lives in the boulder area together with *A. doederleini*, whereas the latter mainly inhabits the sandy area (Kuwamura 1983a). For *A. notatus*, I used a 10×20m quadrat which was set on the boulder slope for the study of *A. doederleini*; for *A. niger*, a 20×60m quadrat was set in the sandy area. All adults of *A. niger* inhabiting the sandy quadrat was individually marked, but *A. notatus* was not all marked in the boulder quadrat because schools of this fish tentatively moved about at the beginning of the breeding season. After marking fish, I measured their standard length (SL mm) and removed a few scales from these fish to estimate the age in the laboratory (**Chapter 2**). Throughout the breeding season, I recorded reproductive experiences for each marked fish by daily observation (**Chapter 2**): post-spawning behavior, which was observed for these two species, helped me to identify spawning pairs (Kuwamura 1985). I also investigated their population dynamics using a capture-recapture method for marked fish (**Chapter 2**). This method also gave information on the individual growth.

The growth pattern is fitted to the von Bertalanffy growth equation (**Chapter 3**),

$$L_t = L_\infty(1 - \exp(-K(t - t_0)))$$

where L_t is the standard length (mm) at age t, L_∞ the asymptotic length, K the growth coefficient, and t_0 the hypothetical time at which the length is zero. To fit this growth equation to the data set, I used the Walford plot for *A. notatus*, while I applied the quasi-Newton's method to *A. niger* whose growth data was scarce. The length of newly-hatched larvae was substituted for L_0 (3.80mmTL for *A. notatus* and 2.45mmTL for *A. niger*; Kuwamura 1983a).

The annual survival rate was calculated from the number of marked fish which survived to recapture divided by all marked fish at capture (**Chapter 2**).

For measurement of egg size (diameter) and brood size (the number of eggs per brood), I captured 28 males *A. notatus* and 15 males *A. niger* outside the quadrat within a day of their spawning and immediately removed broods from their mouths. The standard length of these males and their mates, if caught, were measured and a few scales were removed underwater for age determination.

III. Results

Habitat usage

Adult fish of *Apogon doederleini* and *A. notatus* inhabit the boulder area, while those of *A. niger* inhabits the sandy area. The former two species used the boulder for resting, spawning and sheltering from predators. The potential predators were mainly a scorpionfish *Sebastiscus marmoratus* and rarely a moray *Gymnothorax kidako*. In the boulder habitat, there also existed many other small fish species (also see Sakai et al. 1994). A pile of boulders, which turns out spatial complexity, enables many small species to use this habitat in a variety of forms.

In the sandy habitat, poritid and few acroporid coral colonies were scattered. Adults of *A. niger* used these coral colonies as the spawning and sheltering sites. Large colonies (>50cm in diameter), which are suitable for their shelter, were scarce (0.09 colonies/m^2). In this habitat, there were few fish species that show strong site fidelity throughout the year, but large piscivorous fishes were often found to haunt there (e.g. lizardfishes *Trachinocephalus myops* and *Synodus ulae*, a scorpionfish *Sebastiscus marmoratus*, a flathead *Platycephalus* sp. and a bastard halibut *Pseudorhombus arsius*).

The population density at the beginning of the breeding season was 0.34, 1.51 and 0.03 (fish/m^2) for *A. doederleini* in 1993, *A. notatus* in 1995 and *A. niger* in 1993, respectively. Adults of *A. doederleini* and *A. niger* were usually solitary, whereas those of *A. notatus* was gregarious except for forming pairs in the breeding season.

Life history

The breeding season of *A. notatus* was from June to September. Prior to the breeding season, adult fish formed pairs on the boulder substrata. The number of pairs gradually decreased late in the breeding season and were very few in October. In winter, adults formed large schools consisting of the thousands, while juveniles were rarely seen in the quadrat. The juveniles migrated to the quadrat after growing up yearling in the next breeding season (i.e. 1-year-old fish). The 1-year-old fish started the first reproduction. Oldest fish observed was seven and six years old for males and females, respectively. The annual survival rate for adult fish was 30.7% (N=153). There was a significant sexual difference in the survival rate (male: 42.7%, female: 10.2%; χ^2=14.9, df=1, P<0.0001).

Apogon niger showed a high-fidelity to a certain coral shelter in the non-breeding season. Prior to the breeding season (May-October), both males and females started to move between the shelters to form pairs (Fig. 5-1.1). During the breeding season, marked fish frequently disappeared from the quadrat (Fig. 5-1.2). To confirm whether these disappearances were due to death or to emigration, a census outside the quadrat was conducted over a wide area at the end of the breeding season. Of 25 fish observed outside the quadrat, only two were marked ones. Therefore, most of disappearances cannot be attributed to emigration from the quadrat. The annual adult survival rate was estimated to be 11.7% (N=60). This survival rate was not significantly different between the sexes (Fisher's exact probability test, P>0.6). Because of high adult mortality, the population structure biased toward young age-
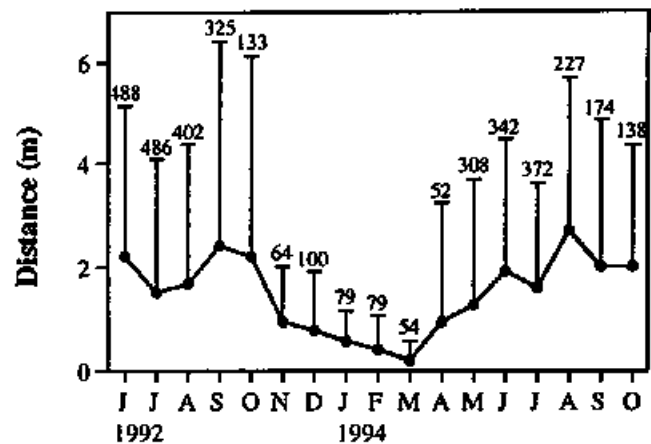
Fig. 5-1.1   The distance of daily shifts between sheltering sites by adult fish of *A. niger*. Vertical lines and numerals indicate the standard deviation and sample size, respectively.
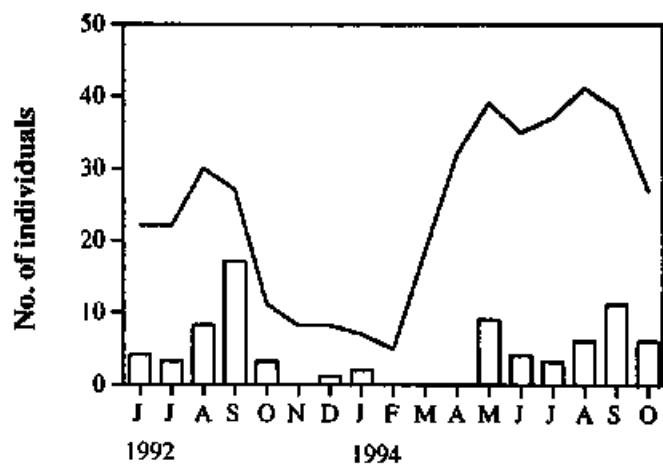
Fig. 5-1.2.   Monthly changes in disappearances of adult *A. niger* from the quadrat. Solid line and open bar indicate a total number of adults inhabiting the quadrat and the number of disappearaces, respectively.

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class (Fig. 5-1.3). Small juveniles appeared during and soon after the breeding season, but were scarce in the quadrat. They used a stone, rope and pipe as the sheltering sites in the stony and sandy area. At the beginning of the next breeding season, they immigrated into the quadrat and used the coral shelters same as adult fish. All 1-year-old fish that was observed throughout the breeding season started the first reproduction.

Life history of *A. doederleini* have been described in **Chapter 2**.

Fig. 5-1.3   The age structure of *A. niger* in the breeding season of 1992 (a) and 1993 (b). Solid, shaded and open bars indicate female, male and individual of unknown sex, respectively.

Growth

In all three species, 1-year-old fish showed a significantly higher growth rate than that of fish in the older age-classes (ANOVA, *A. doederleini*: df=5, F=35.2, P<0.0001, *A. notatus*: df=5, F=125.4, P<0.0001, *A. niger*: not applicable; Scheffe F-test, 1-year-old fish vs. older: all P<0.05 for

Table 5-1.1. Annual individual growth rate of three cardinal fishes. Sample sizes in parentheses.

Age	A. doederleini		A. notatus		A. niger	
1	17.5±5.59 SD	(4)	16.2±4.83 SD	(15)	17.8±10.7 SD	(8)
2	3.33±2.65 SD	(40)	9.90±0.98 SD	(4)	-2.43±3.43 SD	(2)
3	2.03±2.18 SD	(43)	2.09±1.26 SD	(15)	—	
4	0.36±2.07 SD	(16)	0.57±1.06 SD	(23)	—	
5	0.20±1.76 SD	(6)	1.19±1.01 SD	(28)	—	
6	-5.07	(1)	0.10±0.67 SD	(6)	—	

Table 5-1.2. Growth parameters in three cardinal fishes.

Species	Sex	K	L_∞	t_0	L_α	L_α/L_∞
A. doederleini	Male	1.56	86.5	-0.02	69.0	0.80
	Female	1.62	88.6	-0.02	73.0	0.82
A. notatus	Male	1.34	88.7	-0.03	60.0	0.68
	Female	1.29	87.0	-0.03	63.0	0.72
A. niger	Male	1.65	81.2	-0.02	61.5	0.76
	Female	1.48	85.9	-0.02	65.0	0.77

the former two species; Table 5-1.1). There were no significant difference in the growth rate of 1-year-old fish among these species (ANOVA, df=2, F=0.15, P>0.8).

The parameters of the von Bertalanffy growth equation were compared among the three species (Table5-1.2). The growth coefficient K was not much different among cardinal fishes but were among the highest in fishes (Appendix I). The asymptotic length (L_∞) of these species converged to the similar value. The hypothetical growth curve drawn from the von Bertalanffy growth equation was all determinate for these cardinal fishes and did not differ between the sexes in any species (Fig. 5-1.4). For the cardinal fishes, the relative size at maturity to asymptotic size (L_α/L_∞) also showed the nearly highest value among fishes (Appendix I).

Propagule size
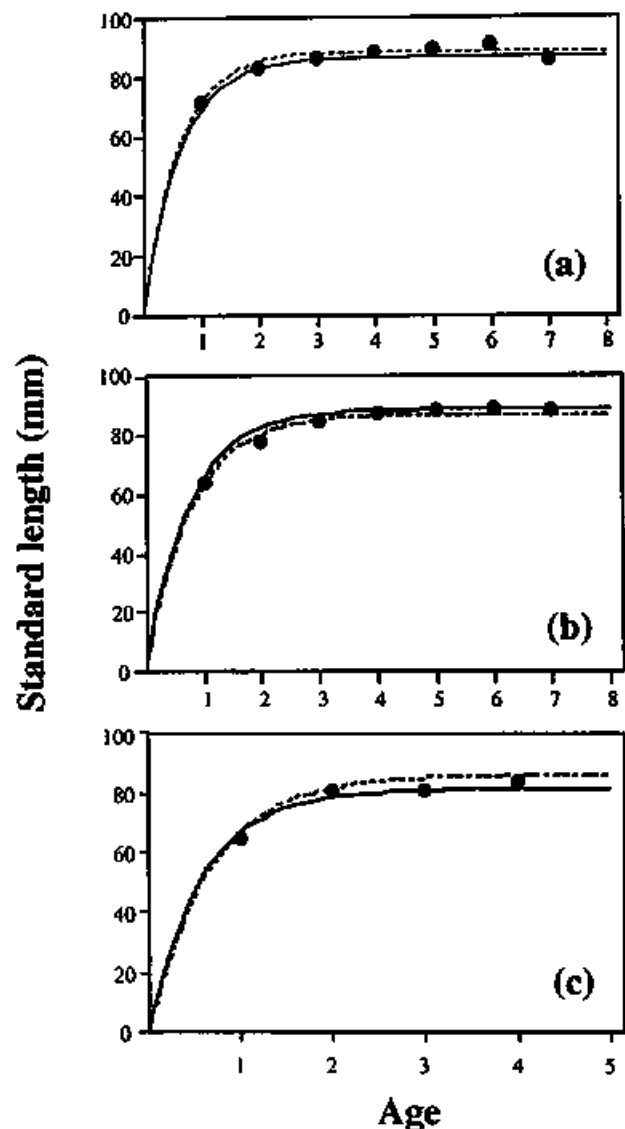
Fig. 5-1.4   Hypothetical growth curves of *A. doederleini* (a), *A. notatus* (b) and *A. niger* (c), drawn from the von Vertalanffy growth equation in Table 5-1.2. Solid and dotted lines are for male and female, respectively. Each plot presents the mean body length.

Table 5-1.3. Interspecific variation in egg size and brood size. Sample size in parentheses.

Species	Egg diameter (mm)	Brood size
A. doederleini	0.88±0.04SD*	8488±2357SD
	(19)	(24)
A. notatus	0.89±0.04SD	3315±1271SD
	(28)	(28)
A. niger	0.70±0.05SD	18248±3679SD
	(14)	(15)

* Eggs are treated by 10% formalin.

Egg size of *A. niger* was significantly smaller than that of *A. doederleini* and *A. notatus* (ANOVA, df=2, F=92.9, P<0.0001; Scheffe F-test *A. niger* vs. *A. doederleini*: P<0.0001, *A. niger* vs. *A. notatus*: P<0.0001, *A. doederleini* vs. *A. notatus*: P>0.6; Table 5-1.3). In contrast, brood size of *A. niger* was the largest of all three species (ANOVA, df=2, F=193.2, P<0.001; Scheffe F-test *A. niger* vs. *A. doederleini*: P<0.0001, *A. niger* vs. *A. notatus*: P<0.0001, *A. doederleini* vs. *A. notatus*: P<0.0001; Table 5-1.3).

In *A. doederleini*, the brood size positively correlated with male body size but not with female body size (see **Chapter 3**). In *A. notatus*, spawning pairs were size-assortative (r^2=0.81, N=95, P<0.0001), and the brood size positively correlated with both males body size (r^2=0.53, N=28, P<0.0001) and females body size (r^2=0.49, N=28, P<0.0001). The stepwise multiple regression analysis revealed that the brood size correlated only with the male body size (R^2=0.53, F=28.8, P<0.0001). In *A. niger*, spawning pairs were very weakly size-assortative (r^2=0.08, N=77, P<0.02). The brood size did not correlate with either the male size or the female size (R^2=0.00, F=0.00, P>0.99).

Reproduction

The breeding season of *A. niger* (May-October) was longer than that of *A. doederleini* (May-

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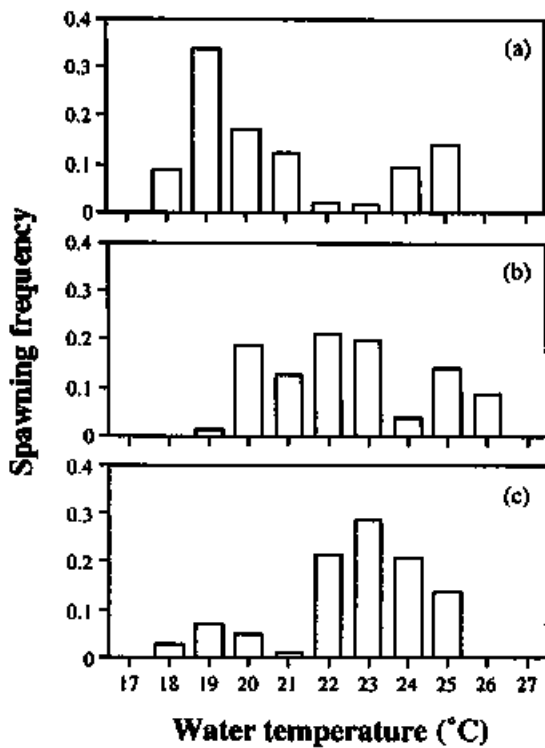
Fig. 5-1.5   Spawning frequency at thermal range during the breeding season of three cardinal fishes, *A. doederleini* (a), *A. notatus* (b) and *A. niger* (c).
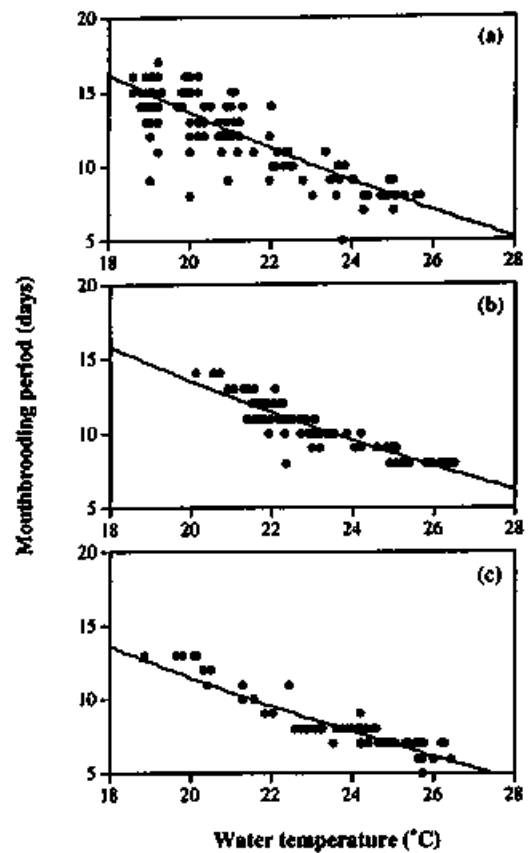
Fig. 5-1.6   Relationships between the mouthbrooding period and ambient water temperature in three cardinal fishes, *A. doederleini* (a), *A. notatus* (b) and *A. niger* (c).

August) and *A. notatus* (June-September) by two months. Spawning occurred within a wide thermal range for all three species (Fig. 5-1.5). *A. niger* tended to frequently reproduce at higher water temperature. The mouthbrooding period of *A. niger* was shorter than that of other two species, partially because of high water temperature (Fig. 5-1.6).

The maximum number of broods that a male raised in a season was 7, 4 and 8 for *A. doederleini*, *A. notatus* and *A. niger*, respectively, and the average was 5.6, 2.5 and 4.1. As a result of short breeding season and high breeding frequency, *A. doederleini* on average spent more time mouthbrooding per breeding cycle (78.6%; 52.5% for *A. notatus* and 58.0% for *A. niger*; ANOVA, df=2, F=83.6, P<0.0001; Scheffe F-test *A. doederleini* vs. *A. notatus*: P<0.0001, *A. doederleini* vs. *A. niger*: P<0.0001, *A. notatus* vs. *A. niger*: P>0.08). For these species, the correlation between male body size and breeding success (the number of broods hatched) in a season was weak (r^2=0.15, N=30, P<0.04 for *A. doederleini*) or nothing (r^2=0.08, N=39, P>0.09 for *A. notatus* and r^2=0.02, N=13, P>0.6 for *A. niger*).

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The correlation between female body size and the number of broods produced in a season was also weak ($r^2=0.12$, N=31, P=0.05 for *A. doederleini*) or nothing ($r^2=0.03$, N=16, P>0.5 for *A. notatus* and $r^2=0.02$, N=12, P>0.6 for *A. niger*). The maximum number of broods produced by a female in a season was 9, 9 and 14 for *A. doederleini*, *A. notatus* and *A. niger*, respectively. Annual reproductive effort, defined as the proportion of total brood weight (the average brood weight multiplied by the maximum number of broods produced per season) to female body weight, was 0.99, 0.92 and 1.74 for *A. doederleini*, *A. notatus* and *A. niger*, respectively.

Reproductive success at age x ($m(x)$), half of the average brood size multiplied by the average number of broods per season, was calculated for both sexes of each species. At age 1, the reproductive success of *A. niger* was by far the greatest both for males and females (Fig. 5-1.7). This was primarily due to their large brood size. In contrast, the reproductive success of male *A. notatus* was very small throughout the adult life. Both for males and females, the reproductive success reached asymptotic at young age (*A. doederleini* and *A. notatus*) or decreased with age (*A. niger*).

From two life history parameters, the reproductive success ($m(x)$) and the survival rate ($l(x)$) at age x, the $l(x)m(x)$ curve was obtained for each species: the $l(x)m(x)$ represents the expectancy of
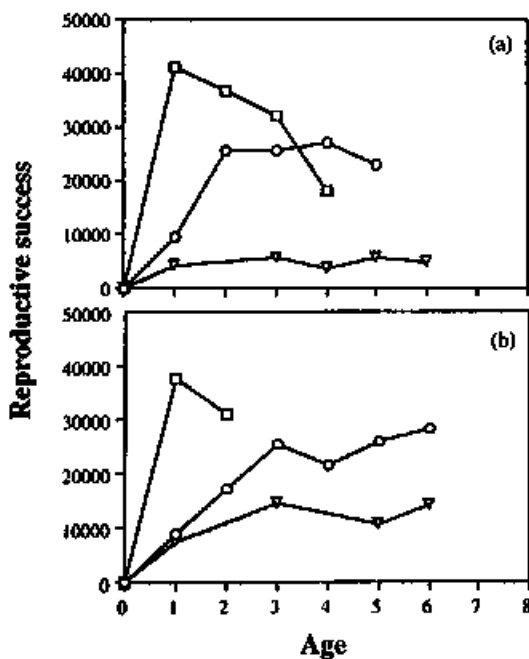
Fig. 5-1.7 The reproductive success during the lifetime for males (a) and females (b) in three cardinal fishes, *A. doederleini* (circles), *A. notatus* (triangles) and *A. niger* (squares).
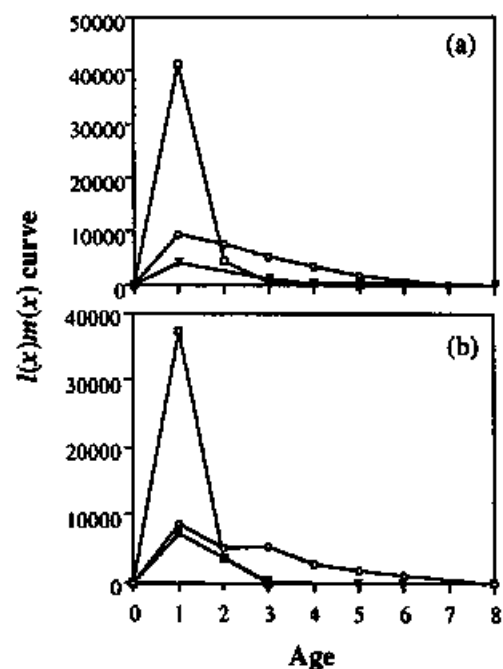
Fig. 5-1.8 The l(x)m(x) curve for males (a) and females (b) in three cardinal fishes, *A. doederleini* (circles), *A. notatus* (triangles) and *A. niger* (squares).

reproductive success at age x. The survival rate at age n ($l(n)$) was calculated from the annual adult survival rate to the n-th power. The $l(x)m(x)$ curve of A. $niger$ was markedly different from that of other two boulder species (Fig. 5-1.8). In this species, the reproductive expectancy was very great at age 1 and thereafter drastically decreased. In other two species, there was a gradual decrease in the reproductive expectancy.

IV. Discussion

Habitat types and mortality

Habitats were categorized into two types: the boulder habitat for *Apogon doederleini* and *A. notatus*, and the sandy habitat for *A. niger*. Sandy dwelling *A. niger* had a higher annual mortality than two boulder dwelling species. In *A. niger*, disappearances of marked fish may have been due mainly to their death because they were seldom found outside the quadrat. As shown in **Chapter 2**, the mortality of male *A. doederleini* was highest in the late breeding season, when their somatic condition lowered. In *A. niger*, their disappearances occurred throughout the breeding season rather than late in the breeding season (Fig. 5-1.2). The seasonal pattern of their disappearances corresponded well with that of the daily shift between shelters (Fig. 5-1.1). Since adult fish and their suitable shelters were sparsely distributed in the sandy area, they need to extensively move between shelters to search for spawning partners in the breeding season. However, such individuals may be vulnerable to predation because large piscivorous fishes often haunt there. Actually, individuals that more extensively moved had a higher mortality (see **Chapter 5-2**). During the breeding season, some adult fish were observed to sustain a gash on the body and one male to be preyed upon by the scorpionfish just after spawning (N. Okuda, personal observation). These results suggest that the high mortality of the sandy species is primarily due to predation.

The boulder species have a plentiful potential refuge from predation and easy access to mates owing to a relatively high population density. In this habitat, since there also exist many small fish species (Sakai et al. 1994; A. Itô, unpublished), the relative abundance of potential predators to prey species will be lower than that in the sandy habitat. For the boulder species, the seasonal pattern and sexual differences in the mortality seem to be caused by any factors other than

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Table 5-1.4. Interspecific comparison of life history traits in three cardinal fishes.

	A. notatus	*A. doederleini*	*A. niger*
Habitat	Boulder area	Boulder area	Sandy area
Population density	Very high	High	Low
Mortality	Low	Low	High
Egg size	Large	Large	Small
Brood size	Very small	Small	Large
Duration of breeding period	Short	Short	Long
Breeding frequency per season	Low	High	High
Annual reproductive effort	Small	Small	Large
Maturity age (year)	1	1	1
$l(x)m(x)$ curve	Gradual decrease	Gradual decrease	Precipitous peak at age 1
Growth pattern	Determinate	Determinate	Determinate

predation (see **Chapter 2** for *A. doederleini* and **Chapter 5-2** for *A. notatus*)

Life history strategy

Interspecific comparison of life history traits in three cardinal fishes is summarized in Table 5-1.4. There were clear differences in some traits between the boulder and sandy species. The sandy living species produced a large number of smaller eggs compared with that of the two boulder living species. Such a trade-off between offspring size and number is common in a variety of plants and animals (reviewed by Roff 1992, Stearns 1992). In cardinal fishes, the brooding space is limited (**Chapter 3**). For them, the egg size reduction may be thus effective in increasing the number of eggs to be accommodated. However, this does not necessarily mean that the sandy species with the larger brood size enjoyed greater reproductive success than the boulder species. The hatched larvae may have a survival advantage of large egg size (Ahnesjö 1992b). It is very difficult to investigate the effect of egg size on the larval survival during the planctonic and post-settlement stages and regrettably, there has been no such study. Therefore, further research needs to be done for the understanding the trade-off between offspring size and number as an universal life history strategy of marine organisms.

The sandy species *A. niger* reproduced at higher water temperature for a longer period than the boulder species did. High water temperature can shorten the embryonic developmental time until hatch. This reproductive pattern enabled males to complete more breeding cycles in a season and consequently allowed females to give more broods to these males. Through the multiple breeding tactics, they can attain the great reproductive success even when in young adult. Actually, *A. niger* showed a markedly different pattern of $l(x)m(x)$ curve from that of the boulder species, reaching a relatively high value at age 1. The general theory of life history evolution predicts that organism should increase the reproductive effort in early life when its adult mortality is high (Hirshfield and Tinkle 1975), and this prediction has been supported by some empirical studies (Minchella and Loverde 1981, Reznick 1990). For an organism with a given high mortality, there are two possible ways to increase the lifetime reproductive success, represented as integration of $l(x)m(x)$. One is to disproportionately increase the reproductive success at older age. However, this way is very difficult for cardinal fishes whose reproductive success is limited by the mouthbrooding ability: both males and females did not increase their reproductive success with age (Fig. 5-1.7). Another way is to increase the reproductive success at younger age. A general demographic model demonstrates that an increase in reproductive success at younger age has large impacts on fitness compared to changes in other life history traits (Cole 1954 but see Meats 1971). Therefore, the increased reproductive effort at younger age for *A. niger* may be a fecundity compensation response to the environment with a high adult mortality.

Among three cardinal fishes, some other life history traits were unvaried, irrespective of their habitats. All these species showed the determinate growth. As discussed in **Chapter 3**, paternal mouthbrooding entails mutual sexual limitation: the reproductive success of either sex is mutually limited by the ability of the other sex which has the lower potential reproductive rate. An optimal energy allocation model presented in **Chapter 3** showed that such a reproductive constraint could prevent fish from indeterminately growing. The growth pattern of these cardinal fishes was the most determinate among diverse taxa of fish. The determinate growth may be common in a family Apogonidae whose care form is a paternal mouthbrooding.

The three cardinal fishes attained maturity at age 1. Their maturity age was earlier than that of other fish species (mean=5.29y, Appendix I). This trend has remained after adjustment for the observed maximum age ($T\alpha/T_{max}$, all species: 0.38, Apogonidae: 0.23). As stated above, the

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earlier maturity is effective in increasing the lifetime reproductive success for species whose reproductive success does not disproportionately increase with age. It has been reported in many cardinal fishes that the maturity age is 1 year (e.g. *A. cyanosoma* (Suzuki and Ueno 1983), *A. semilineatus* (Suzuki and Ueno 1987), *A. lineatus* (Omori and Takahashi 1980), *A. endekataenia* and *A. properuptus* (N. Okuda, unpublished data)). The early maturity may be a life history strategy specific to this family.

V. Summary

A life history strategy was compared among three sympatric cardinal fishes, *Apogon doederleini*, *A. notatus* and *A. niger*. The former two species lives in the boulder area, while the latter lives in the sandy area. The sandy dwelling *A. niger* had a higher adult mortality, suggesting that it was due mainly to predation. The sandy species produced a large number of smaller eggs per brood and had more broods per season. These traits enabled this fish to enjoy the greater reproductive success at young age. The increased reproductive effort at younger age may be a fecundity compensation response to the environment with a high mortality. The other aspects of life history strategy was unvaried across species. They attained maturity at age 1 and their growth pattern was determinate. The early maturity may be effective in increasing the lifetime reproductive success for cardinal fishes whose reproductive success did not disproportionately increase with age. An optimal energy allocation model and comparative methods suggest that their determinate growth can be attributed to reproductive constraints linked with a paternal mouthbrooding.

5-2. Sexual strategy

I. Introduction

Since the advent of sexual reproduction, male and female always have conflicted for interests in reproduction. This is ultimately due to sexual asymmetry of reproductive investment (Parker et al. 1972). In general, the form of investment in zygotes is much different in quality and quantity between the sexes, but their genetic contribution to the zygotes is even. Thus one sex can increase the fitness by exploiting the reproductive investment by the other sex. Here, strategies adopted by the conflicting sexes are defined as sexual strategies (Stockley 1997). The sexual strategy is different from a reproductive strategy in the narrow sense: the former term implies both male and female strategies, whereas the latter term represents the reproductive character of a species without considering sexuality. The sexual strategy of one sex will be influenced by that of the other sex (Stockley 1997) and a compromise between the two conflicting strategies will be also affected by their surroundings (Rowe et al. 1994). We can view the dynamics of sexual conflicts through comparison among different populations within a species (Magurran and Seghers 1994) or among closely related species (Rowe et al. 1994).

In **Chapter 4-2**, we have already seen sexual conflicts in reproduction by a cardinal fish *Apogon doederleini*. Males of this species sustain the cost of mouthbrooding eggs but can benefit from eating them. In contrast, females can increase their reproductive success through polygamous matings but suffer a cost of egg cannibalism. This sexual conflict may prevalently occur in cardinal fishes with paternal mouthbrooding because this care form is usually costly for males but not females. I investigate the incidence of filial cannibalism in two sympatric cardinal fishes *A. notatus* and *A. niger*, and then compare it among three species including *A. doederleini*. I also discuss what kind of environmental factors can influence the balance of sexual conflicts.

II. Methods

Field observation

I studied reproductive biology of *Apogon notatus* and *A. niger* to compare with that of *A. doederleini* (**Chapter 5-1**). I made field observation throughout the breeding season of *A. niger* in 1993 and *A. notatus* in 1995. I marked all individuals of *A. niger* in the sandy quadrat and some individuals of *A. notatus* in the boulder quadrat, and measured their standard length (SLmm). By daily censuses and observations, I investigated reproductive experiences for each marked fish. For *A. notatus*, unmarked fish with whom the marked fish mated were identified by the variation of lines and spots on the head. Since the size distribution of *A. notatus* showed a clear bimodal pattern, the fish were categorized into two size-classes by eye (Fig. 5-2.1). I recaptured the marked fish of both species soon after the breeding season and remeasured their SL to calculate the daily specific growth rate (**Chapter 4-3**).

The courtship frequency and aggression intensity shown by marked fish of *A. notatus* were measured. Each observation was made for 20 minutes. For paired fish, bouts of displays toward a mate and toward fish that approached within 30cm of the pairs were scored (see Kuwamura 1983, for a description of courtship repertoire), and the frequency of these displays was compared between a male and female in the pairs. The pairing period was divided into three phase: the courting phase is from pair formation to the day before spawning, and the pre- and post-spawning phase are before and after spawning during that day, respectively. Unpaired marked fish were also observed for 20 minutes.
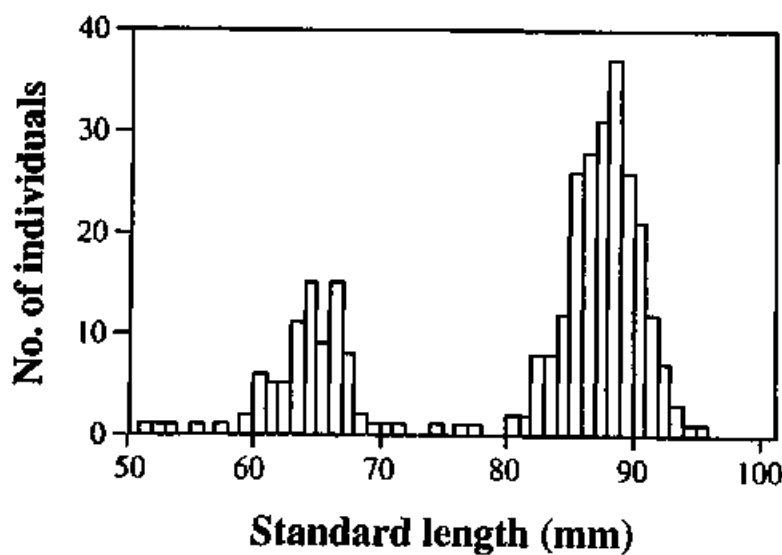
Fig. 5-2.1   The size distribution of *A. notatus*. Small size-class is for fish whose body size is 77mm and less, and large size-class for more than 77mm. Open bars are for 1-year-old fish and shaded bars for two or more.

I sometimes found that broods disappeared from males' mouths before the expected day of hatching. For some of such males, I checked stomach contents using a small syringe to confirm the occurrence of filial cannibalism (Chapter 4-1).

Estimation of operational sex ratio

I estimated the operational sex ratio in the study population of *A. notatus* and *A. niger*, according to the method in **Chapter 4-3**. The adult sex ratio was examined by censuses in the quadrat. Potential reproductive rate (broods/day) was approximated by an inverse of the shortest inter-spawning interval observed for males and females.

III. Results

Reproductive biology of *Apogon notatus*

Sex role

Adult fish formed large aggregations in the middle depths in winter. In April, two months earlier than the breeding season, males and females began to form pairs on the boulder substrata. Pair bond was kept for on average 12.4 days until spawning. During this period, the females showed a significantly higher frequency of courtship behaviors than their mates did (Table 5-2.1). The females occasionally showed extra-pair courtship with another male. The pairs were approached by conspecific fish and a total of 56 other species. A male or female in the pair usually attacked conspecific intruders (79.4%, N=1213), but they seldom attacked heterospecific intruders (3.5%, N=1982). Aggression to the conspecific intruders was more frequently shown by females, while heterospecific aggression was not significantly different between the sexes (Table 5-2.1). The female aggression was more intense during the post-spawning phase ($\bar{x}\pm$SD=9.91$\pm$11.3 per 20 min., N=22) compared with the pre-spawning phase (5.41$\pm$5.42, N=17) and the courting phase (4.20$\pm$5.67, N=93; Kruskal-Wallis test, df=2, H=7.31, P<0.03). In cases in which broods disappeared soon after spawning, females had less intensely showed aggressive behavior than

Table 5-2.1. Sexual differences in courtship frequency and aggression intensity in pairs of *A. notatus*. Numerals are the mean number of bouts and the standard deviation per 20 min observation (N=132).

Behavior	Male	Female	$z^\dagger$
Courtship			
warping or circling	0.09±0.88	23.61±28.20	-9.05 ***
nuzzling	0.63±2.79	5.71±16.76	-2.63 *
parallel-circling	3.14±11.55		—
extra-pair courtship	0.00±0.00	0.38±1.75	-2.93 *
Aggression			
Intraspecific			
attack	1.99±3.58	5.31±7.15	-6.47 ***
being attacked	0.39±1.17		—
no interaction	1.13±2.64		—
Interspecific			
attack	0.06±0.32	0.05±0.24	-0.56 NS
being attacked	0.42±1.59		—
no interaction	14.49±10.50		—

$\dagger$ Wilcoxon signed rank test: * p<0.01, ** p<0.001, *** p<0.0001 and NS not significant

females whose broods were successfully raised by males (Mann-Whitney U-test, z=-3.38, P<0.001).

In 164 of 220 cases, pairs were separated after spawning. The separation usually occurred during the post-spawning phase (95.8%). Soon after the separation, females always invited another unpaired male at their spawning sites. The females showed a high fidelity to the spawning site (also see Usuki 1977; Kuwamura 1985). All of marked females that were observed throughout the breeding season kept paired status until their last spawning, after which they joined schools of conspecific fish. In contrast, males that separated from their mates after spawning remained unpaired status until re-mating. The unpaired mouthbrooding males were floating in the middle depths together with other unpaired fish. These males occasionally approached paired females to display courtship behaviors ($\bar{x}$±SD=0.97±1.75 per 20 min, N=36), but they were usually driven away by a male or female in pairs. Under 15 of 36 observations, they, in groups, interfered with conspecific spawnings by chasing the pre-spawning or post-spawning males. Among the unpaired males, interactions were neutral (5.17±5.40) rather than agonistic (2.33±3.91; Wilcoxon signed

rank test, z=-2.64, P<0.009).

Mating pattern

All females in the large size-class (N=176) mated with males in the large-size class, and most of females in the small size-class (55 of 71) mated with males in the small size-class. Spawning pairs in which the body size of both sexes are known were size-assortative (Spearman rank correlation; p=0.83, ρ<0.001, N=28).

Males took 8-14 days to mouthbrood eggs until the hatch and this period was strongly affected by ambient water temperature, irrespective of male body size and female body size (Stepwise multiple regression analysis, R^2=0.84, F=274.8, P<0.0001). The time taken for males to re-spawn after hatching eggs greatly ranged from 1 to 48 days, independently of water temperature (r^2=0.00, P>0.9, N=83). The inter-spawning interval for females varied seasonally but was not different between size-classes (two-factorial ANOVA, month: F=5.69, df=2, P<0.005, size: F=1.52, df=1, P>0.2 excluding data in September for small sample size). The inter-spawning intervals significantly differed between the sexes throughout the breeding season (Table 5-2.2). The mean interval of females was shorter than that of males and the shortest interval was also recorded in females.

After spawning, females in the large size-class more frequently divorced their mates than females in the small size-class did (χ^2=16.6, df=1, P<0.0001, large: 91.8%, N=159, small: 70.5%,

Table 5-2.2. Inter-spawning interval of males and females in *A. notatus*.

Month		Inter-spawning interval (days)				
		Male		Female		
	N	Mean±SD (Min-Max)	N	Mean±SD (Min-Max)	χ^2 *	*P*
June	31	24.5±7.5 (12-46)	44	15.5±3.9 (9-31)	29.3	<0.0001
July	48	22.4±8.1 (11-59)	77	13.0±5.6 (7-53)	58.1	<0.0001
August	16	24.3±8.2 (15-48)	58	13.5±4.0 (8-27)	25.5	<0.0001
September	0	—	4	15.8±5.5 (11-21)	Not applicable	

* Kolmogorov-Smirnov two-sample test

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N=61). Both small and large females re-spawned more quickly when they changed mates than when they did not so (large: t=6.21, df=129, P<0.0001, small: t=5.15, df=46, P<0.0001). Most of new mates were non-brooder (81.1%). The rate of mate change was significantly higher for large females (χ^2=7.71, df=1, P<0.006; large: 90.9%, N=132, small: 75.0%, N=48). In contrast, neither small nor large males shortened the inter-spawning interval when they changed mates (small: t=0.52, df=25, P>0.6, large: t=-0.69, df=80, P>0.4). The mate change rate by males did not significantly differ between the size-classes (χ2=0.18, df=1, P>0.6; large: 52.9%, N=87, small: 48.1%, N=27). Males showed the lower rate of mate change than females did (χ2=50.9, df=1, P<0.0001).

During the entire breeding season, one female on average spawned 6.5 times (±1.7SD, N=16) and mated with 3.8 different males (±1.3SD, N=16), while one male spawned 3.0 times (±1.1SD, N=39) and mated with 1.9 different females (±0.8SD, N=38). Both values were significantly greater in females (spawning: t=9.27, df=53, P<0.0001, mate: t=6.60, df=52, P<0.0001).

Operational sex ratio

At the peak of the breeding season, the majority of unpaired fish were mouthbrooding (73.6% in July and 76.2% in August; Table 5-2.3). In this period, many males in the small adult pair were also mouthbrooding, whereas males in the large adult pair were usually non-brooder. Judging from observations that marked females always remained paired status and most of unpaired fish were mouthbrooding, the unpaired fish are all considered to be male. Based on these circumstantial evidence, the adult sex ratio (males:females) was estimated. The sex ratio of small adults was slightly male-biased but did not significantly deviate from equality (June: χ2=1.21, df=1, P>0.2, July: χ2=3.34, df=1, P>0.06, August: χ2=2.10, df=1, P>0.1; Table 5-2.3). In contrast, the sex ratio of large adults was significantly male-biased (June: χ2=11.1, df=1, P<0.001, July: χ2=16.5, df=1, P<0.0001, August: χ2=21.0, df=1, P<0.0001). In the late breeding season, the number of pairs decreased, while the number of schooling fish increased (Table 5-2.3). Since the schools consisted of both males and females, the sex ratio in September and October is not known.

From the adult sex ratio and the shortest inter-spawning intervals of two sexes, the

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Table 5-2.3. The sex ratio (males:females) of large and small adults in the quadrat. Numerals in parentheses present the number of mouthbrooding males.

		Jun	July	August	September	October
Large adult*	No. of pairs	54 (0)	48 (5)	40 (8)	32 (2)	13 (0)
	No. of unpaired fish	60 (0)	73 (57)	79 (60)	16 (1)	1 (0)
	Sex ratio	2.11	2.52	2.98	—	—
Small adult	No. of pairs	58 (0)	85 (56)	68 (23)	14 (0)	4 (0)
	No. of unpaired fish	18 (0)	37 (24)	26 (20)	10 (0)	4 (0)
	Sex ratio	1.31	1.44	1.38	—	—
No. of fish in schools		0	0	0	537 (17)	thousands
Total		302	376	321	655	uncountable

* Pairs of a large and small adults are included.

operational sex ratio in each month was calculated. Since there was a highly size-assortative mating, the ratios were examined separately in the two size-classes. The operational sex ratio of small adults was nearly equal, whereas that of large adults was male-biased (Fig. 5-2.2).
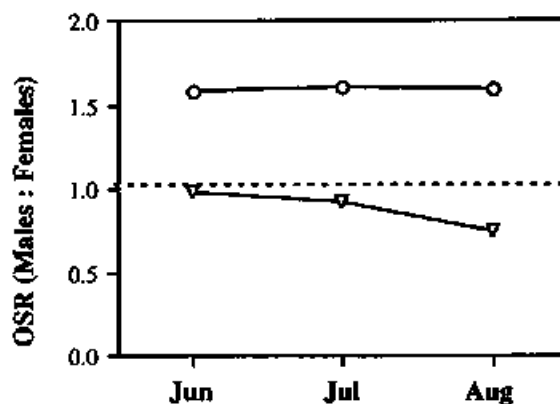
Fig. 5-2.2   The operational sex ratio of large (circles) and small (triangles) adults of A. notatus. Broken line indicates equal sex ratio.

Filial cannibalism

Of 214 spawnings observed, 31 broods disappeared from the male's mouth before the expected day of hatching. For 15 of such males, stomach contents were checked within a few days of spawning. Of them, 12 had eggs in their stomachs. Of the other 16 males, one was observed to swallow the egg mass, five observed to lose their broods just after spawning and ten were unknown about how their broods disappeared. From these data, the rate of filial cannibalism was estimated to range between 6.1 and 10.7% and the rate of brood loss which cannot be attributed to filial cannibalism between 3.7 and 8.4% (N=214).

Males who practiced filial cannibalism changed mates in the next spawning as frequently as males who did not so (Fisher's exact probability test, P>0.9; cannibalism: 50.0% N=8, no cannibalism: 46.4%, N=97). The former males on average took 24.5 days to re-spawn after filial

cannibalism and this time was significantly longer than the time taken for males to re-spawn after hatching eggs (13.0 days; Mann-Whitney U-test, z=-2.66, df=91, P<0.008).

Some fitness parameters were compared between cannibals and non-cannibals; the cannibal is defined as a male who practiced filial cannibalism at least once in a season (Table 5-2.4). The cannibals did not differ from the non-cannibals in the body size and growth rate. The number of broods which the cannibals received in a season was greater than that for the non-cannibals, but the number of broods raised did not differ between them. There was also no significant difference in the annual survival rate between them.

Table 5-2.4. Comparison of fitness parameters between cannibal and non-cannihbal males of *A. notatus*. Sample sizes in parentheses.

	Cannibals	Non-cannibals	Statical test (*P* value)
SL (mm)	84.8±7.2SD (9)	86.8±6.7SD (25)	0.20 [a]
Specific growth rate (%·day^{-1}×10^{-2})	1.01±2.74SD (9)	0.76±2.21SD (19)	0.77 [a]
No. of spawnings	3.7±0.9SD (9)	2.7±0.8SD (25)	0.02 [a]
No. of broods raised	2.4±1.2SD (9)	2.6±0.9SD (25)	0.71 [a]
Annual survival rate (%)	22.2 (9)	44.0 (25)	0.43 [b]

[a] Mann-Whitney U-test; [b] Fisher's exact probability test

Reproductive biology of *Apogon niger*

Sex role

Both males and females usually courted with mates that existed at the same or nearby sheltering site. Courtship was intermittently repeated for a total of 4.1 days until spawning. Since courtship displays (e.g. crossing display; Kuwamura 1985) were simultaneously and cooperatively shown by a male and female in pairs, these could not be separated into male and female roles. Spawning and courtship behaviors were rarely interfered by conspecific fish.

Females more extensively shifted shelters than males did in the breeding season (t=4.25, $P<0.0001$; male: $\bar{x}\pm SD$=1.42±0.87m, N=53, female: 2.34±1.29m, N=48) but not in the non-breeding season (t=1.06, $P>0.2$; male: 0.55±0.54m, N=49, female: 0.72±0.75m, N=22). The daily shifts of shelters were more extensive late in the breeding season (two-way factorial ANOVA, sex: F=21.3, df=1, $P<0.0001$, season: F=17.1, df=1, $P<0.0001$, sex × season: F=0.33, df=1, $P>0.5$). Individuals that disappeared during the breeding season showed the more extensive shifts of shelters (Kormogorov-Smirnov two-sample test, χ^2=7.32, df=1, P=0.05).

Mating pattern

In the early breeding season (May-July), the mean inter-spawning intervals and its shortest value was not significantly different between the sexes (Table 5-2.5). In the late breeding season (August-October), the intervals became shorter both for males and females, with a shorter value for females.

The spawning pairs were very weakly size-assortative (r^2=0.08, N=77, $P<0.02$). Within a few days of spawning, 39 females and 4 males left mates at their spawning sites and 21 pairs simultaneously left there. Cases in which the pair bond was kept until next spawning were only two. The rate of mate desertion was significantly higher for females (χ^2=17.2, df=1, $P<0.0001$). After the separation of spawning pairs, some formed new pairs, while the others were reinstated in the next spawning. Females more frequently re-spawned with the new mate than males did (χ^2=7.18, df=1, $P<0.008$; male: 38.5%, N=78, female: 60.3%, N=73). The inter-spawning interval for females was shorter when they changed their mates only in the late breeding season (Table 5-

Table 5-2.5. The inter-spawning interval in the early and late breeding season for males and females of *A. niger*.

| Breeding season | Spawning interval (days) | | | | | |
| | Male | | Female | | | |
	N	MeanSD (Min-Max)	N	Mean±SD (Min-Max)	χ^2 *	P
Early (May-July)	14	22.0±11.3 (11-56)	14	19.6±9.9 (10-47)	1.29	0.99
Late (August-October)	52	12.9±4.1 (9-24)	50	10.2±3.4 (4-20)	6.89	0.06

* Kolmogorov-Smirnov two-sample test

2.6). The interval for males was not different between when they did and did not change mates.

During the entire breeding season, one male on average spawned 5.1 times (±2.7SD, N=13) and mated with 2.4 different females (±1.4SD, N=8), while one female spawned 4.5 times (±3.8SD, N=12) and mated with 2.4 different males (±1.5SD, N=12). There were no significant differences in these two values between the sexes (Mann-Whitney U-test, spawning: z=-0.98, P>0.3, mate: z=-0.04, P>0.9).

Table 5-2.6. Inter-spawning interval for males and females that did or did not change mates in the early and late breeding season in *A. niger*. Sample sizes in parentheses.

	Female				Male			
	Mate change	No mate change			Mate change	No mate change		
Breeding season	Mean±SD	Mean±SD	z *	P	Mean±SD	Mean±SD	z *	P
Early	20.7±11.4	16.8±4.8	-0.21	0.83	26.1±14.4	16.7±4.7	-1.36	0.17
	(10)	(4)			(7)	(6)		
Late	9.2±4.0	11.0±2.5	-2.14	0.03	12.9±4.2	12.9±4.1	-0.04	0.97
	(26)	(23)			(14)	(36)		

* Mann-Whitney U-test

Operational sex ratio

The adult sex ratio was 0.93 in the early breeding season and 1.05 in the late breeding season. These ratios did not significantly deviate from equality (early: χ^2=0.02, df=1, P>0.8, late: χ^2=0.01, df=1, P>0.9). As a result of higher potential reproductive rate in the female, the operational sex ratio was female-biased (0.85 and 0.47 in the early and late breeding season, respectively).

Filial cannibalism

Of 113 broods, 10 disappeared from males' mouths before the expected day of hatching. In 6 cases where stomach contents were checked, all males had eaten their eggs. Of the other 4 males, three were observed to be potbellied soon after the brood disappearance, suggesting that they cannibalized their own broods (see **Chapter 4-1**). The rate of filial cannibalism was estimated to be 8.0% and the rate of brood loss 0.9%.

After filial cannibalism, these males often changed mates (83.3%). This rate of mate change was higher than that shown by males that did not cannibalize eggs (Fisher's exact probability test, P<0.03). For males who cannibalized eggs, the time taken to re-spawn after filial cannibalism was significantly longer than the time taken to re-spawn after hatching for males that did not practiced cannibalism (Mann-Whitney U-test, z=-2.47, P<0.02; cannibalism: $\bar{x}\pm SD$=21.4±16.0 days, N=5, no cannibalism: 7.9±6.9 days, N=72). Comparison of fitness parameters between cannibals and non-cannibals was the same result as that of *A. notatus* (Table 5-2.7). The cannibals received more broods per season than the non-cannibals, but breeding frequency was not different between them. Both of them had a low survival rate.

Table 5-2.7. Comparison of fitness parameters between cannibal and non-cannihbal males of *A. niger*. Sample sizes in parentheses.

	Cannibals	Non-cannibals	Statical test (*P* value)
SL (mm)	70.1±7.4SD (7)	68.4± 8.0SD (17)	0.63 [a]
Specific growth rate (%·day^{-1}×10^{-2})	3.52±3.94SD (5)	6.85±6.23SD (5)	0.46 [a]
No. of spawnings	7.0±1.2SD (5)	4.3±2.6SD (7)	0.06 [a]
No. of broods raised	5.6±1.5SD (5)	4.1±2.8SD * (7)	0.63 [a]
Annual survival rate (%)	14.3 (7)	11.8 (17)	0.99 [b]

[a] Mann-Whitney U-test; [b] Fisher's exact probability test

IV. Discussion

Female strategy

In all three species, females had the higher potential reproductive rate. This is primarily due to their care form: reproduction of males is limited by their buccal capacity and by a lengthy

mouthbrooding period (**Chapter 3**). Sexual selection theory predicts that one sex with the higher potential more intensely compete for mates of the opposite sex (Clutton-Brock and Vincent 1991, Clutton-Brock and Parker 1992). In these cardinal fishes, females were actually predominant competitor for mates. Females, for example, moved around more extensively to search for mates (*Apogon doederleini* and *A. niger*), they were more aggressive to conspecific fish (*A. notatus*) and they showed more frequent courtship displays (*A. notatus*). Animal with these features is generally defined as sex role reversed species (Vincent et al. 1992, Kvarnemo and Ahnesjo 1996).

In these cardinal fishes, the pair bond throughout the breeding season was weak. Females usually shortened their reproductive cycle by changing mates. This is because female spawning interval is potentially shorter than that of males. Keenleyside (1983) demonstrated that the sex which was ready to more quickly re-spawn was most likely to desert the mates, using sex ratio manipulation experiment of a monogamous cichlid *Herotilapia multispinosa*. In cardinal fishes, the mate desertion appears to be advantageous to females who can re-spawn more quickly. Kuwamura (1983) noted that in *A. notatus*, females sometimes tried to turn mates out of their spawning sites after transferring eggs to these mates. The observed pair bond instability may be an outcome of female decision.

Keenleyside's experiment (1983) also suggests that mate availability is important in determining whether to desert mates. For the sex with a higher reproductive rate, high mate availability will facilitate the mate desertion. In *A. notatus*, females in the large size-class, in which the operational sex ratio was male-biased, showed the higher rate of divorcing mates than females in the small size-class did, and the rate was the highest among three species. Where the operational sex ratio is male-biased, the mate availability is high for females. If the opportunities to quickly re-mate arise, females can enjoy greater mating success by changing mates. The polygamous matings may be therefore an exclusive female strategy in cardinal fishes.

In the sandy species *A. niger*, females did not shorten the inter-spawning interval in the early breeding season even when they changed mates. Since adult fish sparsely distributed, they will have to extensively move to search for a new mate after the separation of pairs. However, the movement between shelters may put them at high risk from predators. Actually, individuals that more extensively moved had a higher mortality. In addition, the fact that spawning pairs of *A. niger* were nearly random rather than size-assortative suggests that a high predation risk prevents them

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from moving between shelters and hence assessing mates. Under such ecological constraints, it will be difficult for females to quickly re-spawn with a new mate ready to spawn. In contrast, the females in the late breeding season extensively moved between shelters and shortened their intervals by changing mates. Since the possibility of adult fish surviving to the next season is very low (**Chapter 5-1**), they will have less future reproductive value in the late breeding season. Therefore, it is likely that they invest more in reproductive activities late in the breeding season.

In *A. notatus*, there was a clear sexual difference in the mortality (**Chapter 5-1**). In this species, female reproductive investment was greater than that of males in terms of gamete production and reproductive activities: they produced more broods than males raised in a season and more frequently showed courtship and aggressive behaviors. The higher mortality in females may result from their greater investment. This sexual difference in the mortality skewed the population sex ratio toward males with the increasing age. In general, the male intense competition and their subsequent high mortality results in monopolization of mates by surviving males (Emlen and Oring 1977, Davies 1991), whereas in sex-role reversed species, females surviving the competition cannot monopolize a disproportionately large number of mates (e.g. pipefishes: 1.8 mates for *Nerophis ophidion* (Berglund et al. 1989), 1.9 for *Syngnathus typhle* (Berglund et al. 1989), cardinal fishes: 2.3 for *Apogon doederleini* (**Chapter 4-1**), 2.3 for *A. niger* (this chapter) and 1.6 for *A. notatus* (this chapter)). This is ultimately due to a limited reproductive potential of females whose egg production basically costs. If a sexual difference in the mortality was greater than that in the potential reproductive rate, then the operational sex ratio will be more affected by the adult sex ratio (Clutton-Brock and Parker 1992). In sex-role reversed species, therefore, escalation of female mating competition can result in the male-biased, but not female-biased, operational sex ratio.

Male strategy

Filial cannibalism by mouthbrooding males occurred in all three species. These males may have eaten eggs to primarily compensate for the cost of parental care (**Chapter 4-1**). In any species, however, the cannibals did not surpass the non-cannibals in their future growth and survival. They could not also disproportionately increase the reproductive success in the next season because of

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brooding constraints (**Chapter 5-1**).Thus, the reproductive loss entailed by filial cannibalism will have to be compensated by the alternative within the current breeding season. Interestingly, the cannibals enjoyed mating success as great as the non-cannibals did over the entire breeding season, although they abandoned some broods. This is because they received more broods than the non-cannibals did. This fact suggests that the cannibals had an opportunity for superfluous matings. Therefore, mate availability for males may be an important factor facilitating filial cannibalism in cardinal fishes (also see **Chapter 4-2**).

The rate of filial cannibalism was different among three species (Table 5-2.8). *A. doederleini* showed the higher rate than *A. notatus* (for underestimated value; $\chi^2=9.71$, df=1, P<0.002) and *A. niger* ($\chi^2=3.58$, df=1, P=0.059). In the former species, cannibals re-mated within a few days of filial cannibalism. These cannibals may have had multiple mate availability before they practiced filial cannibalism (**Chapter 4-2**). Where the operational sex ratio is female-biased, some males can have a chance to mate with multiple females at a time. In the other two species, in contrast, cannibals took a long to re-mate after filial cannibalism. In *A. notatus*, the operational sex ratio was male-biased or nearly equal throughout the breeding season. The mate availability for male *A. notatus* is low compared with that of *A. doederleini*. In *A. niger*, the operational sex ratio was female-biased. However, this does not necessarily mean that multiple females are simultaneously available to a male. For males as well as females, the movement between shelters will be restricted due to the high predation risk. These males may take a long time to encounter new mates ready to spawn after filial cannibalism. The more quickly the cannibals re-mate, the more effectively their reproductive loss can be compensated by the subsequent brood. Thus, for *A. notatus* and *A. niger*, the benefit from filial cannibalism may be smaller than that for *A. doederleini*, as suggested by their low incidence of cannibalism.

Table 5-2.8. The rate of filial cannibalism and brood loss in three cardinal fishes.

	A. notatus	*A. doederleini*	*A. niger*
No. of spawnings	214	207	112
Filial cannibalism rate (%)	6.1-10.7*	15.5	8.0
Brood loss rate (%)	3.7-8.4*	1.0	0.9

* The range represents under- and overestimated values.

In *A. doederleini* and *A. niger*, the brood losses except filial cannibalism rarely occurred, whereas the brood loss rate in *A. notatus* was markedly high (Fisher's exact probability test, *A. notatus* vs. *A. doederleini*: $P<0.0003$, *A. notatus* vs. *A. niger*: $P<0.005$, *A. doederleini* vs. *A. niger*: $P>0.9$; Table 5-2.8). In *A. notatus*, these brood losses may have been due mainly to hetero cannibalism (i.e. the egg consumption by non-related conspecifics), because many conspecific fish ganged up on males that lost broods just after spawning. Hetero cannibalism is very common phenomenon in almost all animals (Hausfater and Hrdy 1984, Elgar and Crespi 1992). This behavior is adaptive because hetero-cannibals energetically benefit by eating conspecifics but not suffer a genetic cost. Hrdy (1979) classified cannibalism (or infanticide) into five categories on the basis of its function: (1) exploitation; (2) resource competition; (3) parental manipulation; (4) sexual selection; and (5) social pathology. The category (1) applies in all case where cannibals consume conspecific. Hetero cannibalism functioning as exploitation will increase through intensified intraspecific competition as the population density increases (Dong and Polis 1992). The population density of *A. notatus* is considerably high compared to that of sympatric cardinal fishes. The high population density may be a primary factor facilitating hetero cannibalism in *A. notatus*.

Hetero cannibalism as sexual selection is of sociobiological interest. In some animals, it has been accepted that hetero cannibalism (or infanticide) functions as the intra-sexual competition by which killers can gain access to mates (Hrdy 1979; FitzGerald and van Havre 1987). In *A. notatus*, unpaired males that often interfered with rival's spawning are considered the main cannibals, but this study could not show if these cannibals increased the future mating success.

Sexual conflicts

In the study species, females could benefit from polygamous matings, while males could benefit from filial cannibalism. This is a common sexual strategy in three species. However, the balance of sexual conflicts varied among species. In the boulder species *A. doederleini*, the female mating strategy caused a female-biased operational sex ratio, and as a result, it facilitated the male cannibalism strategy. In the sandy species *A. niger*, on the other hand, both female polygamous trend and male cannibalistic trend were on the decline. This suggests that the sexual strategies are restrained by ecological factors such as a sparse distribution of adult fish and high predation risk.

Even in the same habitat, the sexual strategies thoroughly changed. In another boulder species *A. notatus*, the population density was very high (**Chapter 5-1**). In this fish, frequent intraspecific interaction due to the high population density provoked female to be aggressive to conspecific fish which are the potential egg predator. The increased reproductive investment by females caused a sexual difference in the mortality, resulting in the male-biased sex ratio. Where the operational sex ratio was male-biased, males was hetero cannibalistic rather than filial cannibalistic. Hetero cannibalism could be also a male strategy, where cannibals benefit by eating non-related eggs. Conversely, male cannibalism, whether it is filial or hetero, inflicts a cost of brood loss on females.

In such ways, males and females of cardinal fishes conflicted for interests. Early studies on reproductive strategies did not refer to the conflicting two strategies. However, the recent interest has been aimed at the sexual conflict because it helps our understanding of sexual selection and mating system (Rowe et al. 1994; Stockley 1997). The sexuality should be more taken into consideration to investigate the reproductive strategy. This study showed not only that a strategy of either sex could be affected by that of the other, but also that the respective strategies could vary depending on ecological and social factors. To view the dynamics of sexual conflicts, the comparison between populations within a species or among closely related species is a fruitful method.

V. Summary

Sexual strategy was compared among three sympatric cardinal fishes, *Apogon doederleini*, *A. notatus* and *A. niger*. Because of paternal mouthbrooding, the potential reproductive rate was usually higher in females. In all species, females practiced polygamous matings to enjoy greater reproductive success, while males practiced filial cannibalism to compensate for the care cost. The male and female sexual strategies varied among species. In the boulder species *A. doederleini*, female polygamous matings caused the female-biased operational sex ratio and consequently facilitated filial cannibalism by males. In the sandy species *A. niger*, such sexual strategies were restrained by two ecological factors, a sparse distribution of adult fish and high predation risk. In another boulder species *A. notatus* in which a population density is very high, increased

reproductive investment by females caused a significant sexual difference in the mortality, resulting in the male-biased operational sex ratio. In this fish, males more often practiced hetero, but not filial, cannibalism.

Chapter 6

General discussion

Adaptation and constraint

Through the comparative study of cardinal fishes, we have seen differences in life history traits in relation to environments (Chapter 5-1). The life history theory assumes that a set of traits which offer the greater fitness for individuals in the population is favored by the natural selection (Stearns 1992). One may conclude that individuals with a certain trait have adapted to their surroundings, using the optimality model which mathematically shows that they enjoy the greater fitness than individuals with the other trait. However this is not necessarily true. Adaptationists often commits this fallacy when they try to explain the evolution of trait in question. We cannot give an adaptive explanation for interspecific variation in the traits unless the causal relation is elucidated. The comparison among the currently existing species only shows us a correlation between traits and environments (Harvey and Pagel 1991).

Strictly speaking, the concept of adaptation should be founded on the comparison of an individual, a population or a species between two different points of a time series. In this study, the interspecific comparison gives us no information about which species is ancestral: the ancestor is the boulder species or the sandy species, and solitary or gregarious. If a phylogenetic relationship is known, then it will be easy to deduce the evolutionary process. Therefore, further work needs to be done for the understanding the adaptation in cardinal fishes. One of effective ways to know the evolutionary history is a molecular phylogenetic analysis: the phylogeny represents the course of history which organisms have experienced and in general, the pattern of DNA sequence reflects the phylogeny. At the present day, DNA sequence analysis to draw phylogenetic tree has been a commonplace, as molecular biological technique increasingly advances. The molecular phylogenetic tree is a useful tool to test evolutionary hypotheses.

More often, we find similarities in life history traits among related species even if their surroundings are greatly different. In cardinal fishes, for example, the growth pattern of three

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species was all determinate (**Chapter 5-1**). An optimal allocation model predicted that their determinate growth could be attributed to reproductive constraints linked with paternal mouthbrooding (**Chapter 3**). This prediction can be tested by comparing among fishes in which there exist reproductive constraints to a various extent. This comparison actually showed that the growth of a family Apogonidae was the most determinate among diverse fish taxa (**Appendix I**). We can know that such a similarity is due to a phylogenetic constraint only when comparing among higher taxonomic groups. The adaptation and constraint are the continuum, which often confuses us because of the inconsistent conclusion drawn from comparison at a different taxonomic level. In practicing the comparative methods, more important is to appropriately choose the taxonomic group within which traits in question should be compared. The appropriate comparative methods will help our understanding of adaptation and constraint.

Sexual conflict and sexual selection

Sexual reproduction always involves a conflict for interests between the sexes (Halliday 1994). In fishes, the prevalence of paternal care may be also an evolutionary consequence of sexual conflicts (Clutton-Brock 1991). Filial cannibalism by males is common in fishes, especially in paternal care species, whereas maternal cannibalism is less frequent even in species with maternal care (reviewed by Dominey and Blumer 1984, FitzGerald and Whoriskey 1992). This difference is ultimately due to sexual asymmetry in gametic investment: male sperm is energetically cheap but female egg is expensive (Parker et al. 1972). A cost of eating zygotes is negligible for males unless they invest in caring for the zygotes. In paternal species, filial cannibalism by males whose ration is restricted by the parental care may be a parasite on the production of females (Rohwer 1978).

Also in cardinal fishes, filial cannibalism by mouthbrooding males was a consequence of sexual conflicts (**Chapter 4-2, 5-2**). The prevalent occurrence of filial cannibalism in this family may be primarily due to a large energetic cost of mouthbrooding (**Chapter 2, 4-1**). Males can compensate for the care cost by eating their own eggs. A male's benefit from filial cannibalism is achieved at a female's cost. The balance of this conflict may be determined by the relative costs and benefits involved for both sexes: male cannibalism strategy is more profitable as the female benefit from polygamous mating strategy increases, and vice versa (**Chapter 5-2**). The comparative study

revealed not only that male and female strategies were mutually affected within a species, but also that both strategies varied among species. This variation in the sexual strategies may reflect the ecological and social differences in the environments which surround each species.

The evolution of sexual reproduction brought forth another important concept. Since Darwin (1871) proposed the concept of sexual selection to explain the evolution of sex differences, this field has been enthusiastically controversial. Two epochal ideas, operational sex ratio and potential reproductive rate offered by Emlen and Oring (1977) and Clutton-Brock and Vincent (1991), respectively, provoked theoreticians and empirical workers to take a further interest in studies of sexual selection. These two indicators enable us to predict on which sex the sexual selection operates more strongly, as supported by numerous empirical studies (Clutton-Brock and Vincent 1991; Kvarnemo and Ahnesjö 1996). In cardinal fishes, mouthbrooding usually retarded male reproductive rate below that of females (Chapter 4-2, 5-2). In this family, sex role reversal may therefore be a natural consequence of their care form, as is often the case in paternal egg bearers (Gwynne 1991, Rosenqvist 1993). Nevertheless, the study of *Apogon notatus* showed an unusual case to us. In this fish, females were more active in reproduction but the operational sex ratio was male-biased over the breeding season. This does not seem to agree with the general rule of sexual selection theory, that is, competition for mates is higher in the most abundant sex. Recently, I have collected some circumstantial evidence that the sexual selection would more strongly operate on males, but not females, in *A. notatus* (N. Okuda, in preparation). This comparative study showed that the intensity and direction of sexual selection could vary depending on environments to which species are exposed.

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Appendix I

Growth parameters in fishes. For K, L_∞, L_α and L_α/L_∞, see the text. $Tmax$ is the observed maximum age and T_α the age at maturity. M and F represent male and female, respectively.

Family	Species	K	L_∞(mm)	L_α(mm)	L_α/L_∞	$Tmax$	T_α	Sex	Refs[†]
Chondorichthyes									
Lamniformes									
Lamnidae	*Isurus oxyrinchus*	0.27	3020	1820	0.60	4.5	3	M	1
		0.20	3450	2580	0.75	11.5	7	F	
Carcharhiniformes									
Triakididae	*Triakis semifasciata*	0.09	1499	1000	0.67	24	7	M	2
		0.07	1602	1050	0.66	24	10	F	
Carcharhinidae	*Rhizoprionodon terraenovae*	0.36	1080	800	0.74	10	4	M	3
		0.36	1080	870	0.81	10	5	F	
	Carcharhinus plumbeus	0.05	2570	1550	0.6	15	13	M	4
		0.04	2990	1550	0.52	21	12	F	
	Carcharhinus falciformis	0.15	2910	2100	0.72	12.8	6	M	5
		0.15	2910	2250	0.77	13.8	7	F	
Sphyrnidae	*Sphyrna lewini*	0.07	3290	1800	0.55	11.6	10	M	5
		0.07	3290	2500	0.76	16.8	15	F	
Squaliformes									
Squalidae	*Squalus acanthias* a)	0.09	847	681*	0.80	38	14	M	6
		0.03	1251	810*	0.65	52	23	F	
	Squalus acanthias b)	0.07	961	681*	0.71	35	14	M	6
		0.03	1291	810*	0.63	64	23	F	
	Squalus acanthias c)	0.07	1018	720	0.71		11	M	6
		0.04	1529	935	0.61		20	F	
	Squalus acanthias d)	0.21	797	600	0.75		5	M	6
		0.11	1014	820	0.81		11	F	
Rajiformes									
Dasyatididae	*Dasyatis akajei*	0.10	1500	440	0.29		3.5	M&F	7
Osteichthyes									
Clupeiformes									
Clupeidae	*Clupea h. harengus* a)	0.38	300	240	0.80		4.5	M&F	7
	Clupea h. harengus b)	0.38	290	235	0.81		5	M&F	7
	Clupea h. harengus c)	0.39	295	240	0.81		4.3	M&F	7
	Clupea h. harengus d)	0.27	340	280	0.82		6.4	M&F	7
	Clupea h. harengus e)	0.21	360	205	0.57		7.5	M&F	7
	Clupea h. pallasi	0.19	385	290	0.75		7.4	M&F	7
	Sardinops caerulea a)	0.39	260	185	0.71		3.2	M&F	7

Family	Species	K	L_∞(mm)	L_0(mm)	L_0/L_∞	Tmax	T_0	Sex	Refs[†]
	Sardinops caerulea b)	0.45	300	225	0.75		3.1	M&F	7
Salmoniformes									
Salmonidae	*Coregonus clupeaformis* a)	0.13	500	270	0.54		6	M&F	7
	Coregonus clupeaformis b)	0.09	490	270	0.55		8.9	M&F	7
	Coregonus kiyi	0.51	280	180	0.64		2	M&F	7
	Salvelvinus namaycush	0.07	560	184	0.33		5.7	M&F	7
	Salmo trutta	0.36	300	240	0.80		4.5	M&F	7
	Salvelinus alpinus	0.03	1400	450	0.32		12	M&F	7
Osmeridae	*Osmerus mordax dentex*	0.22	325	200	0.62	15	6	M&F	8
Esocidae	*Esox lucius* a)	0.35	770	400	0.52	10	2	M	9
		0.24	1000	420	0.42	9	2	F	
	Esox lucius b)	0.21	1100			5		M	9
		0.21	1150			12		F	
	Esox lucius c)	0.38	690					M	9
		0.26	940					F	
	Esox lucius d)	0.36	770					M	9
		0.28	1160					F	
	Esox lucius e)	0.16	1410					M&F	9
Cypriniformes									
Cyprinidae	*Phoxinus phoxinus*	0.55	90	38	0.42		1	M&F	7
	Leuciscus leuciscus a)	0.19	265	92	0.35	9	2	M	10
		0.17	258	160	0.62	10	4	F	
	Leuciscus leuciscus b)	0.28	265	113	0.42	9	2	M	10
		0.22	275	111	0.41	10	2	F	
	Leuciscus leuciscus c)	0.30	260					M&F	10
	Leuciscus leuciscus d)	0.18	210					M&F	10
	Leuciscus leuciscus e)	0.14	300					M&F	10
	Leuciscus leuciscus f)	0.32	240					M&F	10
	Leuciscus leuciscus g)	0.37	287					M&F	10
	Leuciscus leuciscus h)	0.32	247					M&F	10
Cobitidae	*Rutilus arcasii* a)	0.26	120	44	0.37	4	2	M	11
		0.26	120	40	0.33	5	2	F	
	Rutilus arcasii b)	0.27	133	42	0.32	4	2	M	11
		0.27	133	36	0.27	6	1	F	
	Rutilus arcasii c)	0.40	117					M&F	11
	Rutilus arcasii d)	0.43	103					M&F	11
	Rutilus rutilus a)	0.25	240	118	0.49	11	3	M	12
		0.15	370	120	0.32	13	3	F	
	Rutilus rutilus b)	0.14	400			13		M	12

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Family	Species	K	L∞(mm)	Lα(mm)	Lα/L∞	Tmax	Tα	Sex	Refs†
		0.13	430			13		F	
Batrachoidiformes									
Batrachoididae	Opsanus tau a)	0.15	407			11		M	13, 14
		0.39	272	161*	0.60	9	2	F	
	Opsanus tau b)	0.11	381					M	13
		0.41	241					F	
Gadiformes									
Gadidae	Gadus minutus	0.40	240	130	0.54		2	M&F	7
	Gadus virens	0.19	1070	710	0.66		5.7	M&F	7
	Melanogrammus aeglefinus	0.20	530	260	0.49		3.4	M&F	7
Merlucciidae	Merluccius merlucius	0.10	600	270	0.45		6	M&F	7
Beryciformes									
Holocentridae	Myripristis amaena	0.22	194	149*	0.77	14 >	6	M&F	15
	Sargocentron diadema	1.13	168					M&F	15
	Holocentrus diadema	1.47	153					M&F	15
	Holocentrus ascensionis	0.39	230					M&F	15
Gasterosteiformes									
Gasterosteidae	Gasterosteus aculeatus	0.64	67	36	0.54		1.2	M&F	7
	Pungitius pungitius	1.60	43	37	0.86		1.2	M&F	7
Scorpaeniformes									
Scorpaenidae	Sebastiscus marmoratus	0.51	188	152*	0.81	6	3	M	16, 17
		0.55	174	145*	0.84	6	3	F	
	Sebastes thompsoni	0.22	332			9		M&F	18
Hexagrammidae	Oxylebius pictus a)	0.32	184	123	0.67	5	2	M	19
		0.32	184	140	0.76	6	3	F	
	Oxylebius pictus b)	0.43	214	143	0.67	6	2	M	19
		0.43	214	171	0.80	8	3	F	
Cottidae	Cottus gobi a)	0.40	73	42	0.58		2.1	M&F	7
	Cottus gobi b)	0.50	65	50	0.77		2.9	M&F	7
	Cottus pitensis	0.07	259	56*	0.22	5	2	M&F	20
	Cottus asperrimus	0.18	92	44*	0.48	5	2	M&F	20
	Cottus klamathensis macrops	0.28	98	55*	0.57	5	2	M&F	20
Perciformes									
Serranidae	Plectropomus maculatus	0.21	600			12		M&F	21
	Mycteroperca phenax	0.07	1090			21		M&F	15
Priacanthidae	Priacanthus tayenus	1.25	290			2		M&F	15
Apogonidae	Apogon doederleini	1.56	87	69	0.80	6	1	M	31

Family	Species	K	L∞(mm)	Lα(mm)	Lα/L∞	Tmax	Tα	Sex	Refs[†]
		1.62	89	73	0.82	7	1	F	
	Apogon notatus	1.34	89	60	0.68	7	1	M	31
		1.29	87	63	0.72	6	1	F	
	Apogon niger	1.65	81	62	0.76	4	1	M	31
		1.48	86	65	0.77	2	1	F	
Percidae	*Perca fluviatilis*	0.20	300	160	0.53		3.8	M&F	7
Lutjanidae	*Lutjanus kasmira*	0.29	340			6		M&F	22
	Ocyurus chrysurus	0.28	451			14		M&F	23
Haemulidae	*Haemulon plumieri*	0.11	640			13		M&F	15
Sparidae	*Calamus nodosus*	0.21	459			17		M&F	15
Lethrinidae	*Lethrinus lentjan*	0.29	440			7		M&F	24
	Lethrinus mahsena	0.21	495			7		M&F	24
Sciaenidae	*Micropogonias undulatus*	0.27	419			8		M&F	25
Chaetodontidae	*Chaetodon rainfordi*	0.31	119	62	0.52	10	1	M&F	26
	Chaetodon plebius	0.72	94			7		F	26
	Chelmon rostratus	0.50	123			10		M&F	26
Pomacentridae	*Pomacentrus moluccensis*	0.53	47			9		M&F	27
	Pomacentrus wardi	0.51	72			10		M&F	27
	Dascyllus albisella	0.23	130	113	0.87	11		M&F	28
Blenniidae	*Blennius pholis*	0.30	170	80	0.47		2.1	M&F	7
Trichiuridae	*Lepidopus caudatus*	0.23	2018	970	0.48	8	2	M	29
		0.24	2000	1110	0.56	8	2	F	
Scombridae	*Pnematophorus diego*	0.4	400	320	0.80		4	M&F	7
Pleuronectiformes									
Bothidae	*Citharichthys sorididus*	0.30	300	190	0.63		3.3	M&F	7
Pleuronectidae	*Parophrys vetulus*	0.17	485	387*	0.80	21	6	F	30
	Pleuronectes platessa	0.08	700	280	0.40		6.4	M&F	7
	Hippoglossoides platessoides	0.07	600	400	0.67		15	M&F	7

Letter following species name means different sampling locality.

* The length back-calculated from age at maturity from the von Bertalanffy equation.

[†]References 1, Pratt et al. 1983; 2, Kusher et al. 1992; 3, Branstetter 1987a; 4, Casey et al. 1985; 5, Branstetter 1987b; 6, Ketchen 1975; 7, Roff 1984; 8, Haldorson and Craig 1984; 9, Mann 1976; 10, Mann 1974; 11, Rincon and Lobon-Cervia 1989; 12, Mann 1973; 13, Radtke et al. 1985; 14, Wilson et al. 1982; 15, Dee and Radtke 1989; 16, Yokogawa et al. 1992; 17, Yokogawa and Iguchi 1992; 18, Suzuki et al. 1978; 19, DeMartini and Anderson 1980; 20, Daniels 1987; 21, Ferreira and Russ 1992; 22, Morales-Nin and Ralston 1990; 23, Johnson 1983; 24, Wassef 1991; 25, Barger 1985; 26, Fowler 1991; 27, Fowler and Doherty 1992; 28, Hill and Radtke 1988; 29, Demestre et al. 1993; 30, Dygert 1990; 31, present study.