Determinate growth in a paternal mouthbrooding fish whose reproductive success is limited by buccal capacity

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Summary

The life history of the paternal mouthbrooding cardinal fish *Apogon doederleini* was investigated in the temperate waters of Japan, with particular reference to its growth and reproductive rate. Both males and females almost ceased to grow at age 3 years, although living to 7 years of age. 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's 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 based on data of *A. doederleini*, a simulation model of energy allocation without considering sexual interaction revealed that the optimal growth pattern shows an indeterminate growth that differs greatly from the actual growth pattern of *A. doederleini*. This suggests that there are some brooding constraints to size-advantage of reproductive success in this species. The possible mechanism of such reproductive constraint is discussed.

Keywords: apogonid fish; growth pattern; life history; optimal energy allocation; reproductive rate

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 a fecundity advantage. As the internal space to accommodate eggs or embryos increases with body size, clutch size will increase in proportion to 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 non-existent or consists of non-depreciable behaviours, such as anti-predator guarding, where costs do not increase in proportion to 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 offspring body size may depend on maternal body size (Blueweiss *et al.*, 1978). This obscure size–fecundity relationship is due in part 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 fledgling or weaning, irrespective of parental size. For example, avian clutch size is restricted strongly by the ability of parents to feed young (Lack,

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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 possess a particular set of brooding constraints. Here we 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, we describe a case study of the cardinal fish *Apogon doederleini*, a paternal mouthbrooder, focusing on its growth pattern and size–fecundity and age–fecundity relationships. Second, using a modified version of the model of Kozlowski and Uchmanski (1987), we discuss if determinate growth is linked with brooding constraints in *A. doederleini*.

Materials and methods

Study species

Apogon doederleini inhabits shallow waters of the west Pacific. Males and females individually establish their sheltering and breeding sites, and their site fidelity is strong throughout the year (Okuda and Yanagisawa, 1996a). Spawning occurs in pairs, usually between a neighbouring male and female. Immediately after the release of a cohesive egg mass by the female, the male takes it into his mouth (Kuwamura, 1985). The paternal mouthbrooding of the egg mass continues for 5–17 days until hatching, depending on ambient water temperature (Okuda and Yanagisawa, 1996b). Mouthbrooding males do not feed, while females, which provide no parental care, forage after spawning. In one breeding season (May to August), a female produces several egg masses and a male completes several breeding cycles.

Measurement of life-history parameters

The life history of this species was investigated at Murote Beach, Shikoku Island, Japan. A 10×20 m quadrat was set on the boulder slope at a depth of 5.8–9.0 m. At the beginning of the breeding season in 1992, all individuals of this fish whose sheltering sites were in the quadrat were captured and marked individually underwater by extracting two or three dorsal and/or anal fin rays. A few scales from the body were removed and preserved in 10% formalin to age the fish in the laboratory. The fish were released at the capture sites after measurement of their standard length. Prior to the breeding seasons of 1993 and 1994, these procedures were repeated for all surviving marked individuals and new residents.

For ageing fish from scales, we followed the methods of Suzuki and Ueno (1983, 1987) and Ueno *et al.* (1987). Because in some apogonid fishes an annulus on the scale is formed prior to or during the breeding season, the number of annuli corresponds with age. The application of this method to *A. doederleini* was validated in two ways: monthly collection of specimens and examination of scales from the same individuals at two different times, prior to and soon after the breeding season. Both methods showed that the annulus was formed during the breeding season.

From 3 years, mark-recapture data, the annual individual growth rate and adult survival rate were calculated. The growth rate (G_t) at age t is given by:

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

where L_t represents the standard length (mm) at age t. The growth pattern is fitted to the von Bertalanffy growth equation as follows:

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

where L_t is the length at age t, L_∞ is the asymptotic length, K is a growth coefficient and t_0 is the hypothetical time at which the length is zero. K determines the shape of the growth curve: the larger the value of 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 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 (3.15 mm; Kuwamura, 1983) was substituted for L_0.

The annual adult survival rate is 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 (Okuda and Yanagisawa, 1996b).

Measurement of reproductive success

Daily observations throughout the breeding season of 1993 enabled us to obtain data on the number of broods which each female produced and each male received from his mates in the season (Okuda and Yanagisawa, 1996a). To determine the number of eggs per brood, we captured 62 males outside the quadrat at two different mouthbrooding phases: within a day of spawning ($n = 11$) and 1–2 days before the expected day of hatching ($n = 51$). After they were anaesthetized with quinaldine, their broods were removed and their standard length measured. In 47 cases in which their mates could be identified, the standard length of these females was also measured.

Results

Life history

The first recruitment of juveniles took place in early June, 2 weeks after the onset of reproduction. Their minimum size was 9.0 mm. At this stage, they occurred in small shoals near rocks, but gradually became solitary with growth. All 1-year-old fish established their sheltering sites and attained maturation. Very few fish survived to age 1 year in both 1993 and 1994 (Fig. 1), although a substantial recruitment of juveniles occurred each year. The survival rate for juveniles could not be estimated because their recruitment and disappearance occurred simultaneously during June to September.

The annual survival rate for adult fish did not differ significantly among age groups (Table 1; d.f. $= 4$, $\chi^2 = 6.86$, $P > 0.1$, 5- and 6-year-old fish combined). The oldest males and females were 5 and 7 years old, respectively. 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), but this was non-significant (d.f. $= 1$, $\chi^2 = 3.38$, $P > 0.06$ in 1992; d.f. $= 1$, $\chi^2 = 1.70$, $P > 0.1$ in 1993).

Growth

Body size differed significantly among age groups (Table 1; ANOVA, d.f. $= 6$, $F = 51.0$, $P < 0.0001$). When body size was compared between two successive age groups, however, the difference was significant only between 1- and 2-year-old fish (Scheffé 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 ANOVA, $P > 0.8$). The minimum size at maturity was 69.0 mm for males and 73.0 mm for females.
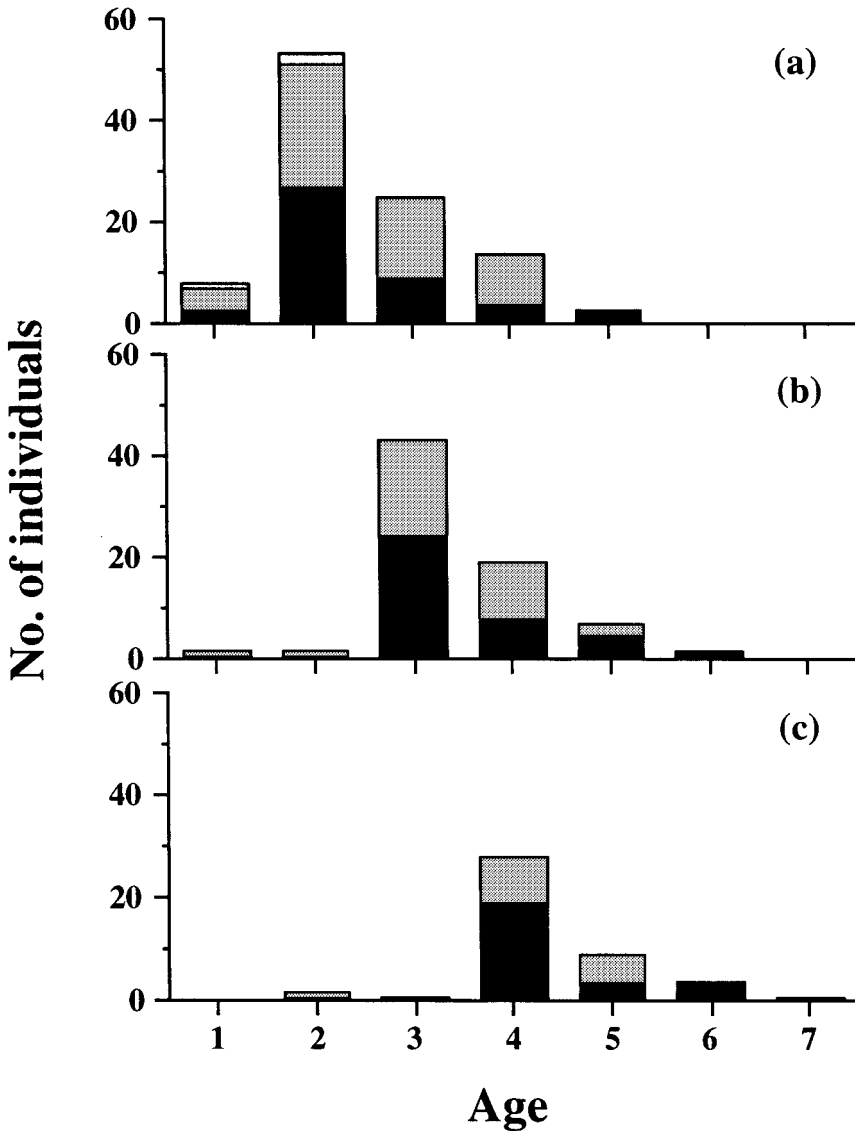
Figure 1. The age structure of *A. doederleini* at Murote Beach in 1992 (a), 1993 (b) and 1994 (c). Solid, shaded and open bars indicate female, male and individual of unknown sex, respectively.

One-year-old fish grew at a fast rate but the growth of fish more than 1 year old decreased dramatically (Table 1); the growth rate of 1-year-old fish was significantly faster than that of fish in any other age class (Scheffé F-test, $P < 0.05$ for all). No difference was seen between the sexes in growth rate in the same age groups (two-way ANOVA, $P > 0.2$).

From the linear regression of L_{t+1} against L_t, the three parameters of the von Bertalanffy equation were as follows: $K = 1.56$, $L_{\infty} = 86.5$, $t_0 = -0.02$ for males ($r^2 = 0.86$, $n = 48$,

Table 1. Annual growth rate and survival rate in *Apogon doederleini* (sample size in parentheses)

Age (years)	Standard length (mm)[a]	Annual growth rate (%)[a]	Annual survival rate (%)
1	71.0 ± 3.32 (9)	17.5 ± 5.59 (4)	30.0 (10)
2	82.8 ± 3.43 (55)	3.33 ± 2.65 (40)	69.1 (55)
3	86.2 ± 3.31 (69)	2.03 ± 2.18 (43)	63.2 (68)
4	87.9 ± 2.93 (59)	0.36 ± 2.07 (16)	51.6 (31)
5	89.1 ± 2.71 (19)	0.20 ± 1.76 (6)	60.0 (10)
6	90.8 ± 1.78 (6)	−5.07 (1)	50.0 (2)
7	85.5 (1)	–	–

Data from 1992 to 1994 are pooled. Body size in each age group did not differ between years (two-way ANOVA).
[a]Mean ± S.D.

$P < 0.0001$) and $K = 1.62$, $L_\infty = 88.6$, $t_0 = -0.02$ for females ($r^2 = 0.71$, $n = 71$, $P < 0.0001$). The growth curves were similar between the sexes (Fig. 2).

Reproductive success

The size of broods removed just before hatching ($\bar{x} \pm$ S.D. $= 8567 \pm 1641$, $n = 51$) was significantly smaller than that of broods removed on the day following spawning ($10{,}177 \pm 1580$, $n = 11$; $t = 2.97$, $P < 0.005$), although there was no significant difference in body size of the parents between the two groups ($t = -1.48$, $P > 0.1$ for males; $t = -0.37$, $P > 0.7$ for females). Spawning pairs were size-assortative ($r^2 = 0.71$, $P < 0.0001$, $n = 39$), and brood size just before hatching correlated positively with body size of the male ($r^2 = 0.44$, $P < 0.0001$, $n = 51$) and body size of the female ($r^2 = 0.29$, $P < 0.0005$, $n = 39$). Stepwise multiple regression analysis, however, showed that 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) (mm standard length) is expressed by the following allometric equation: $y = 1.44x^{1.96}$.
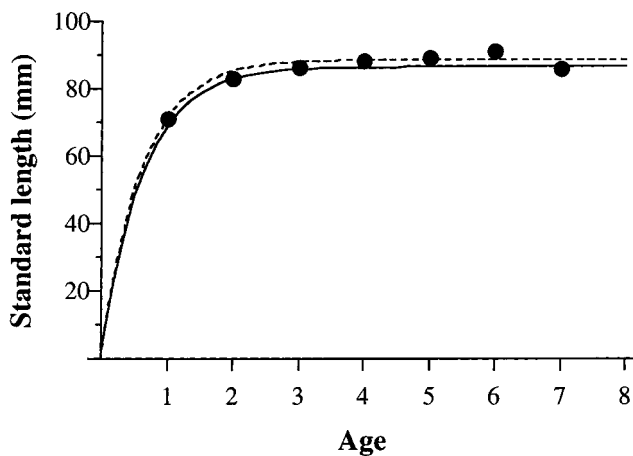

Figure 2. Hypothetical growth curves drawn from the von Bertalanffy growth equation. Solid and dotted lines are for males and females, respectively. Each plot presents the mean body length in Table 1.

Brood size close to hatching increased with age of the male (Table 2). However, 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 did not correlate with age of the female either ($r^2 = 0.05$, $P > 0.1$, $n = 39$).

The number of broods that a male received from mates in one breeding season was 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 of occasional brood cannibalism by mouthbrooding males (Okuda and Yanagisawa, 1996a,b), 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 was weakly correlated 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 ($r^2 = 0.10$, $n = 31$, $P > 0.09$).

Based on the above results, two life-history parameters were obtained for each sex: the probability that a 1-year-old fish survives to age x (l_x), and annual reproductive rate (m_x) at age x. The latter is expressed as half the average brood size close to hatching multiplied by the average number of broods hatched in a breeding season (Table 2). The annual reproductive rate increases until age 2 years in males and until age 3 years in females; thereafter it remains almost constant. The reproductive expectancy ($l_x \cdot m_x$), which is defined here as the expectancy of reproduction at age x for 1-year-old fish, is greatest at age 1 year for both sexes, and the contribution to lifetime reproductive success decreases dramatically with age (Fig. 3).

Discussion

Growth pattern

The growth of *Apogon doederleini* showed a marked decrease at age 2 years and became nearly asymptotic at age 3 years. The relative size at maturity to asymptotic size (L_α/L_∞), which is an index of determinate growth, was 0.80 for males and 0.82 for females. The value of L_α/L_∞ varies greatly among fish species, from 0.22 to 0.87 (Appendix) with a 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, and higher than the mean values of snakes (0.68; Shine and Charnov, 1992) and lizards (0.74; Shine and Charnov, 1992), although 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 $= 0.33$, Appendix). A high value of K also effectively indicates determinate growth.

K varies considerably, even among populations of a fish species (Appendix). The growth pattern of fishes is greatly affected by biotic and abiotic factors (Wootton, 1991), of which food availability and predation pressure are the most influential in natural populations (Mann, 1973; Nakashima and Leggett, 1975; DeMartini and Anderson, 1980; Schmitt and Hubert, 1983; Noltie, 1988; Chisnall, 1989). It has been reported for some species that populations experiencing 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 (N. Okuda, unpublished data). At our study site, gammarids, 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.

Table 2. A life table of *Apogon doederleini* showing survival rate, $l(x)$, and annual reproductive rate, $m(x)$ (sample size in parentheses)

Age (years)	$l(x)^a$	Males			Females		
		Brood size	No. of hatched broods	$m(x)$	Brood size of mate[b]	No. of hatched broods	$m(x)$
1	1.00	4577 ± 717 (3)	4 (1)	9 154	5788	3 (1)	8 682
2	0.30	8469 ± 899 (6)	6 (1)	25 407	8493	4 (1)	16 986
3	0.21	8720 ± 1322 (36)	5.82 ± 1.02 (17)	25 375	8748	5.74 ± 1.20 (19)	25 107
4	0.13	9679 ± 1682 (5)	5.56 ± 0.73 (9)	26 908	8166	5.20 ± 1.64 (5)	21 232
5	0.07	9014[c]	5.00 ± 0.00 (2)	22 943	8991	5.75 ± 2.22 (4)	25 849
6	0.04	–	–	–	9375	6 (1)	28 125
7	0.02	–	–	–	–	–	–

[a]Relative values calculated from the annual survival rate in Table 1.
[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.
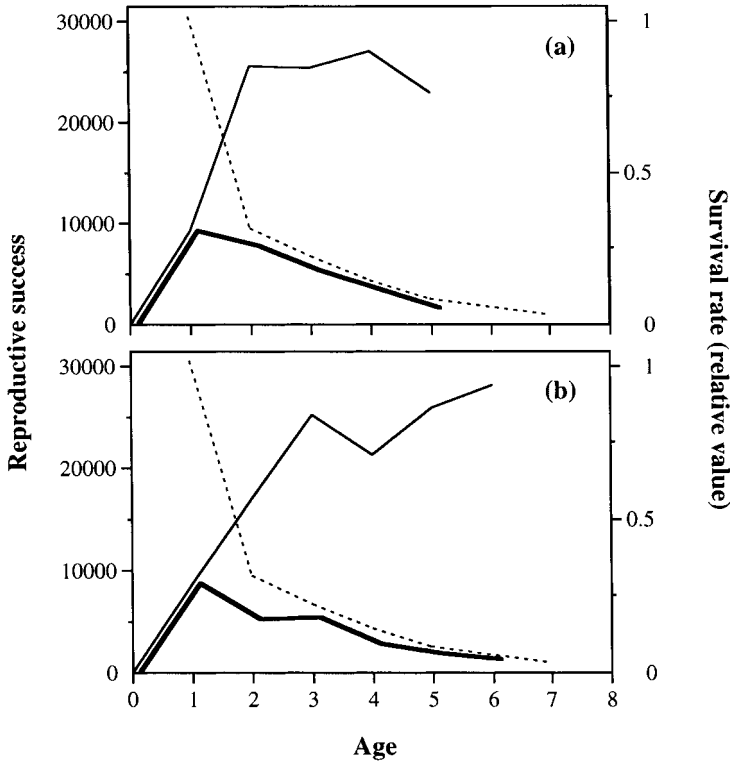
Figure 3. The reproductive expectancy $l(x) \cdot m(x)$ (bold lines) calculated from $l(x)$ (dotted lines) and $m(x)$ (thin lines) in Table 2 for males (a) and females (b), respectively.

Optimal allocation to growth and reproduction

We examine here 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. Based on these assumptions, a set of optimal switching times $(t_1, \ldots, t_\omega)$ that maximizes the lifetime reproductive success $R_0 = \sum_{k=1}^{\omega} R_k(t_1, \ldots, t_k)$ is calculated, where ω is the lifespan and R_k and t_k are the number of offspring and the switching time at age k, respectively.

Now, let us consider a model species for *A. doederleini*, which has annual survivability q and lives to age 7 years. 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

We estimated $f(L)$ to be $79.3L^{0.0476}$ from juvenile growth of *A. doederleini* within 4 months of settlement (N. Okuda, unpublished data), when the maximum growth rate is expected. The reproductive rate $H(L)$ was estimated to be $10.1L^{1.96}$, which is equal to the reproductive rate of a male that raised seven broods per season. We 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 $L \geq L^*$ (Fig. 4). We consider three stages of limitation: $H_1(L)$ is without limitation, $H_2(L)$ has an upper limitation at $L^* = 176.0$ mm and $H_3(L)$ has an upper limitation at $L^* = 88.0$ mm, which is equal to the asymptotic length of *A. doederleini*. From Table 1, annual survival q is represented as 0.3 and 0.7.

We 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 (Fig. 5). With high survival ($q = 0.7$; Fig. 5a), stronger limitation makes the model species mature at a younger age (3.67, 1.86 and 0.95 y for $H_1(L)$, $H_2(L)$ and $H_3(L)$, respectively) and at smaller size (324, 159 and 78.5 mm). In any case, it shows an extremely determinate growth ($L_\alpha/L_\infty = 0.93$, 0.90 and 0.89). In contrast, with low survival ($q = 0.3$; Fig. 5b), age and size at maturity are similar for $H_1(L)$, $H_2(L)$ and $H_3(L)$ (0.93, 0.93 and 0.81 y and 76.7, 76.7 and 66.4 mm). As the limitation becomes stronger, the model species shows a more 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 fits field data well, 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 differ greatly 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 some factors do 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 the frequent occurrence of partial brood cannibalism (Okuda and Yanagisawa, 1996b). A possible function of partial brood cannibalism in parental males is to adjust the number of off-spring to their buccal capacity, rather than to provide a nutritive benefit. Since mouthbrooding
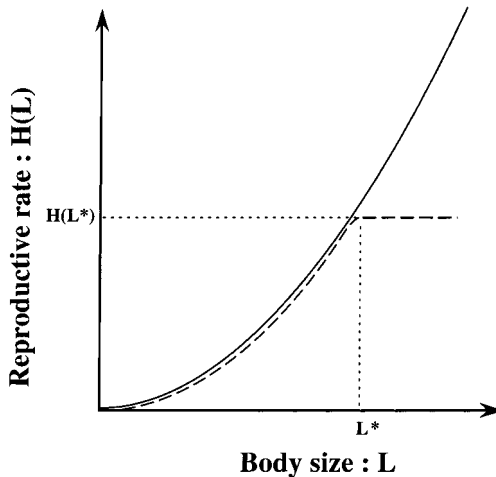
Figure 4. The reproductive rate with respect to body size in a species with no reproductive constraints (solid line) and with reproductive constraints (broken line), in which it is assumed that the reproductive rate becomes constant at a critical size L^*.
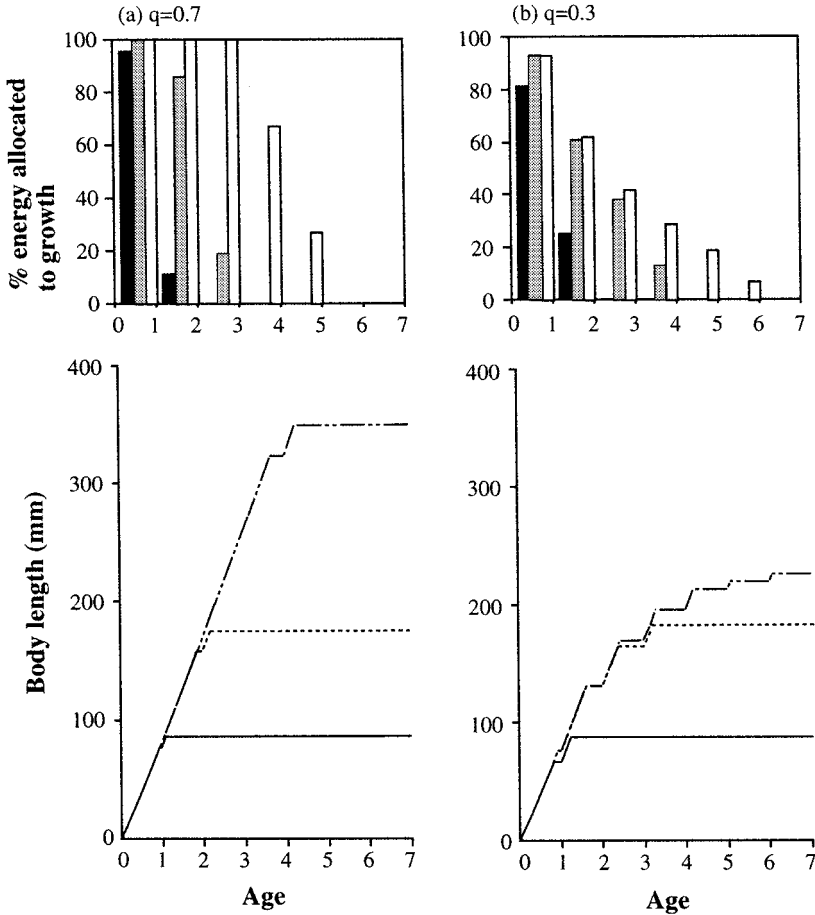
Figure 5. Optimal energy allocation to growth at each age when $q = 0.7$ (a) and $q = 0.3$ (b) (top) and the individual growth curve resulting from the optimal allocation (bottom). Open, shaded and solid bars and chain, dotted and solid lines show cases of no reproductive limitation, an upper limitation at $L^* = 176$ mm and at $L^* = 88$ mm, respectively.

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. Brood size correlates closely with the volume of the male buccal cavity (M. Miyazaki, unpublished data). Thus male reproductive success may be limited primarily by 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 their time mouthbrooding in the breeding season (Okuda and Yanagisawa, 1996b), there would be little scope 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, 1996a). 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 cost of care (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, 1996a). Females are the predominant competitors for mates, as in other apogonid fishes (Kuwamura, 1985; Okuda and Yanagisawa, 1996a). 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, 1996a). That the number of broods produced by one female in a breeding season is 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 depends greatly on the brooding characteristics of males, especially their buccal capacity.

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

Acknowledgements

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Appendix

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

Family	Species	K	$L_{\infty\,(mm)}$	$L_{\alpha\,(mm)}$	L_α/L_∞	T_{max}	T_α	Sex	Reference
Chondorichthyes									
Lamniformes									
Lamnidae	*Isurus oxyrinchus*	0.27	3020	1820	0.60	4.5	3	M	Pratt *et al.* (1983)
		0.20	3450	2580	0.75	11.5	7	F	
Carcharhiniformes									
Triakidae	*Triakis semifasciata*	0.09	1499	1000	0.67	24	7	M	Kusher *et al.* (1992)
		0.07	1602	1050	0.66	24	10	F	
Carcharhinidae	*Rhizoprionodon terraenovae*	0.36	1080	800	0.74	10	4	M	Branstetter (1987a)
		0.36	1080	870	0.81	10	5	F	
	Carcharhinus plumbeus	0.05	2570	1550	0.60	15	13	M	Casey *et al.* (1985)
		0.04	2990	1550	0.52	21	12	F	
	Carcharhinus falciformis	0.15	2910	2100	0.72	12.8	6	M	Branstetter (1987b)
		0.15	2910	2250	0.77	13.8	7	F	
Sphyrnidae	*Sphyrna lewini*	0.07	3290	1800	0.55	11.6	10	M	Branstetter (1987b)
		0.07	3290	2500	0.76	16.8	15	F	
Squaliformes									
Squalidae	*Squalus acanthias*[a]	0.09	847	681*	0.80	38	14	M	Ketchen (1975)
		0.03	1251	810*	0.65	52	23	F	
	Squalus acanthias[b]	0.07	961	681*	0.71	35	14	M	Ketchen (1975)
		0.03	1291	810*	0.63	64	23	F	
	Squalus acanthias[c]	0.07	1018	720	0.71		11	M	Ketchen (1975)
		0.04	1529	935	0.61		20	F	
	Squalus acanthias[d]	0.21	797	600	0.75		5	M	Ketchen (1975)
		0.11	1014	820	0.81		11	F	
Rajiformes									
Dasyatididae	*Dasyatis akajei*	0.10	1500	440	0.29		3.5	M & F	Roff (1984)
Osteichthyes									
Clupeiformes									
Clupeidae	*Clupea h. harengus*[a]	0.38	300	240	0.80		4.5	M & F	Roff (1984)
	Clupea h. harengus[b]	0.38	290	235	0.81		5	M & F	Roff (1984)

Family	Species	K	$L_{\infty(mm)}$	$L_{\alpha(mm)}$	L_α/L_∞	T_{max}	T_α	Sex	Reference
	Clupea h. harengus[c]	0.39	295	240	0.81		4.3	M & F	Roff (1984)
	Clupea h. harengus[d]	0.27	340	280	0.82		6.4	M & F	Roff (1984)
	Clupea h. harengus[e]	0.21	360	205	0.57		7.5	M & F	Roff (1984)
	Clupea h. pallusi	0.19	385	290	0.75		7.4	M & F	Roff (1984)
	Sardinops caerulea[a]	0.39	260	185	0.71		3.2	M & F	Roff (1984)
	Sardinops caerulea[b]	0.45	300	225	0.75		3.1	M & F	Roff (1984)
Salmoniformes									
Salmonidae	*Coregonus clupeaformis[a]*	0.13	500	270	0.54		6	M & F	Roff (1984)
	Coregonus clupeaformis[b]	0.09	490	270	0.55		8.9	M & F	Roff (1984)
	Coregonus kiyi	0.51	280	180	0.64		2	M & F	Roff (1984)
	Salvelinus namaycush	0.07	560	184	0.33		5.7	M & F	Roff (1984)
	Salmo trutta	0.36	300	240	0.80		4.5	M & F	Roff (1984)
	Salvelinus alpinus	0.03	1400	450	0.32		12	M & F	Roff (1984)
Osmeridae	*Osmerus mordax dentex*	0.22	325	200	0.62	15	6	M & F	Haldorson and Craig (1984)
Esocidae	*Esox lucius[a]*	0.35	770	400	0.52	10	2	M	Mann (1976)
		0.24	1000	420	0.42	9	2	F	
	Esox lucius[b]	0.21	1100			5		M	Mann (1976)
		0.21	1150			12		F	
	Esox lucius[c]	0.38	690					M	Mann (1976)
		0.26	940					F	
	Esox lucius[d]	0.36	770					M	Mann (1976)
		0.28	1160					F	
	Esox lucius[e]	0.16	1410					M & F	Mann (1976)
Cypriniformes									
Cyprinidae	*Phoxinus phoxinus*	0.55	90	38	0.42		1	M & F	Roff (1984)
	Leuciscus leuciscus[a]	0.19	265	92	0.35	9	2	M	Mann (1974)
		0.17	258	160	0.62	10	4	F	
	Leuciscus leuciscus[b]	0.28	265	113	0.42	9	2	M	Mann (1974)
		0.22	275	111	0.41	10	2	F	
	Leuciscus leuciscus[c]	0.30	260					M & F	Mann (1974)
	Leuciscus leuciscus[d]	0.18	210					M & F	Mann (1974)
	Leuciscus leuciscus[e]	0.14	300					M & F	Mann (1974)

Family	Species	K	$L_{\infty \text{(mm)}}$	$L_{\alpha \text{(mm)}}$	L_α / L_∞	T_{max}	T_α	Sex	Reference
	Leuciscus leuciscus[f]	0.32	240					M & F	Mann (1974)
	Leuciscus leuciscus[g]	0.37	287					M & F	Mann (1974)
	Leuciscus leuciscus[h]	0.32	247					M & F	Mann (1974)
Cobitidae	*Rutilus arcasii*[a]	0.26	120	44	0.37	4	2	M	Rincon and
		0.26	120	40	0.33	5	2	F	Lobon-Cervia (1989)
	Rutilus arcasii[b]	0.27	133	42	0.32	4	2	M	Rincon and
		0.27	133	36	0.27	6	1	F	Lobon-Cervia (1989)
	Rutilus arcasii[c]	0.40	117					M & F	Rincon and
									Lobon-Cervia (1989)
	Rutilus arcasii[d]	0.43	103					M & F	Rincon and
									Lobon-Cervia (1989)
	Rutilus rutilus[a]	0.25	240	118	0.49	11	3	M	Mann (1973)
		0.15	370	120	0.32	13	3	F	
	Rutilus rutilus[b]	0.14	400			13		M	Mann (1973)
		0.13	430			13		F	
Batrachoidiformes									
Batrachoididae	*Opsanus tau*[a]	0.15	407			11		M	Radtke *et al.* (1985),
		0.39	272	161*	0.60	9	2	F	Wilson *et al.* (1982)
	Opsanus tau[b]	0.11	381					M	Radtke *et al.* (1985)
		0.41	241					F	
Gadiformes									
Gadidae	*Gadus minutus*	0.40	240	130	0.54		2	M & F	Roff (1984)
	Gadus virens	0.19	1070	710	0.66		5.7	M & F	Roff (1984)
	Melanogrammus aeglefinus	0.20	530	260	0.49		3.4	M & F	Roff (1984)
Merlucciidae	*Merluccius merlucius*	0.10	600	270	0.45		6	M & F	Roff (1984)
Beryciformes									
Holocentridae	*Myripristis amaena*	0.22	194	149*	0.77	14>	6	M & F	Dee and
									Radtke (1989)
	Sargocentron diadema	1.13	168					M & F	Dee and
									Radtke (1989)

Appendix (contd.)

Family	Species	K	$L_{\infty\text{(mm)}}$	$L_{\alpha\text{(mm)}}$	L_α/L_∞	$T_{\max}$	T_α	Sex	Reference
	Holocentrus diadema	1.47	153					M & F	Dee and Radtke (1989)
	Holocentrus ascensionis	0.39	230					M & F	Dee and Radtke (1989)
Gasterosteiformes									
Gasterosteidae	*Gasterosteus aculeatus*	0.64	67	36	0.54		1.2	M & F	Roff (1984)
	Pungitius pungitius	1.60	43	37	0.86		1.2	M & F	Roff (1984)
Scorpaeniformes									
Scorpaenidae	*Sebastiscus marmoratus*	0.51	188	152*	0.81	6	3	M	Yokogawa *et al.* (1992),
		0.55	174	145*	0.84	6	3	F	Yokogawa and Iguchi (1992)
	Sebastes thompsoni	0.22	332			9		M & F	Suzuki *et al.* (1978)
Hexagrammidae	*Oxylebius pictus*[a]	0.32	184	123	0.67	5	2	M	DeMartini and
		0.32	184	140	0.76	6	3	F	Anderson (1980)
	Oxylebius pictus[b]	0.43	214	143	0.67	6	2	M	DeMartini and
		0.43	214	171	0.80	8	3	F	Anderson (1980)
Cottidae	*Cottus gobi*[a]	0.40	73	42	0.58		2.1	M & F	Roff (1984)
	Cottus gobi[b]	0.50	65	50	0.77		2.9	M & F	Roff (1984)
	Cottus pitensis	0.07	259	56*	0.22	5	2	M & F	Daniels (1987)
	Cottus asperrimus	0.18	92	44*	0.48	5	2	M & F	Daniels (1987)
	Cottus klamathensis macrops	0.28	98	55*	0.57	5	2	M & F	Daniels (1987)
Perciformes									
Serranidae	*Plectropomus maculatus*	0.21	600			12		M & F	Ferreira and Russ (1992)
	Mycteroperca phenax	0.07	1090			21		M & F	Dee and Radtke (1989)
Priacanthidae	*Priacanthus tayenus*	1.25	290			2		M & F	Dee and Radtke (1989)
Apogonidae	*Apogon doederleini*	1.56	87	69	0.80	6	1	M	Present study
		1.62	89	73	0.82	7	1	F	Present study

Family	Species	K	$L_{\infty\text{(mm)}}$	$L_{\alpha\text{(mm)}}$	L_α/L_∞	$T_{\max}$	T_α	Sex	Reference
Percidae	*Perca fluviatilis*	0.20	300	160	0.53		3.8	M & F	Roff (1984)
Lutjanidae	*Lutjanus kasmira*	0.29	340			6		M & F	Morales-Nin and Ralston (1990)
	Ocyurus chrysurus	0.28	451			14		M & F	Johnson (1983)
Haemulidae	*Haemulon plumieri*	0.11	640			13		M & F	Dee and Radtke (1989)
Sparidae	*Calamus nodosus*	0.21	459			17		M & F	Dee and Radtke (1989)
Lethrinidae	*Lethrinus lentjan*	0.29	440			7		M & F	Wassef (1991)
	Lethrinus mahsena	0.21	495			7		M & F	Wassef (1991)
Sciaenidae	*Micropogonias undulatus*	0.27	419			8		M & F	Barger (1985)
Chaetodontidae	*Chaetodon rainfordi*	0.31	119	62	0.52	10	1	M & F	Fowler (1991)
	Chaetodon plebius	0.72	94			7		F	Fowler (1991)
	Chelmon rostratus	0.50	123			10		M & F	Fowler (1991)
Pomacentridae	*Pomacentrus moluccensis*	0.53	47			9		M & F	Fowler and Doherty (1992)
	Pomacentrus wardi	0.51	72			10		M & F	Fowler and Doherty (1992)
	Dascyllus albisella	0.23	130	113	0.87	11		M & F	Hill and Radtke (1988)
Blenniidae	*Blennius pholis*	0.30	170	80	0.47		2.1	M & F	Roff (1984)
Trichiuridae	*Lepidopus caudatus*	0.23	2018	970	0.48	8	2	M	Demestre *et al.* (1993)
		0.24	2000	1110	0.56	8	2	F	
Scombridae	*Pnematophorus diego*	0.40	400	320	0.80		4	M & F	Roff (1984)
Pleuronectiformes									
Bothidae	*Citharichthys sordidus*	0.30	300	190	0.63		3.3	M & F	Roff (1984)
Pleuronectidae	*Parophrys vetulus*	0.17	485	387*	0.80	21	6	F	Dygert (1990)
	Pleuronectes platessa	0.08	700	280	0.40		6.4	M & F	Roff (1984)
	Hippoglossoides platessoides	0.07	600	400	0.67		15	M & F	Roff (1984)

*Length back-calculated from age at maturity from the von Bertalanffy equation. Superscript letters following species names denote different sampling localities.