

Size-dependent reproductive traits of *Yoldia notabilis* (Bivalvia: Protobranchia)

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ABSTRACT: Between-site variation in age and size at maturity, egg size, fecundity and reproductive effort was measured in a population of the bivalve *Yoldia notabilis* in Otsuchi Bay, northeastern Japan, and tests were conducted to address whether these reproductive traits are dependent on size or age. The diameter of mature oocytes increased with age and size, as did fecundity and reproductive effort. Most individuals were mature at 3 yr of age (Age 3) at the shallower station (10 m depth) and at Age 4 at the deeper station (14 m), although the size at maturity was similar (between 15 and 20 mm shell length) at the 2 stations. This is the size at which the bivalve escapes heavy predation from the crab *Paradorippe granulata*. Age-specific reproductive effort was higher at the shallower station than at the deeper one; however, reproductive effort did not differ significantly between stations when compared on the basis of size. These lines of evidence suggest that the onset of reproduction and the schedule of reproductive effort depend more on size than age. The observed size-dependency of reproduction is considered to be associated with size-dependent mortality rate due to predation, as well as with size-limited reproductive capacity due to morphological constraints in shell volume.

KEY WORDS: *Yoldia notabilis* · Life history · Age and size at maturity · Reproductive effort · Between-site variation

INTRODUCTION

Reproductive traits of organisms, e.g. the age at first reproduction, the number of offspring (clutch size), the size of eggs or young, and the proportion of energy allocated to reproduction, usually change with either body size or age. The elucidation of causes and consequences of the variation in such age- and/or size-specific reproductive schedules has been one of the central objectives in studies on life history evolution (Stearns 1976, 1992, Charlesworth 1980).

A considerable amount of research has examined whether demographic parameters and life history traits of organisms depend on either age or size (see reviews in Groenendael et al. 1988). In modular organisms, such as plants and corals, in which size and age are not always correlated, it has been often reported that size is more important than age in determining population dynamics and reproductive traits (Werner & Caswell 1977, Chapman 1986, Ang 1991, Babcock 1991, but see Hughes & Connell 1987). However, only a few studies have examined independent effects of size and age on

the life history pattern of solitary animals, including marine bivalves (Kautsky 1982, Peterson 1983, 1986, Harvey & Vincent 1989). Nevertheless, some vital traits of bivalve populations, especially mortality, are strongly dependent on size (Hughes 1970, Paine 1976, Blundon & Kennedy 1982, Goshima 1982, Peterson 1982a, b, Arnold 1984, Juanes 1992, Zwarts & Blomert 1992). In such circumstances, it may well be that reproductive traits are also more closely tied to animal size rather than age, because reproductive traits of organisms generally evolve in association with other vital rates, such as growth rate and survival rate, so as to maximize fitness under specified conditions (Stearns 1976, 1992, Roff 1992).

Yoldia notabilis is a protobranch bivalve inhabiting the shallow soft bottom (between 8 and 20 m depth) in Otsuchi Bay, northeastern Japan (Nakaoka 1993). It is a long-lived iteroparous bivalve, its maximum lifespan exceeding 15 yr (Nakaoka & Matsui 1994). Nakaoka (1992b) reported that this bivalve showed large microhabitat variation in growth rate among individuals within a population. This variation in growth rate

causes variation in age-specific survivorship through size-dependent predation by crabs and other benthic predators (Nakaoka 1993). Under these conditions of varying growth rate and survivorship, some reproductive traits of *Y. notabilis* are also expected to change within a population. By comparing reproductive traits between individuals of different sizes but of similar age, or vice versa, it is possible to examine the effects of size and age on the variation in reproductive traits separately.

In the present paper, I report between-site variation of reproductive traits of *Yoldia notabilis* within a population in Otsuchi Bay. The main objective is to examine whether the reproductive traits of the bivalve are dependent on size or age by comparing 2 stations at which the individuals exhibit different growth rates. Further, I discuss the adaptive significance of observed reproductive traits in relation to other population parameters, such as survivorship and individual growth rate, as well as to physiological and morphological constraints of the bivalve.

MATERIALS AND METHODS

Samples for this study were collected at 2 stations established within the inner portion of Otsuchi Bay; Stn YA (39° 19.7' N, 141° 54.6' E, 10 m depth) and Stn YD (39° 19.8' N, 141° 54.8' E, 14 m). The reproductive cycle of *Yoldia notabilis* is highly synchronous and seasonal; almost all adults possess developed gonads in autumn until spawning occurs over the short periods between the end of November and December (Nakaoka 1989, 1993). It is thus possible to examine reproductive traits by collecting mature clams prior to the spawning season. I programmed and carried out the samplings in October 1990 and 1991. In 1990, however, the number of collected individuals was not sufficient for analyses. I therefore added specimens taken in September and November 1990 to the October samples for the analyses described below. Bivalves were collected using a Smith-McIntyre grab sampler and their shell length was measured with a caliper. They were then fixed with 5% seawater formalin and transferred to 70% ethanol after 1 mo. More detailed information on the locality, environmental conditions, sampling procedure and sample treatments is given in Nakaoka (1992b).

Age of the *Yoldia notabilis* specimens was determined by counting the annual external growth lines on the outer shell surface (Naka-

oka 1992a) for individuals younger than 8 yr old (<Age 8), and by counting the internal growth lines within a shell cross-section (Nakaoka & Matsui 1994) for the older individuals. Individual shell growth from February to October was determined from the difference between shell length at the shell margin and that at the outermost growth line which was produced in the previous February (Nakaoka 1992a). Since the growing season of *Y. notabilis* is restricted to spring (Nakaoka 1992b), this shell increment is equivalent to annual growth rate.

For each year and station, 40 to 93 individuals with shell lengths larger than 5 mm were randomly selected for the examination of reproductive traits. After removal of the shell, the presence or absence of ripe gonads was observed, and if gonads were present, sexes were identified under a dissecting microscope. For females, mature oocytes were isolated from soft tissue by dissection and cleaned by sonication. Fecundity was determined by counting the number of mature oocytes in each female. Mean oocyte size of each female was determined by measuring the diameter of 100 randomly selected mature oocytes using a profile projector (Mitsutoyo, Model PJ311).

Reproductive effort (*RE*) of each female was defined according to Bayne et al. (1983) as follows:

$$RE (\%) = [Pr / (Pr + Pg)] \times 100 \quad (1)$$

where *Pr* is gonad production and *Pg* is somatic production during the year. *Pr* and *Pg* are generally measured and expressed in the same unit (e.g. weight or joule). In *Yoldia notabilis*, however, the gonads spread into body gaps among other organs. This made it impossible to isolate them from the remaining portion of soft tissue without damage and to weigh them separately. Therefore, I alternatively expressed *Pr* as the total egg volume, while *Pg* was expressed as the annual increment of wet weight of soft tissue to calculate reproductive effort, assuming (1) the density of egg to be 1 and (2) the energy content per unit mass or volume is equal between the gonads and other part of

Table 1 *Yoldia notabilis*. Spatial and annual variation in shell length (mm) in October. Data are expressed as mean \pm SD (no. of specimens)

Age (yr)	Stn YA 1990	Stn YD 1990	Stn YA 1991	Stn YD 1991
1	– (0)	2.9 \pm 0.6 (23)	6.8 (1)	4.3 \pm 0.4 (9)
2	12.1 \pm 1.5 (10)	7.0 \pm 1.5 (21)	– (0)	7.6 \pm 1.9 (4)
3	19.2 \pm 2.0 (55)	13.0 \pm 2.2 (54)	20.9 \pm 2.3 (9)	13.1 \pm 1.7 (8)
4	24.3 \pm 1.3 (3)	20.5 \pm 1.3 (4)	26.3 \pm 1.9 (19)	19.5 \pm 2.1 (31)
5	27.9 \pm 0.6 (2)	22.4 \pm 1.1 (5)	28.6 \pm 1.8 (6)	26.1 \pm 0.3 (2)
6	30.2 \pm 3.2 (4)	26.8 \pm 3.1 (12)	28.9 (1)	26.3 \pm 2.2 (9)
7	32.9 \pm 1.7 (5)	31.5 \pm 3.3 (7)	34.7 \pm 2.3 (4)	30.5 \pm 1.9 (23)

soft tissue. *Pr* was determined as the product of egg number and egg volume, the latter calculated from oocyte diameter. *Pg* was approximated by the somatic increase in wet weight of soft tissue from February to October each year. Somatic wet weight (*WW*, mg) was estimated using the following formulae:

$$\text{Stn YA: } WW = 0.0069 \text{ SL}^{3.54} \quad (2)$$

($r = 0.997, p < 0.001$)

$$\text{Stn YD: } WW = 0.0118 \text{ SL}^{3.38} \quad (3)$$

($r = 0.995, p < 0.001$)

where SL is shell length (mm) at the shell margin (October estimates) or that at the outermost growth line (February estimates). The allometric equations were obtained from the data in February 1990 and 1991, when bivalves were non-reproductive.

All statistical analyses were performed using SAS (SAS Institute 1988), except the test of sex ratio for which a χ^2 test was employed (Ishii 1980, p. 135).

RESULTS

Spatial and annual variation in shell length

The mean shell length of each year class (between Ages 1 and 7) was compared between Stn YA and Stn YD, and between October 1990 and October 1991 (Table 1). Mean shell length at each age was always larger at Stn YA than Stn YD in both years, a result in accordance with Nakaoka (1992b). A 2-way ANOVA showed significant differences in shell length ($p < 0.005$) between stations except for the Age 6 class, and insignificant differences ($p > 0.1$) between years except for the Age 5 class (Table 2).

Sex ratio

The number of females and males collected was 33 and 31, respectively, at Stn YA in 1990, 20 and 23 at Stn YD in 1990, 18 and 20 at Stn YA in 1991, and 33 and 35 at Stn YD in 1991. A χ^2 test revealed no significant differences from the expected 1:1 sex ratio in any sites and years ($p > 0.50$). The sex ratio did not change with age or size (Figs. 1 & 2). A Kolmogorov-Smirnov 2-sample test did not show significant differences in size- and age-frequency distributions between females and males at any station or in any year ($p > 0.30$).

Table 2. *Yoldia notabilis*. Results of 2-way ANOVA testing for differences in shell length at each age between stations (Stns YA and YD) and between years (1990 and 1991)

Age (yr)	Source	df	SS	MS	F	p
3	Stn	1	700.28	700.28	134.60	0.0001
	Year	1	14.08	14.08	2.71	0.1026
	Error	112	634.72	5.20		
4	Stn	1	166.65	166.65	42.62	0.0001
	Year	1	1.76	1.76	0.45	0.5054
	Error	53	207.27	3.91		
5	Stn	1	46.01	46.01	23.34	0.0004
	Year	1	14.36	14.36	7.60	0.0187
	Error	11	20.79	1.89		
6	Stn	1	24.35	24.35	3.00	0.0970
	Year	1	2.24	2.24	0.28	0.6046
	Error	22	178.30	8.10		
7	Stn	1	49.69	49.69	10.17	0.0030
	Year	1	1.04	1.04	0.21	0.6478
	Error	35	171.09	4.89		

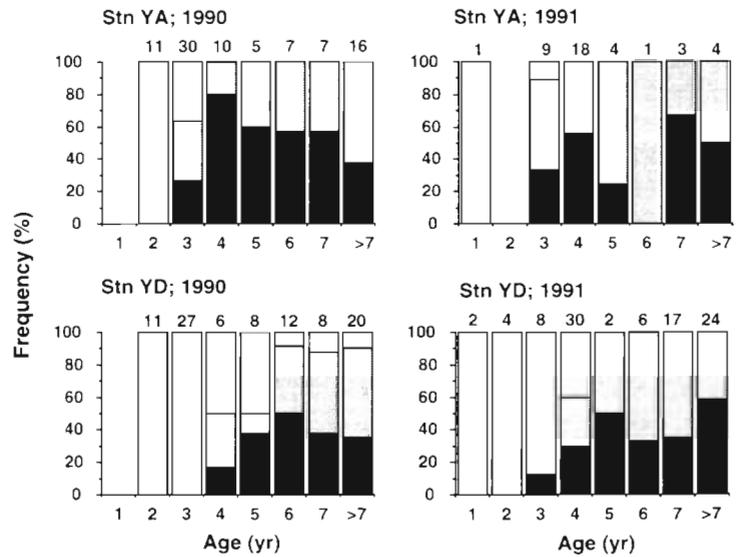


Fig. 1. *Yoldia notabilis*. Age-frequency distributions of immature individuals, males and females at Stns YA and YD in 1990 and 1991. Numerals above columns indicate sample sizes

Age and size at first reproduction

More than half the individuals were mature at Age 3 at Stn YA in both 1990 and 1991. At Stn YD, on the other hand, only a small proportion (less than 15%) of individuals (1991) or no individuals (1990) were mature at Age 3, indicating a delay in the onset of reproduction (Fig. 1).

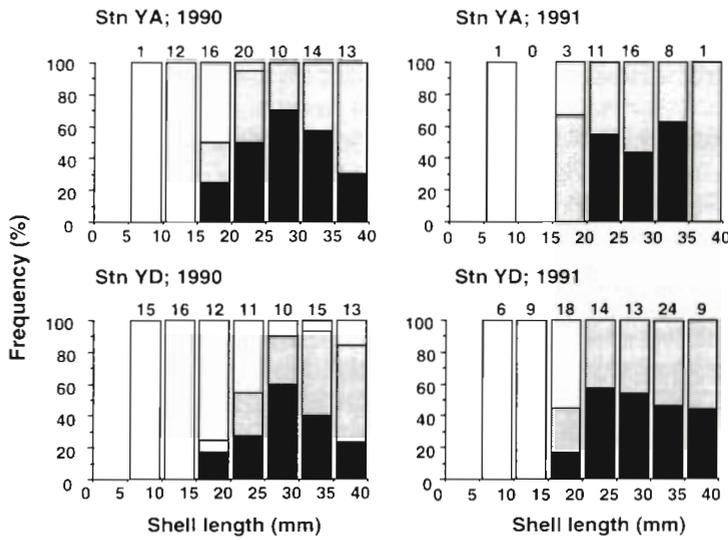


Fig. 2. *Yoldia notabilis*. Size-frequency distributions of immature individuals, males and females at Stns YA and YD in 1990 and 1991. Numerals above columns indicate sample sizes

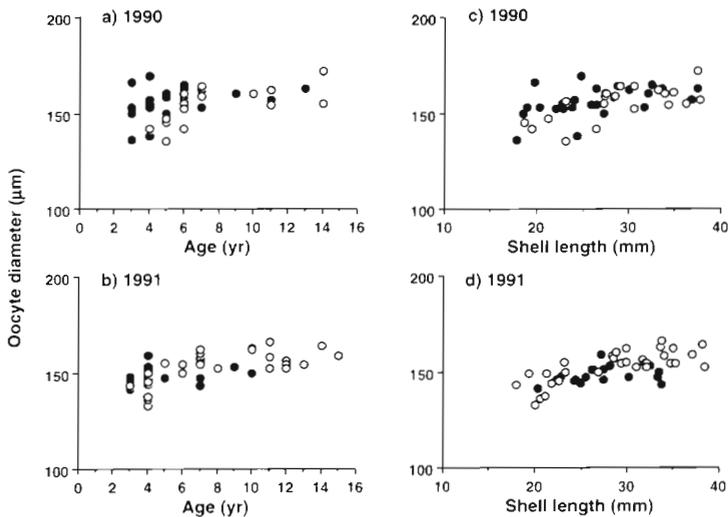


Fig. 3. *Yoldia notabilis*. Relationships between age and diameter of ripe oocyte (a: 1990, b: 1991), and between shell length and oocyte diameter (c: 1990, d: 1991) at Stn YA (●) and Stn YD (○). Each point represents the mean oocyte diameter of 100 randomly selected oocytes in each female

In contrast, size at maturity was similar between stations and years (Fig. 2). The smallest mature individual appeared between 15 and 20 mm in shell length. Minimum adult size was 17.8 mm for females and 16.5 mm for males. More than 50% of the individuals were mature between 20 and 25 mm, and all individuals larger than 25 mm had ripe gonads except at Stn YD in 1990, where about 10% of the individuals (> 25 mm) did not contain mature gonads (Fig. 2).

Oocyte size

The mean oocyte size in each female varied between 133 and 172 µm, and tended to increase slightly with age and shell length (Fig. 3). The age-oocyte size relationship is statistically significant only at Stn YD in 1991, whereas the relationship between shell length and oocyte size was significant at Stn YA in 1990, and at Stn YD in both 1990 and 1991 (Table 3). Analysis of covariance (ANCOVA) was performed to test for the differences in age- and size-specific changes in oocyte size between stations and years (Table 4). A significant difference ($p < 0.005$) was found between years, but not between stations ($p > 0.10$) (Table 4a, b).

Fecundity

The number of oocytes per female increased with age between Ages 3 and 7, and it became nearly constant (ca 10^5) in females older than Age 7 (Fig. 4a, b). In contrast, the number of oocytes increased exponentially with shell length throughout the entire size range (Table 5). The minimum number of oocytes per female was 140 and the maximum 2.54×10^5 .

In both years, females at Stn YA had greater age-specific and size-specific fecundities than those at Stn YD (Fig. 4). ANCOVA showed significant differences in both the age-egg number relationship and the shell length-egg number relationship between stations ($p < 0.001$), but not between years ($p > 0.09$) (Table 4c, d).

Reproductive effort

Reproductive effort of females varied from 0.1 to 97.0%. It increased asymptotically with age, increasing steadily between Ages 3 and 10, and becoming nearly constant thereafter (Fig. 5a, b). At younger ages, between Ages 3 and 5, age-specific reproductive effort was 2 to 15 times higher at Stn YA than at Stn YD (Table 6), and its range of distribution never overlapped (Fig. 5a, b). For Age 4 in 1991 and Age 5 in 1990, where sufficient data were collected, the differences were significant between the stations (Table 6). Reproductive effort became similar for females older than Age 5 (Fig. 5a, b), and no significant differences were detected at Ages 6 and 7 (Table 6). In these age classes, however,

Table 3. *Yoldia notabilis*. Parameters of linear equations fitted between age or shell length and oocyte diameter for each station and year. The equations were obtained by regression analysis and are expressed as $ED = ax + b$, where x is age (yr) or shell length (mm) and ED is mean oocyte diameter (μm) for each female. n : no. of specimens. t -test: ^{ns} $p > 0.5$, * $0.01 < p < 0.05$, ** $0.001 < p < 0.01$, *** $p < 0.001$

Location, year	a	b	n	r	t	Location, year	a	b	n	r	t
Age \times Oocyte diameter						Shell length \times Oocyte diameter					
Stn YA, 1990	1.17	150.0	26	0.388	2.06 ^{ns}	Stn YA, 1990	0.67	138.5	26	0.469	2.60*
Stn YD, 1990	1.16	145.0	18	0.427	1.89 ^{ns}	Stn YD, 1990	1.04	124.8	20	0.674	3.88**
Stn YA, 1991	0.29	140.4	18	0.266	1.10 ^{ns}	Stn YA, 1991	0.34	146.7	18	0.159	0.64 ^{ns}
Stn YD, 1991	1.46	141.3	31	0.645	4.55***	Stn YD, 1991	1.00	124.0	31	0.750	6.11***

shell length also did not differ significantly, except for Age 7 at Stn YD in 1991 (Table 6). ANCOVA, which was employed assuming linear increase in reproductive effort between Ages 3 and 10, revealed significant difference in the age-reproductive effort relationship between stations ($p < 0.001$) but not between years ($p = 0.49$) (Table 4e).

In contrast, reproductive effort increased linearly with shell length from the smallest to the largest females (Fig. 5c, d). The shell length-reproductive effort relationship did not vary significantly either between stations or between years (ANCOVA, $p > 0.2$; Table 4f).

DISCUSSION

Yoldia notabilis became sexually mature 1 yr earlier at Stn YA than at Stn YD (Fig. 1). In addition, age-specific reproductive effort was considerably higher at Stn YA than at Stn YD in young females (between Ages 3 and 5, Fig. 5a, b). However, when these 2 traits were compared on the basis of shell length, size at maturity (between 15 and 20 mm) was the same at the 2 stations (Fig. 2), and the shell length-reproductive effort relationship also did not differ significantly between stations (Table 4f). These results suggest that the schedule and magnitude of reproductive effort (including the onset of reproduction) depend more on size than age in *Y. notabilis*. Similar size-dependent reproductive traits have been reported in other marine bivalves such as *Macoma balthica* (Harvey & Vincent 1989), *Mercenaria mercenaria* (Peterson 1983, 1986) and *Mytilus edulis* (Kautsky 1982, Bayne et al. 1983).

The variation in life history traits within a population has 2 main sources: (1) genetic variation among individuals; and (2) environmental variation among microhabitats (Roff 1992, Stearns 1992). In the case of *Yoldia*

Table 4. *Yoldia notabilis*. Results of ANCOVA testing for differences in size- and age-specific reproductive traits (oocyte diameter, oocyte number and reproductive effort) between individuals collected at different stations (Stns YA and YD) and years (1990 and 1991). Individuals older than 10 yr and larger than 35 mm were excluded from analysis in order to balance the ranges of shell length and age between stations and years

Source	df	SS	MS	F	p
(a) Oocyte diameter \times Age					
Stn	1	122.1	122.1	2.67	0.1068
Year	1	459.8	459.8	10.04	0.0022
Age	1	1173.7	1173.7	25.63	0.0001
Error	73	3342.6	45.8		
(b) Oocyte diameter \times Shell length					
Stn	1	1.3	1.3	0.03	0.8578
Year	1	645.9	645.9	15.47	0.0002
Shell length	1	1468.2	1468.2	35.16	0.0001
Error	73	3048.1	41.8		
(c) log(Oocyte number) \times log(Age)					
Stn	1	12.91	12.91	49.96	0.0001
Year	1	0.74	0.74	2.86	0.0949
Age	1	24.31	24.31	94.02	0.0001
Error	73	18.87	0.26		
(d) log(Oocyte number) \times log(Shell length)					
Stn	1	2.96	2.96	18.50	0.0001
Year	1	0.02	0.02	0.11	0.7435
Shell length	1	31.52	31.52	197.36	0.0001
Error	73	11.66	0.16		
(e) Reproductive effort \times Age					
Stn	1	3307.3	3307.3	21.31	0.0001
Year	1	74.1	74.1	0.48	0.4916
Age	1	45370.9	45370.9	292.35	0.0001
Error	73	11329.1	155.2		
(f) Reproductive effort \times Shell length					
Stn	1	318.8	318.8	1.59	0.2108
Year	1	185.9	185.9	0.93	0.3382
Shell length	1	42097.9	42097.9	210.46	0.0001
Error	73	14602.1	200.0		

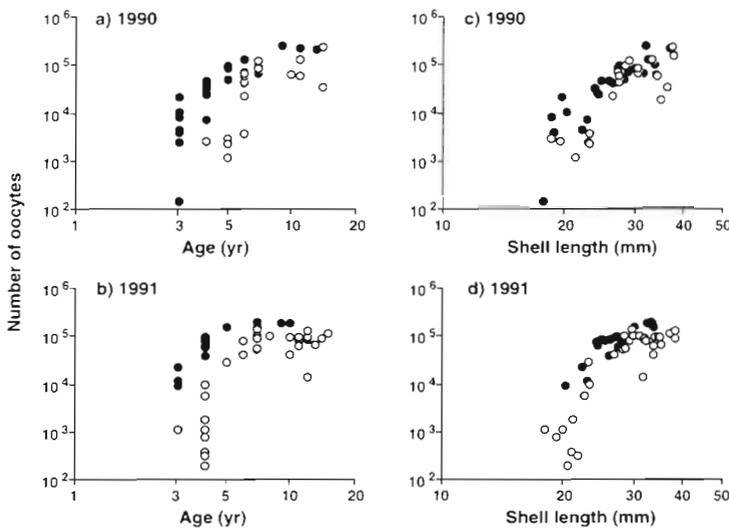


Fig. 4. *Yoldia notabilis*. Relationships between age and number of oocytes (a: 1990, b: 1991), and between shell length and number of oocytes (c: 1990, d: 1991) of females at Stn YA (●) and Stn YD (○)

notabilis, the observed difference in age-specific reproductive traits between stations was unlikely to be due to genetic differences because the 2 stations are close enough in distance (ca 500 m) for gene flow to occur. Since pelagic larvae of this bivalve can transit the 500 m distance in 3 d (Nakaoka unpubl.), genetic separation is unlikely. It is thus more likely that the variation in age-specific reproductive traits is due to environmental variation between the 2 stations. Nakaoka (1992b) found that the food supply to the benthic community varied greatly between the stations, and that their variation causes the difference in growth rate of *Y. notabilis*. The bivalve initiates reproduction when it becomes larger than 15 mm in shell length, and allocates more resources to reproduction as it grows larger in size, regardless of actual age. This size-dependent reproductive strategy, therefore, leads to between-site variation in the age-specific traits as a result of variation in growth rate.

Table 5. *Yoldia notabilis*. Parameters of allometric equations fitted between shell length and the number of oocytes per female for each station and year. The equations were obtained by regression analysis and are expressed as $EG = aSL^b$, where SL is shell length (mm) and EG is the number of mature oocytes per female. n: no. of specimens. t-test: ***p < 0.001

Location, year	a	b	n	r	t
Stn YA, 1990	6.24×10^{-6}	6.85	26	0.850	7.91***
Stn YD, 1990	1.84×10^{-5}	6.33	20	0.825	6.20***
Stn YA, 1991	1.40×10^{-3}	5.38	18	0.879	7.39***
Stn YD, 1991	2.79×10^{-8}	8.21	31	0.872	9.58***

The size and age at maturity of organisms is generally influenced by growth rate and survivorship, and it shows variation within a species or even within a population (Roff 1984, Stearns & Koella 1986, Stibor 1992). Although the size at maturity of *Yoldia notabilis* is similar between the 2 stations in Otsuchi Bay, it is 5 to 10 mm larger than that of the population of Hakodate Bay, which is found 300 km north of Otsuchi Bay (S. Goshima pers. comm.). This implies that the size at maturity in Otsuchi Bay is not strictly determined by phylogenetic or physiological constraints on the species. Alternatively, it seems to be more dependent on the local ecological conditions. Nakaoka (1993) found that small juveniles of *Y. notabilis* in Otsuchi Bay suffer high mortality due to predation by the crab *Paradorippe granulata*, and that they can escape from the severe predation at sizes greater than 15 mm in shell length. This size coincides with the size at first reproduction.

The onset of reproduction at a size which provides refuge from high mortality has also been reported in another infaunal bivalve, *Mya arenaria* (Goshima 1982). Seed & Brown (1978) argued that, in marine invertebrates whose survivorship increases with size, selection favors the strategy which devotes all available energy to rapid growth in juvenile stages and postpones reproductive development until individuals have outgrown the size range most susceptible to mortality. Since predation pressure is nearly the same between the 2 stations in Otsuchi Bay (suggested by the similar densities of *P. granulata*; Nakaoka 1993), this argument may explain the size-dependent initiation of reproduction of *Y. notabilis* in Otsuchi Bay.

An increase in reproductive effort with age and size has been generally observed in iteroparous marine invertebrates (see reviews in Browne & Russell-Hunter 1978, Bayne et al. 1983), and is considered to be the consequence of the trade-off between reproduction at younger ages and subsequent survivorship or future reproductive potential (Williams 1966a, b, Gadgil & Bossert 1970, Hirshfield & Tinkle 1975, Calow 1979). In *Yoldia notabilis*, reproductive effort increased asymptotically with age, while it increased linearly with size (Fig. 5). In particular, the relationship between reproductive effort and shell length did not differ between stations (Table 4f). One of the possible causes for this consistency can be attributed to the size-limited reproductive capacity of bivalves (Calow 1983, Sebens 1987). Maximum reproductive output of bivalves is often limited by the inner shell volume (Kautsky 1982, Bayne et al. 1983, but see Kabat 1985). Morphological constraints may shift maximum energy allocation to

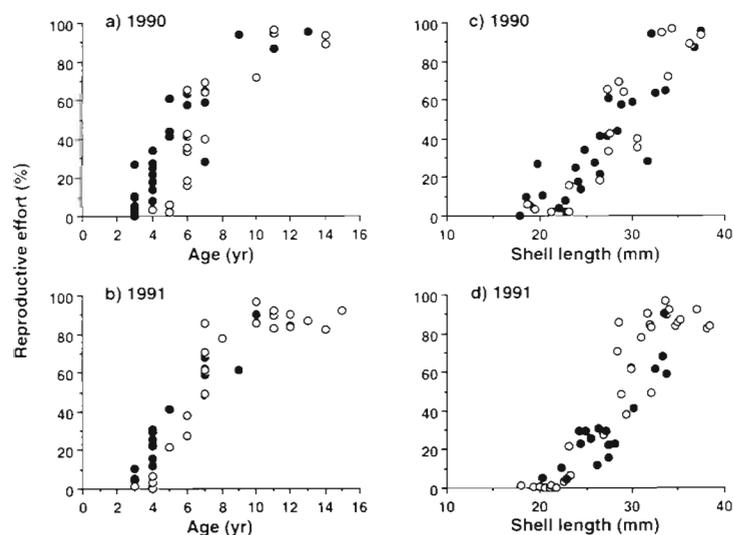


Fig. 5. *Yoldia notabilis*. Relationships between age and reproductive effort (a: 1990, b: 1991), and between shell length and reproductive effort (c: 1990, d: 1991) of females at Stn YA (●) and Stn YD (○)

reproduction to a size greater than that predicted theoretically based strictly on bioenergetic considerations (Calow 1981, Sebens 1982, 1987). In the case of *Y. notabilis*, total annual production ($Pr + Pg$ in Eq. 1) is maximized at 25 mm in shell length. Assuming that an individual of this size devotes all its production to reproduction, the total gamete production reaches ca 610 ml in volume, corresponding to more than 80% of the shell cavity volume. It is thus virtually impossible to invest all surplus energy into reproduction, because the somatic tissue already occupies nearly 80% of the shell cavity volume (Nakaoka unpubl.).

Since shell cavity volume of *Yoldia notabilis* increases with the 3rd power of shell length (estimated

by isometric shell growth in 3 dimensions; Nakaoka unpubl.), as does somatic tissue in non-reproductive season (Eqs. 2 & 3), the upper limits of the reproductive capacity are also expected to increase with the 3rd power of shell length. However, fecundity was found to increase with an exponent greater than 5 (Table 5), which implies that size-limited reproductive capacity cannot solely explain the observed relationship between reproductive effort and shell length. Iwasa (1981) theoretically analyzed the problems of optimal schedule for growth and reproduction, and described conditions under which the strategy of simultaneous investment in somatic tissue and gametes appears. This type of strategy is favorable when (1) the increase in production is slow compared to that of body size, (2) adult survivorship is unpredictable, (3) mortality rate is a decreasing function of body size, and (4) reproduction occurs seasonally. The *Y. notabilis* population in

Otsuchi Bay satisfied at least conditions (1) (Nakaoka unpubl.), (3) (Nakaoka 1993) and (4) (Nakaoka 1989). Specifically, conditions (1) and (3) may be responsible for the constant relationship between size and reproductive effort.

Because of this size-dependent reproductive effort, age-specific fecundity and reproductive effort of young individuals were lower at Stn YD where the food supply was poorer than at Stn YA (Nakaoka 1992b). Reduction in reproductive effort with environmental stress or food depletion has been reported in other marine invertebrates (Menge 1974, Bayne et al. 1983, McDonald & Thompson 1985a, b, Grémare et al. 1988, Harvey & Vincent 1989, Iglesias & Navarro

Table 6. *Yoldia notabilis*. Age-specific data on reproductive effort and shell length of females used for the analyses of reproductive traits. Data are expressed as mean \pm SD (no. of specimens). Differences between stations tested by *t*-test: ^{ns} $p > 0.5$, ^{**} $0.001 < p < 0.01$, ^{***} $p < 0.001$

Age (yr)	Reproductive effort (%)		<i>t</i>	Shell length (mm)		<i>t</i>
	Stn YA	Stn YD		Stn YA	Stn YD	
1990						
3	8.1 \pm 8.9 (7)	— (0)	—	20.0 \pm 1.9	—	—
4	20.6 \pm 8.8 (7)	2.9 (1)	—	24.6 \pm 1.3	19.5	—
5	48.2 \pm 10.6 (3)	3.3 \pm 2.2 (3)	7.17 ^{**}	27.6 \pm 0.6	21.0 \pm 2.3	4.79 ^{**}
6	54.0 \pm 11.4 (3)	35.1 \pm 18.2 (6)	1.62 ^{ns}	29.3 \pm 3.0	27.1 \pm 2.4	1.21 ^{ns}
7	50.6 \pm 20.0 (3)	57.8 \pm 15.7 (3)	0.49 ^{ns}	31.7 \pm 1.8	29.4 \pm 1.1	1.92 ^{ns}
1991						
3	6.9 \pm 3.2 (3)	1.2 (1)	—	21.8 \pm 1.4	18.0	—
4	24.0 \pm 6.3 (10)	1.7 \pm 2.2 (8)	11.52 ^{***}	26.1 \pm 1.4	21.2 \pm 1.3	7.70 ^{***}
5	41.5 (1)	21.3 (1)	—	30.2	23.2	—
6	— (0)	32.5 \pm 7.5 (2)	—	—	28.1 \pm 1.8	—
7	63.5 \pm 6.5 (2)	62.8 \pm 13.9 (6)	0.06 ^{ns}	33.5 \pm 0.3	29.5 \pm 1.4	3.83 ^{**}

1991). In the present case, food conditions at Stn YD were not so poor as to cause a decrease in survivorship of adult individuals (Nakaoka 1993). In addition, food supply and annual growth rate are known to vary greatly from year to year (Nakaoka & Matsui 1994), which suggests that Stn YD is not consistently poor in food condition. In such circumstances, it may be advantageous for organisms to reduce reproductive effort in years with poor food availability and save resources for future reproduction (Goodman 1979, Thompson 1984). A size-dependent reproductive strategy enables such adaptive adjustment of reproductive effort according to the fluctuations in food supply and growth rate.

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