

# Spatial and seasonal variation in growth rate and secondary production of *Yoldia notabilis* in Otsuchi Bay, Japan, with reference to the influence of food supply from the water column

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**ABSTRACT:** A 1 yr field study of a long-lived protobranch bivalve, *Yoldia notabilis* Yokoyama, in Otsuchi Bay, northeastern Japan, revealed that there was a large seasonal and spatial variation in growth rate and secondary production, and that primary production in the water column and following organic supply to the bottom were responsible for the variation. Both shell and soft tissue growth of each of 9 year-classes were rapid in spring, and slow or even negative in other seasons. The rapid growth coincided well with the occurrence of spring phytoplankton bloom in the water column and the peak of organic flux to the bottom. Mean shell length and mean soft tissue weight of each year-class were larger, and the growth rates of shell and soft tissue as well as the secondary production were higher at the shallower station (10 m deep) than at the deeper station (14 m). The differences in size, growth rate and production between the 2 stations were consistent with the local difference in food supply from the water column to the bottom, but not related to other environmental factors such as temperature, salinity, organic content in the sediment and density of *Y. notabilis*. Annual production was 1.38 and 0.89 g ash-free dry wt  $0.1 \text{ m}^{-2} \text{ yr}^{-1}$ , giving P/B ratios of 0.76 and 0.41 for the shallow and deep station respectively. Food intake by *Y. notabilis* between February and April 1991 was estimated to be 26.4 and 13.9 g C  $\text{m}^{-2}$  (shallow and deep respectively), which amounted to ca 10 % of the primary production and 30 to 40 % of the organic supply to the bottom. These estimates suggested that the *Y. notabilis* population plays an important role in the energy flow from pelagic to benthic communities.

## INTRODUCTION

Many benthic animals are known to exhibit large temporal and spatial variation in parameters such as recruitment, growth, survivorship and reproduction within a population. Detection of the factors causing such intrapopulation variation is of great importance in understanding how the population is maintained over time and in its distributional area. In infaunal bivalves, variation in growth rate has been studied in a variety of species, and several biotic and abiotic factors such as temperature, food availability and intra/inter-specific competition have been proposed as being responsible for the variation (e.g. Ansell 1968, Green & Hobson 1970, Beukema et al. 1977, 1985, Rae 1979, Peterson & Andre 1980, Peterson & Beal 1989, Irlandi & Peterson 1991). Among them, a few studies focused on the rela-

tionship between pelagic or benthic primary production and growth rate of animals. For example, Hummel (1985a, c) demonstrated that seasonal changes in food intake and growth rate of *Macoma balthica* were mainly regulated by the seasonal pattern in the primary production in the water column. Similarly, Thompson & Nichols (1988) showed in the same species that seasonal and spatial variation in growth rate coincided with the fluctuations in planktonic and benthic chlorophyll *a* (chl *a*) concentrations. However, quantitative studies which couple primary production to growth rate of bivalves are still scarce and restricted to a small number of lamellibranch species.

The purpose of this paper is to demonstrate that primary production in the water column and organic supply to the bottom can influence the seasonal and spatial variation in growth rate and secondary produc-

tion of the protobranch bivalve *Yoldia notabilis* Yokoyama. Based on 1 yr benthic samplings, I examined age-specific growth rate of a *Y. notabilis* population in Otsuchi Bay, northeastern Japan, and compared its variation with those of food supply and other environmental factors.

The species belonging to the genus *Yoldia* are long-lived protobranch bivalves widely distributed in high latitudes (Cowan 1968). *Yoldia* spp. are primarily surface and subsurface deposit feeders (Rhoads 1963, Bender & Davis 1984), but are also known to feed on suspended materials (Stasek 1965, Davenport 1988). In spite of its importance in soft-bottom communities (Rhoads & Young 1970, Levinton 1977, Lopez 1988), there have only been a few studies on life history and population dynamics of this group. Sanders (1956) and Lewis et al. (1982) investigated population structure and production of *Y. limatula* along the northwestern coast of the Atlantic. Hutchings & Haedrich (1984) described growth and age structure of *Y. thraciaeformis* in the deep sea of the Atlantic.

*Yoldia notabilis* is distributed along northwestern coast of the Pacific, from the Kamchatka Peninsula, Russia to Honshu Island, Japan (Matsukuma et al. 1991). It is one of the dominant benthic animals in the soft-bottom community of Otsuchi Bay (Horikoshi et al. 1976). Nakaoka (1989) revealed that the bivalve reproduces once a year during winter. Juvenile growth is very slow, achieving only 1.3 mm in shell length at the end of the first year; then growth becomes rapid, shell length reaching 32.0 mm at 7 yr (Nakaoka 1992). This bivalve has annual rings on the external shell surface (Nakaoka 1992), which enabled me to determine density and growth rate of each year-class separately.

## MATERIALS AND METHODS

**Study site.** The research was carried out at the inner part of Otsuchi Bay (Fig. 1). A population of *Yoldia notabilis* is distributed at 5 to 20 m in depth (Horikoshi et al. 1979). Bottom substratum consists of muddy sand; molluscs and polychaetes dominate among the macrobenthic fauna of the area (Horikoshi et al. 1976).

Seasonal changes in water temperature (Kutsuwada et al. 1990, 1991) and chl *a* content in the water (Iizumi et al. 1990) of Otsuchi Bay are presented in Fig. 2. Water temperature varied seasonally from 21.8°C in September 1990 to 7.1°C in March 1991. Chl *a* content

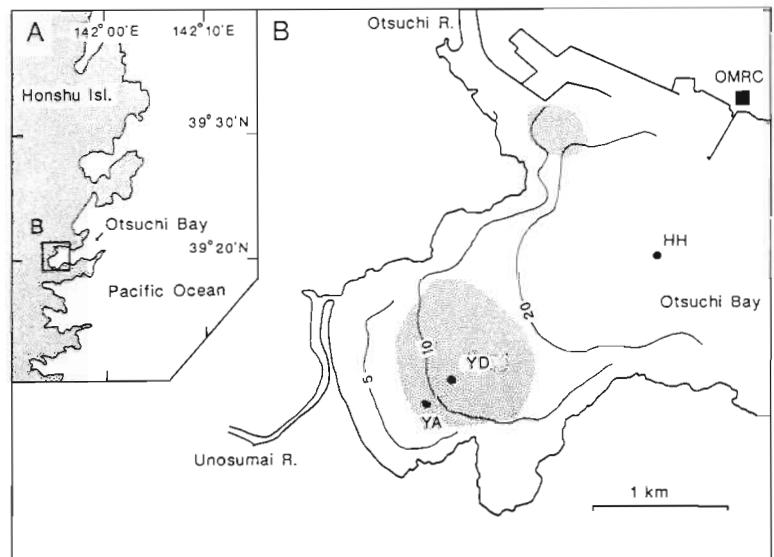


Fig. 1. Location and bathymetry (in m) of the study site in Otsuchi Bay, northeastern Japan. YA and YD: *Yoldia notabilis* sampling stations; HH: station where chl *a* content was monitored by Iizumi et al. (1990); OMRC: Otsuchi Marine Research Center, Ocean Research Institute, University of Tokyo. Shaded area indicates the distribution of *Y. notabilis*

had a clear peak in March 1991. This peak was consistent with the occurrence of the spring phytoplankton bloom in Otsuchi Bay (Iizumi et al. 1990).

**Field surveys and laboratory analyses.** Two sampling stations were established for the study (Fig. 1). Stn YA was 10 m in depth and located near the shallower limit of the distribution of *Yoldia notabilis*; Stn YD was 14 m deep and positioned around the center of its distribution.

Environmental conditions were monitored at both stations. Temperature and salinity were measured on the bottom on 3 occasions (August 1991, January and April 1992) using a STD (Alek, model AST-1000S).

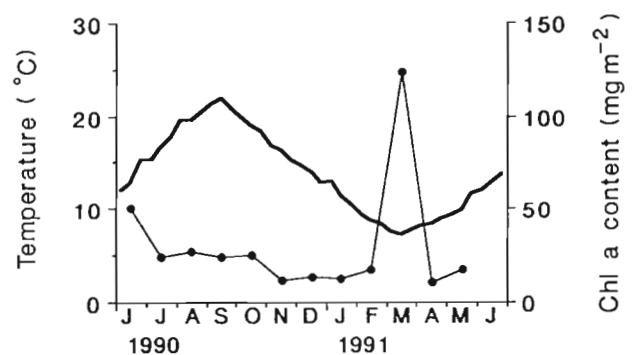


Fig. 2. Seasonal changes in water temperature (bold line) and chl *a* content (●) in Otsuchi Bay. Data on temperature are derived from Kutsuwada et al. (1990, 1991) and chl *a* content from Iizumi et al. (1990)

Sediment properties (silt-clay content, organic carbon and nitrogen contents) were analyzed on 4 occasions (September and December 1990, March and June 1991). Sediments were taken using a Smith-McIntyre grab sampler and the top 1 cm layer was extracted using subcores 10.2 cm<sup>2</sup> in area. Half of each sediment sample was sieved with a mesh of 63 µm openings and divided into sand and silt-clay fractions. Both fractions were then dried in an oven at 60 °C and weighed on a Mettler balance (model AC 100) for the determination of silt-clay content. The other half of the sediment sample was dried at 60 °C, decalcified with 0.2N HCl and dried again. Organic carbon and nitrogen contents were then measured using a CN corder (Yanagimoto, Model MT-600). Organic matter supply to the bottom was measured monthly between October 1990 and August 1991 (except July 1991) using cylindrical sediment traps, 50 cm in depth and 16.5 cm in diameter. Each sediment trap contained 4 compartments of 32.2 cm<sup>2</sup> each. The sediment traps were moored 1 m above the bottom surface without fixate solutions (e.g. formalin), and were retrieved 2 to 4 d after deployment. Trap contents were then filtered on a GF/F filter and decalcified with 0.2N HCl, and organic carbon and nitrogen were quantified with a CN corder after drying at 60 °C.

Sampling of *Yoldia notabilis* was conducted monthly between June 1990 and June 1991. Four to nine samples were taken monthly at each station using a 0.1 m<sup>2</sup> Smith-McIntyre grab sampler. After extracting the subcores described above, the collected sediments were sieved through a 1 mm mesh sieve and all specimens of *Y. notabilis* retained on the sieve were sorted alive. Because of their slender shell, juveniles smaller than 1.7 mm in shell length were washed away through the sieve. In order to collect these juveniles, 3 to 4 subsamples of 0.01 m<sup>2</sup> each were taken each month (except from August 1990 to March 1991 at Stn YA, and in March 1991 at Stn YD) and bivalves retained on a 0.5 mm mesh sieve were collected under a dissecting microscope. For all the collected individuals, shell length was measured with a caliper or with a micrometer to the nearest 0.1 mm.

*Yoldia notabilis* age was determined by counting the number of external rings on the shell which were deposited annually in winter (Nakaoka 1992). Nine year-classes (Classes 1983 to 1991) and 1 compound class which recruited before 1983 (Class <1983) were separated by this method, and mean shell length and density of each year-class were calculated for each month and station. Age determination was not performed in 10.3 % of the collected specimens due to ambiguity of the ring pattern or shell damage. These individuals were excluded from the analyses of growth but included in the estimation of density by assuming their age to be the one with the nearest mean shell length.

Growth and biomass in terms of soft tissue weight was estimated by converting the data on shell length to soft tissue ash-free dry weight (AFDW), using the regression equation determined from 10 to 29 individuals of various sizes [mean shell length 24.7 mm ± 9.0 (SD)] randomly selected for each month and station. To determine AFDW, soft tissue was removed from the shells, dried for 48 h at 60 °C, weighed on a Mettler balance to 0.1 mg accuracy, ashed for 12 h in a muffle furnace at 500 °C and reweighed.

Secondary production,  $P$ , of each year-class was estimated using Allen's method (Crisp 1984, p. 305) by the following formula:

$$P = \int Ndw = \sum (1/2)(N_t + N_{t+\Delta t}) \Delta w \quad (1)$$

where  $N_t$  = density of individuals at time  $t$  (see Table 3), and  $\Delta w$  = mean AFDW increment during the period  $\Delta t$ .

All statistical analyses were performed using SAS (SAS Institute 1988).

## RESULTS

### Spatial variation in environment

Bottom water temperature and salinity, measured on 3 occasions, were virtually identical at the 2 stations (Table 1). Silt-clay content in the sediment was significantly higher at Stn YD than at Stn YA in March 1991 but not in other months (Fig. 3a). Organic carbon and nitrogen contents in the sediment did not differ significantly between the 2 stations in any month (Fig. 3b, c).

Organic carbon and nitrogen fluxes had 2 peak seasons (Fig. 4). The first peak, occurring between November 1990 and January 1991, had a C/N ratio of more than 10. Microscopic observation revealed that the contents of the sediment traps consisted mainly of inorganic sediment particles, and it is likely that massive resuspension of the bottom sediment occurred during this period due to winter storms. In contrast, the second peak, recorded in March 1990 had the lowest C/N ratio (6.8 at Stn YA and 7.0 at Stn YD). This peak was consistent with the occurrence of spring phytoplankton bloom in this season (Fig. 2), and the trap contents were almost entirely made up of centric diatoms (*Thalassiosira nordenskiöldi*, *Coscinodiscus*

Table 1. Bottom water temperature and salinity at 2 stations in Otsuchi Bay, Japan

Date	Temperature (°C)		Salinity (‰)	
	Stn YA	Stn YD	Stn YA	Stn YD
28 Aug 1991	20.4	20.3	33.33	33.32
21 Jan 1992	9.3	9.7	33.86	33.81
17 Apr 1992	6.5	6.5	33.45	33.44

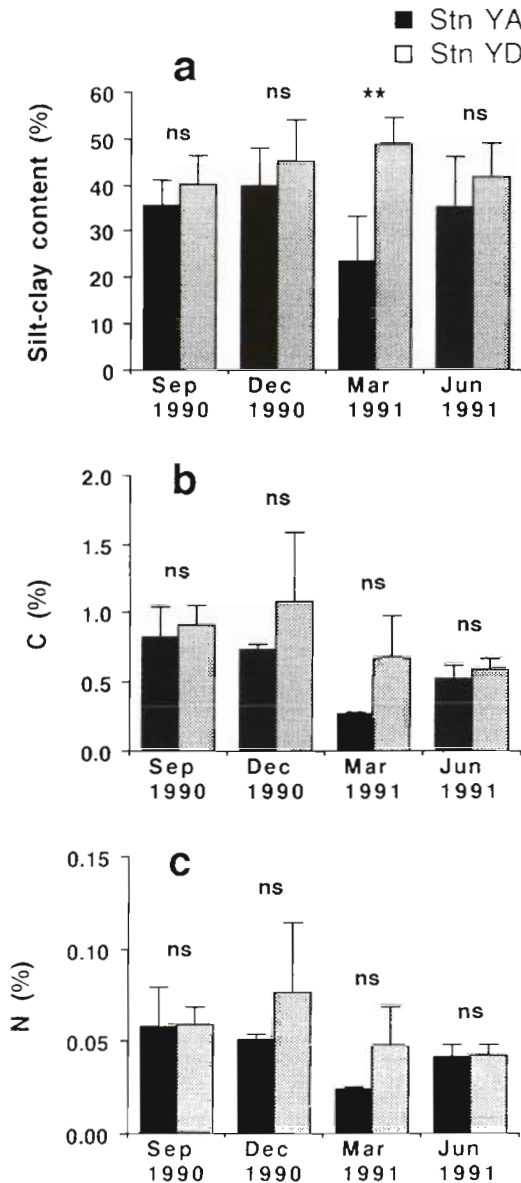


Fig. 3. (a) Silt-clay content, (b) organic carbon content and (c) nitrogen content in the top 1 cm layer of the sediments for 4 mo at Stns YA (solid) and YD (shaded). Vertical bars indicate SD of the mean.  $n = 3$  to 6 for each plot. Results of  $t$ -test of the arcsine-transformed data between the stations are presented above the columns; \*\* $0.001 < p < 0.01$ , ns:  $p > 0.05$

spp., and *Chaetoceros compressus* and *C. debilis*). The organic supply at Stn YA was significantly higher than at Stn YD in November, February (only in N), March and June, but the difference was not detected in other months (Fig. 4)

#### Numerical abundance and biomass

Annual mean density and biomass of *Yoldia notabilis* retained on a 1 mm mesh sieve were 17.9 ind.  $0.1 \text{ m}^{-2}$

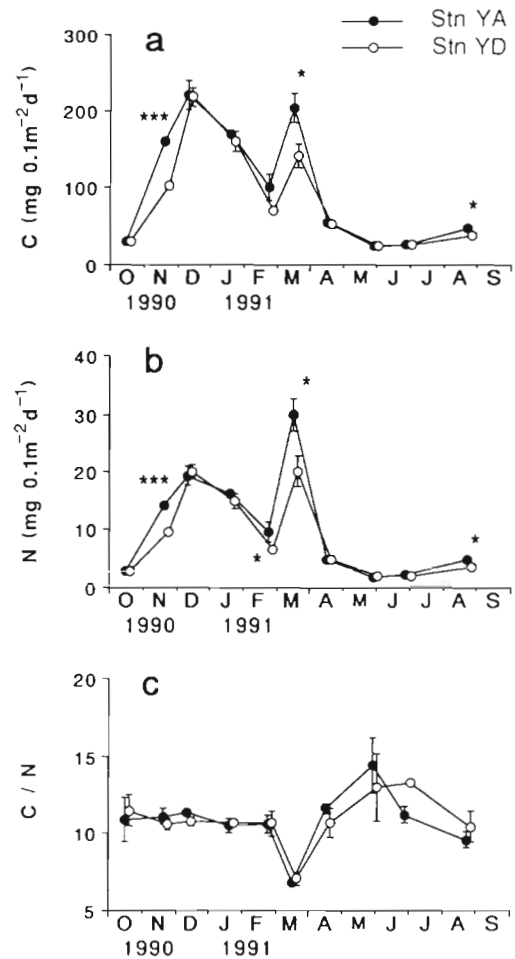


Fig. 4. Seasonal changes in (a) organic carbon flux, (b) nitrogen flux and (c) C/N ratio of the flux to the bottom measured using materials collected by sediment traps at Stns YA (●) and YD (○). Vertical bars, SD of the mean.  $n = 2$  to 3 for each plot. Results of  $t$ -test between the stations are presented in (a) and (b) by asterisks; \*\*\* $p < 0.001$ , \* $0.01 < p < 0.05$ , no mark:  $p > 0.05$

and 1.82 g AFDW  $0.1 \text{ m}^{-2}$  at Stn YA, and 20.6 ind.  $0.1 \text{ m}^{-2}$  and 2.14 g AFDW  $0.1 \text{ m}^{-2}$  at Stn YD.

Monthly mean density of *Yoldia notabilis* from June 1990 to October 1990 was higher than in the other months at Stn YD, whereas such a temporal change was not detected at Stn YA. Mann-Whitney's  $U$ -test revealed no significant differences in the density between the 2 stations except in August 1990 (Table 2).

Monthly mean biomass decreased from summer to early spring, reaching a minimum in February 1991 at Stn YA and in March 1991 at Stn YD. Then it increased rapidly from March to June 1991 with the maximum value recorded in June 1991 at both stations. Mann-Whitney's  $U$ -test again showed no significant differences in the biomass between the 2 stations (Table 2).



Table 2. *Yoldia notabilis*. Monthly mean density and biomass at 2 stations

Month	Stn YA Mean $\pm$ SD (n)	Stn YD Mean $\pm$ SD (n)	Mann-Whitney's <i>U</i> -test	
			<i>U</i> <sub>cat</sub>	p
<b>Density (ind. 0.1 m<sup>-2</sup>)</b>				
Jun 1990	18.0 $\pm$ 9.1 (4)	27.3 $\pm$ 5.8 (6)	4.0	0.088
Jul 1990	21.6 $\pm$ 7.0 (5)	25.8 $\pm$ 5.7 (8)	12.5	0.272
Aug 1990	15.8 $\pm$ 6.0 (5)	29.1 $\pm$ 1.8 (6)	0.0	0.006
Sep 1990	18.6 $\pm$ 10.1 (5)	25.4 $\pm$ 6.7 (6)	8.0	0.199
Oct 1990	21.5 $\pm$ 6.4 (4)	26.3 $\pm$ 9.6 (7)	10.0	0.450
Nov 1990	21.0 $\pm$ 8.3 (5)	20.1 $\pm$ 6.8 (9)	24.0	0.841
Dec 1990	18.8 $\pm$ 8.5 (5)	19.9 $\pm$ 3.7 (7)	12.0	0.368
Jan 1991	21.2 $\pm$ 5.0 (5)	16.9 $\pm$ 2.8 (8)	30.0	0.139
Feb 1991	15.0 $\pm$ 8.4 (5)	17.4 $\pm$ 5.5 (9)	16.0	0.384
Mar 1991	16.0 $\pm$ 6.5 (5)	13.3 $\pm$ 4.1 (7)	24.0	0.289
Apr 1991	16.5 $\pm$ 10.9 (6)	17.0 $\pm$ 3.8 (6)	14.0	0.520
May 1991	14.1 $\pm$ 3.6 (5)	18.6 $\pm$ 2.8 (8)	7.0	0.055
Jun 1991	17.6 $\pm$ 8.9 (5)	15.8 $\pm$ 2.7 (6)	11.0	0.188
<b>Biomass (g AFDW 0.1 m<sup>-2</sup>)</b>				
Jun 1990	1.81 $\pm$ 0.99 (4)	2.46 $\pm$ 0.84 (6)	7.0	0.286
Jul 1990	1.97 $\pm$ 0.61 (5)	2.66 $\pm$ 0.61 (8)	7.0	0.057
Aug 1990	1.61 $\pm$ 1.00 (5)	2.56 $\pm$ 0.46 (6)	5.0	0.068
Sep 1990	1.72 $\pm$ 1.61 (5)	2.45 $\pm$ 0.68 (6)	7.0	0.144
Oct 1990	1.58 $\pm$ 0.30 (4)	2.09 $\pm$ 0.91 (7)	10.0	0.450
Nov 1990	1.61 $\pm$ 0.70 (5)	1.84 $\pm$ 0.78 (9)	16.0	0.386
Dec 1990	1.37 $\pm$ 0.58 (5)	1.70 $\pm$ 0.70 (7)	11.0	0.291
Jan 1991	1.22 $\pm$ 0.28 (5)	1.43 $\pm$ 0.60 (8)	18.0	0.770
Feb 1991	1.13 $\pm$ 0.61 (5)	1.66 $\pm$ 0.70 (9)	14.0	0.257
Mar 1991	1.21 $\pm$ 0.84 (5)	1.20 $\pm$ 0.42 (7)	15.0	0.685
Apr 1991	2.51 $\pm$ 2.02 (6)	2.25 $\pm$ 0.75 (6)	16.0	0.749
May 1991	2.46 $\pm$ 0.61 (5)	2.86 $\pm$ 0.79 (8)	11.0	0.188
Jun 1991	3.34 $\pm$ 1.83 (5)	3.12 $\pm$ 0.43 (6)	13.0	0.715

Mean density of successive year-classes fluctuated widely from one year-class to another (Table 3). The year-class recruited in 1987 (Class 1987) was most abundant at Stn YA, while Classes <1983, 1987 and 1990 were abundant at Stn YD. In contrast, Classes 1985 and 1989 at Stn YA, and Classes 1985 and 1986 at Stn YD were less abundant. Most notably, individuals belonging to Class 1989 were never seen at Stn YA during the study period (Table 3).

#### Seasonal change in growth rate

Shell growth from June 1990 to June 1991 was estimated from the monthly change in mean shell length for each year-class (Fig. 5). In all year-classes, growth was slow from summer to winter, and then became rapid in spring. This seasonal change in growth rate was obvious in the youngest 6 classes (Classes 1985 to 1990), but less obvious in the oldest 3 classes (Classes <1983 to 1984). Mean shell length of each corresponding year-class was 2 to 8 mm larger at Stn YA than at Stn YD in Classes 1985 to 1988, and 1 to 4 mm larger at Stn YA in the last 3 mo of Class 1990, but the difference was not evident in the oldest 3 classes (Fig. 5).

Growth in terms of soft tissue AFDW was negligible from June 1990 to March 1991, and negative growth was even detected in older year-classes (Fig. 6). This period was followed by the rapid growing season from March to June 1991. AFDW increased nearly 2- to 5-fold during these 3 mo. In all year-classes, AFDW was heavier (except in the winter months of Class <1983) and the growth rate during spring was higher at Stn YA than at Stn YD (Fig. 6).

#### Production

Similar to the soft tissue AFDW changes (Fig. 6), total monthly production for all 9 year-classes was low or negative from summer to winter and became high in spring at both stations (Fig. 7). The peak production, recorded between March and April 1991, was 1.31 g AFDW 0.1 m<sup>-2</sup> 30 d<sup>-1</sup> at Stn YA and 0.82 g AFDW 0.1 m<sup>-2</sup> 30 d<sup>-1</sup> at Stn YD.

Total annual production was estimated to be 1.38 g AFDW 0.1 m<sup>-2</sup> yr<sup>-1</sup> at Stn YA and 0.89 g AFDW 0.1 m<sup>-2</sup> yr<sup>-1</sup> at Stn YD. Comparing the data with the annual mean biomass, the P/B ratio was calculated to be 0.76 and 0.41 for Stns YA and YD, respectively.

#### DISCUSSION

This 1 yr study on the *Yoldia notabilis* population in Otsuchi Bay revealed that there was large seasonal and spatial variation in both growth rate and secondary production.

Growth in shell length was most rapid in spring in 1991 (Fig. 5), which was consistent with the results from 1989 and 1990 (Nakaoka 1989, Nakaoka 1992). In addition, growth in soft tissue and secondary production were also found to be at a maximum in spring; specifically, soft tissue weight increased very rapidly from March to April 1991 (Fig. 6), and secondary production during this period contributed to more than 90 % of total annual production at each of the 2 stations (Fig. 7). The rapid growth and high production in this season coincided well with the occurrence of spring phytoplankton bloom in Otsuchi Bay (Fig. 2). Data from the sediment trap samples also showed that there was a large amount of organic flux, consisting mainly of diatoms, to the bottom during this season (Fig. 4) and this indicates that the peak in primary production in the water column was certainly supplied to the bottom communities. In contrast, primary production

Table 3. *Yoldia notabilis*. Monthly mean density (ind.  $0.1 \text{ m}^{-2}$ ) of each of 10 year-classes separated using the external growth rings on shell. Density of 1990 and 1991 year-classes was not determined in some month because specimens in the small size-fraction (between 0.5 and 1.0 mm mesh sieves) were not collected

Month	Year-class									
	<1983	1983	1984	1985	1986	1987	1988	1989	1990	1991
<b>Stn YA</b>										
Jun 1990	0.5	0.5	2.5	0.5	2.3	9.1	2.5	0.0	13.1	–
Jul 1990	1.2	1.8	1.0	0.4	3.0	12.1	2.0	0.0	10.0	–
Aug 1990	1.6	1.2	0.6	0.2	1.8	8.1	2.2	0.0	–	–
Sep 1990	1.6	0.8	1.4	0.6	2.2	9.3	2.6	0.0	–	–
Oct 1990	1.8	1.3	1.0	0.5	0.8	13.6	2.5	0.0	–	–
Nov 1990	2.2	1.6	1.0	0.0	0.6	12.1	3.4	0.0	0.0	–
Dec 1990	1.6	1.0	1.0	0.4	2.2	10.3	2.2	0.0	–	–
Jan 1991	1.6	1.4	0.2	0.4	2.0	13.3	2.2	0.0	–	–
Feb 1991	2.0	2.0	0.6	0.0	1.6	7.1	1.6	0.0	–	–
Mar 1991	1.0	1.0	1.8	0.2	1.2	9.3	1.4	0.0	–	–
Apr 1991	1.2	1.0	1.0	0.3	2.2	7.9	2.5	0.0	0.3	0.0
May 1991	1.2	0.4	2.0	1.0	1.2	6.3	1.4	0.0	0.6	0.0
Jun 1991	0.8	1.2	1.0	0.2	2.0	9.9	2.2	0.0	0.2	0.0
<b>Stn YD</b>										
Jun 1990	5.4	2.2	2.9	1.3	0.8	6.6	3.7	4.4	6.5	–
Jul 1990	5.9	3.2	2.5	0.9	0.5	4.8	3.2	4.8	20.0	–
Aug 1990	4.7	3.4	2.7	0.8	1.2	7.9	1.7	6.7	10.0	–
Sep 1990	5.1	3.0	2.7	1.7	1.0	5.7	1.7	4.5	16.7	–
Oct 1990	6.1	2.5	2.3	0.9	0.4	7.8	3.0	3.3	6.7	–
Nov 1990	3.3	2.6	3.8	1.0	1.0	6.2	1.9	0.3	23.3	–
Dec 1990	3.2	3.0	2.9	1.2	1.2	5.6	1.9	1.0	10.0	–
Jan 1991	3.4	2.7	2.4	0.5	0.5	5.7	1.4	0.4	5.0	0.0
Feb 1991	3.4	3.6	2.4	0.8	0.4	6.1	0.7	0.1	2.5	0.0
Mar 1991	2.5	1.3	2.6	1.2	0.9	3.9	0.9	0.1	–	–
Apr 1991	2.5	1.3	3.4	1.5	0.7	6.6	0.3	0.0	0.7	0.0
May 1991	3.4	2.9	3.2	0.8	1.1	3.8	1.1	0.1	2.1	0.0
Jun 1991	4.5	1.5	3.7	0.5	0.2	3.4	0.2	0.7	1.2	5.0

and the organic flux were low or poor in quality from summer to winter, and growth and production of *Yoldia notabilis* were negligible or even negative during this period. These facts strongly suggest that the growth and production of *Y. notabilis* are food-limited, i.e. the bivalves can grow only in spring when food is abundant, but not during the rest of the year.

Synchronization of growth with phytoplankton bloom has been reported in a suspension/surface-deposit feeding bivalve, *Macoma balthica* (Hummel 1985a, Thompson & Nichols 1988). Tellinacean bivalves, including this species, are capable of switching feeding mode in response to water current or sediment transport (Ólaffson 1986, Levinton 1991), and are able to respond quickly to the increase in food concentration in water or on the bottom (Hummel 1985a, b). Although the protobranch bivalves *Yoldia* spp. have been generally believed to be infaunal deposit feeders (Rhoads & Young 1970, Lopez 1988), evidence of surface-deposit feeding or suspension feeding has been recorded in several species such as *Y. ensifera* (Stasek 1965), *Y. limatula* (Bender & Davis 1984), *Y. eightsi* (Davenport 1988) and *Y. notabilis* (Nakaoka

unpubl.). It may well be that, by switching feeding mode, *Y. notabilis* is able to utilize fresh food on the surface or in suspension when it becomes abundant in spring.

Bivalve size and growth rate of corresponding year-classes, and the estimates of production were detected to be larger at Stn YA than at Stn YD (Figs. 5, 6 & 7). This type of a spatial variation within such a short distance can be commonly found in a variety of marine benthic animals, and can be explained by the differences in temperature (Green & Hobson 1970), salinity (McLusky & Allan 1976), food availability (Beukema et al. 1977, Thompson & Nichols 1988, Irlandi & Peterson 1991) and density effects (Rae 1979, Broom 1982, Peterson 1982). In the present case, temperature and salinity were identical at the 2 stations (Table 1), and organic content in the sediment as well as biomass and density of *Yoldia notabilis* did not differ significantly between the stations (Fig. 3, Table 2); therefore these factors were not related to the spatial variation in *Y. notabilis*. In contrast to these factors, organic carbon and nitrogen fluxes from the water column to the bottom were 1.4 to 1.5 times higher at Stn YA than at

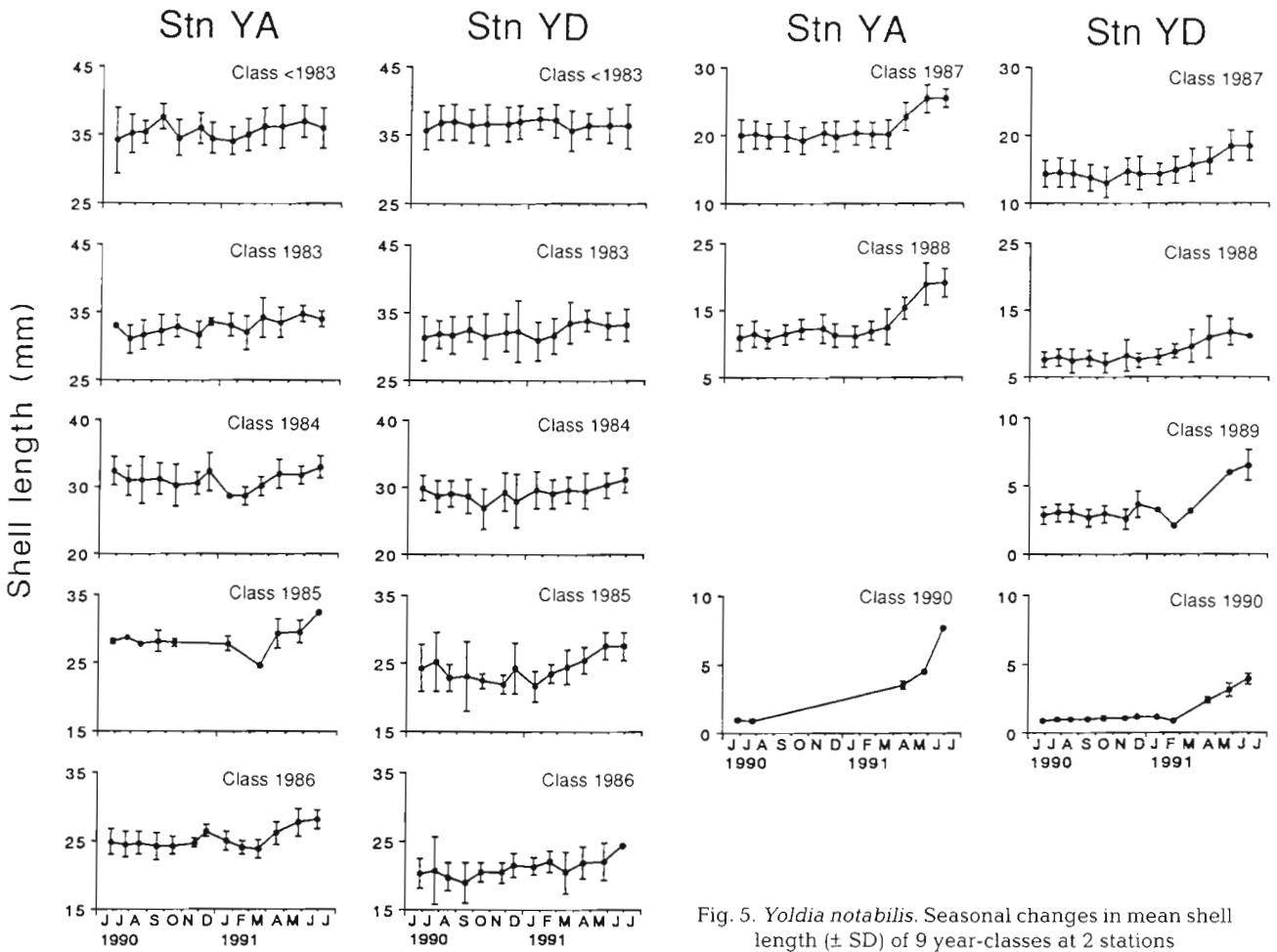


Fig. 5. *Yoldia notabilis*. Seasonal changes in mean shell length ( $\pm$  SD) of 9 year-classes at 2 stations

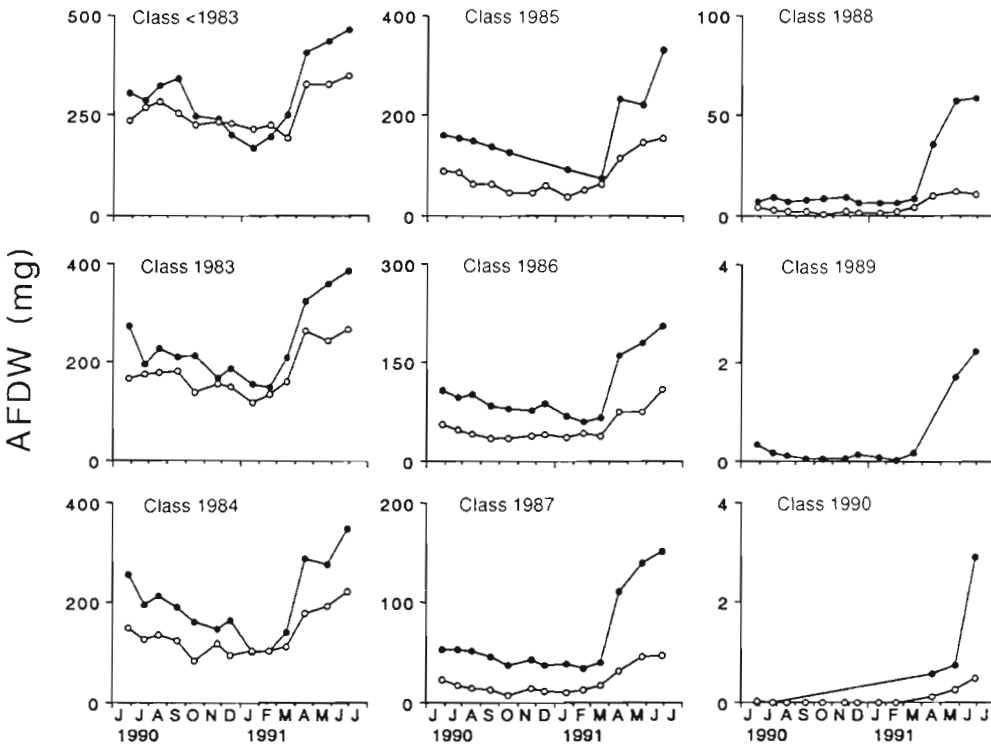


Fig. 6. *Yoldia notabilis*. Seasonal changes in soft tissue AFDW of an individual with mean shell length for each of 9 year-classes at Stns YA (●) and YD (○)

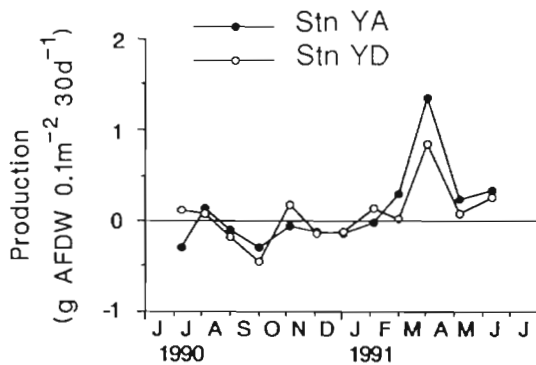


Fig. 7 *Yoldia notabilis*. Seasonal changes in monthly secondary production at Stns YA (●) and YD (○)

Stn YD in March 1991 (Fig. 4), and this coincided well with the spatial variation in shell and somatic growth rates and secondary production of *Y. notabilis* in spring. These data support the view that, as in the case of the seasonal variation which was discussed above, spatial variation in growth rate and production is caused by the local differences in food supply from the water column. Iizumi et al. (1990) reported that spring phytoplankton bloom occurs more intensely in shallower areas in the inner part of Otsuchi Bay because of abundant nutrient supply from the rivers. This probably results in better food conditions at the shallower Stn YA.

Secondary production of *Yoldia notabilis* from February to April 1991 was estimated to be 16.5 g AFDW m<sup>-2</sup> at Stn YA and 8.7 g AFDW m<sup>-2</sup> at Stn YD (calculated from Fig. 7). Converting the data into organic carbon basis (1 g AFDW equals 0.4 g C; Nakaoka unpubl.) and assuming net growth efficiency to be 25% [an average value for several bivalves in Hughes (1970) and Hummel (1985c)], assimilation of *Y. notabilis* is calculated to be 26.4 and 13.9 g C m<sup>-2</sup> for Stns YA and YD, respectively. These values amounted to ca 10% of the primary production in the water column in spring (ca 200 g C m<sup>-2</sup>, Takahashi 1991), and 30 to 40% of the organic flux during February–April 1991 (calculated from Fig. 4). Although the actual values are probably somewhat lower, since other nutrient sources such as benthic primary production and bacterial production have not been taken into account, the data suggests that the *Y. notabilis* population plays an important role in the energy flow supplied from pelagic layer to the bottom communities.

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