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Production and Respiration of a Bivalve *Theora lubrica* in Northern Bingo-Nada, the Seto Inland Sea

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Abstract Density of a small semelid bivalve *Theora lubrica*, which occupied 61-67 % of the macrobenthic community in northern Bingo-Nada in 1986-1987, reached a maximum in June (2,038 ind./m^2) and thereafter decreased markedly to near zero in mid summer. The bivalves immediately after settlement were collected during a year except August, and divided into seven cohorts on the basis of seasonal change in the size compositions.

Estimates of the production and respiratory energy loss were made on each cohort, and totaled to 21.1 g dry weight/m^2/year and 80.6 g dry weight/m^2/year, respectively. Seasonal change of the respiratory energy loss, which was influenced by the biomass and sediment temperature, was larger than that of the production. It is assumed to be caused mainly by a large amount of the respiratory energy loss that the production hardly increased in June - July, when the biomass was maximum and ambient temperature was on the rise.

Key words: bivalve, cohort, eutrophication, production, respiration, *Theora lubrica*.

INTRODUCTION

The semi-enclosed shallow waters and bays, e.g., the Seto Inland Sea and Tokyo Bay, have been eutrophicated because of urban drainage and industrial waste water. These eutrophications influence the macrobenthic community to a large extent, in which organisms with a behavior of small movement are increased (KIKUCHI, 1991). A small semelid bivalve *Theora lubrica*, a biological indicator for oxygen-deficient waters, is predominant at the muddy sediment of eutrophic waters. It is, therefore, considered that the bivalve plays a major role in cycle of eutrophic matters. Estimates of the production are made in the strait region of Bingo-Nada of the Seto Inland Sea (MUKAI, 1974), and in Tomoe Bay of Kyushu (TANAKA and KIKUCHI, 1970), based on the seasonal change in the population density. However, the population is sustained by several cohorts, whose settlements from the pelagic to benthic lives are vulnerable to ambient oxygen level (IMABAYASHI, 1986; IMABAYASHI and IWATANI, 1988). These facts indicate that the production also is influenced by the environmental variable. Therefore, population dynamics at the benthic life varies largely with the habitat (IMABAYASHI and TSUKUDA, 1984).

The present study deals with the production estimation of *Theora lubrica* by examining a seasonal change in the density of each cohort in northern Bingo-Nada, where the population dynamics is different from the above-mentioned waters. The respiratory energy loss also is estimated to evaluate its role in cycle of eutrophic matters, because dissolved oxygen is closely connected with the settlement and survival.

MATERIALS AND METHODS

Sampling and measurement

Sampling was conducted at three stations (SH3, SH4, SH5) off Sensui Island in northern Bingo-Nada, the Seto Inland Sea (Fig. 1), where hydrogen sulfide was abundantly produced in summer with decreasing dissolved oxygen at bottom layer, and bottom sediment was composed of organic matters with an ignition loss of over 8 % (IMABAYASHI and TSUKUDA, 1984). Sampling stations with a depth of 7 to 10 m undergo a large fluctuation of tidal level, i.e., 2.9 m in spring range (NATIONAL ASTRONOMICAL OBSERVATORY, 1990).

Macrobenthos was collected from April 1986 to March 1987, using a Ekman-Birge bottom grab (sampling area: 0.025-0.04 m^2). Quantitative bottom samples were taken 2-7 times at every sampling on each of the three stations. Individuals retained on a 1 mm mesh sieve were preserved in 10 % buffered formalin, then identified to Polychaeta, Mollusca, Crustacea and Others. In particular, dominant benthos, e.g., *Theora lubrica*, were identified to species and counted.

The length-weight relationship in the bivalve was obtained as follows. The shell length was measured to the nearest 0.1 mm by a means of an ocular micrometer. The dry ash-free weight was determined by burning off the organic matters 2 hrs at 500℃, after the bivalve including shell was dried 8 hrs at 110℃.

Estimation of respiratory energy loss

The respiration of benthos is generally expressed by the equation $Q=a \cdot W^b$, where Q is the amount of respiration, W, the body weight, a is a constant, and b the exponent. In the case of the bivalve, the following equations at three levels of temperatures are reported by IMABAYASHI (1989):

$$10℃,\ Q=0.315 \cdot W^{0.755}$$
$$15℃,\ Q=0.489 \cdot W^{0.781}$$
$$20℃,\ Q=0.829 \cdot W^{0.642}$$

where Q and W are the units of mlO_2/hr/individual and mg dry weight, respectively.

The respiration at any given temperature can be calculated from the fact that the relation of temperature to Log a is linear (CRISP, 1984), using the above equations. Therefore, respiratory energy loss (g dry weight/m^2/day) of the bivalve population was estimated by multiplying the biomass by the respiration observed at each sampling time, assuming that calorie of the bivalve was assumed 4

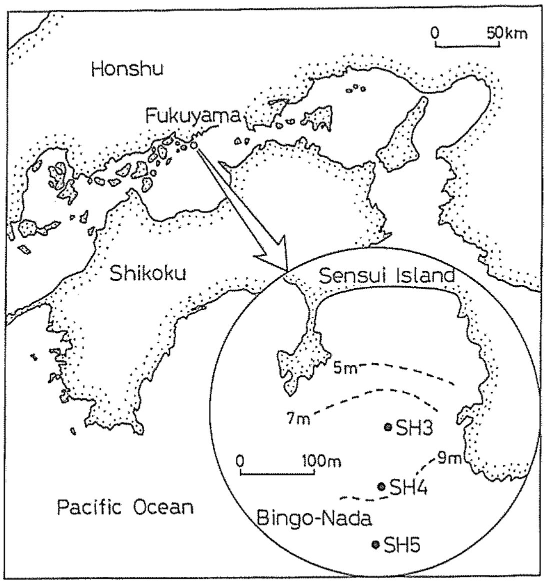

Fig. 1. Location of the sampling stations (solid circle) in northern Bingo-Nada during 1986 to 1987.

cal/mg dry ash-free weight, and 1 ml of oxygen at n.t.p. was equivalent to 4.8 cal (CRISP, 1984). The dry ash-free weight was 14 % of the dry weight in the bivalve.

Estimation of production

Production is the amount of organic matters produced in a unit time by organisms. In the wild population of the bivalve, which is composed of several cohorts (IMABAYASHI and TSUKUDA, 1984), the production is estimated by combining a change of the density and a process of the growth in each cohort. Growth increment of average body size in the cohort, which was attained in a given period, was added to all of the individuals. The growth increment is expressed as $N \cdot (dW/dt) \cdot \Delta t = N \cdot \Delta W$, where N is the number surviving at time t, and ΔW the growth increment of average body weight W. Therefore, the production P by all individuals of the cohort over any period t_1-t_2 is obtained by the following equation:

$$P_{(t_1\text{-}t_2)} = \sum_{t=t_1}^{t=t_2} N \cdot \Delta W$$

The yearly production of the population was the summation of that of all cohorts.

RESULTS

Sediment temperature

Seasonal change of the sediment temperature at Stns.SH3, SH4 and SH5 was shown in Fig. 2. Temperature increased at a rate of approximately 3℃/month from April (10.2℃) to summer, and decreased in turn. The peak was reached in August at Stns.SH3 and SH4 of 26.3-26.8℃, and in September at Stn.SH5 of 24.5℃. The minimum (9.7-10.0℃) was observed in winter.

In this way, no or little difference in temperature was seen between sampling stations except August, whereas the yearly change was large.

Fauna of macrobenthic community

The fauna of macrobenthic community hardly differed among Stns.SH3, SH4 and SH5, and was dominated by Mollusca and Polychaeta during a year (Table 1). Especially *Theora lubrica* occupied a high number ratio of 61-65% in the macrobenthic community over the sampling area. In Polychaeta, *Paraprionospio* sp.type B, *Prionospio ehlersi, Nephtys polybranchia, Sigambra tentaculata* and *Notomastus latericeus* were collected almost during a year.

Five species of spionid polychaetes, e.g., *Paraprionospio* sp.type B, showed a number ratio of 14 % in the macrobenthic community. Crustacea, e.g., *Alpheus japonicus* and small gammaridean species, occurred in low numbers (2%).

Most of the species of Mollusca and Polychaeta, except *Notomastus latericeus*, decreased in summer. Therefore, density of all macrobenthos changed largely during a year, when the maiximun (1,638 ind./m^2)and minimum (125 ind./m^2) were observed in June and August, respectively.

The fact that total density was controlled mainly by the predominant species *Theora lubrica* was seen at three stations (Figs. 3, 4).

Density and size composition of the bivalve

Pattern of the seasonal change in the density of *Theora lubrica* was similar among three stations (Fig. 4). The bivalve was abundant in spring, when Stn.SH3 reached a maximum density of 2,038 ind./m^2 in June, and thereafter decreased remarkably to almost nothing in August, when bottom oxygen decreased with increasing temperature. In autumn and

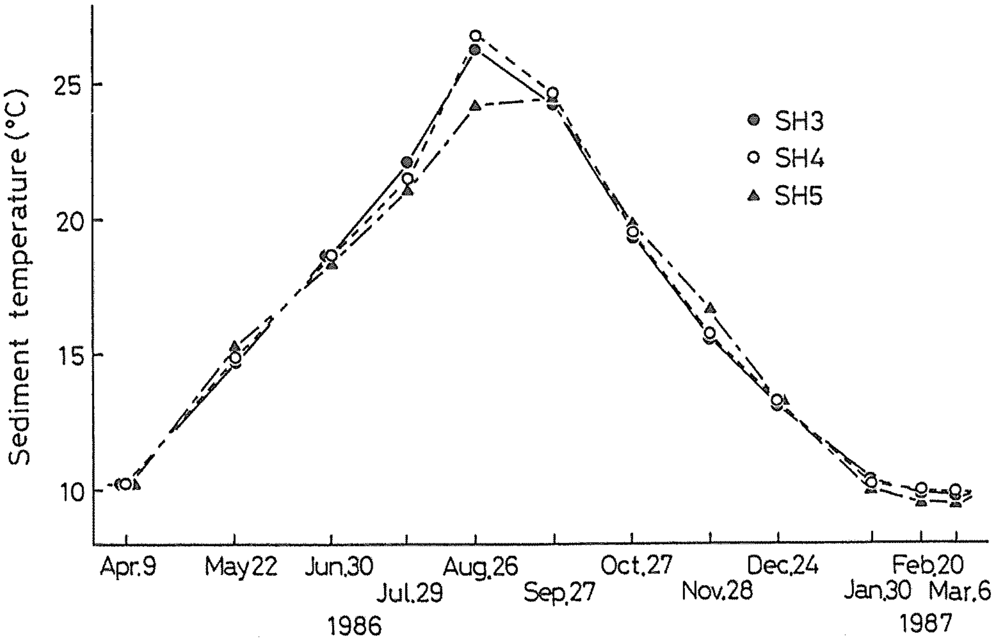

Fig. 2. Seasonal changes in sediment temperature at Stns.SH3, SH4 and SH5.

Table 1. Seasonal change in the composition and density (ind./m^2) of macrobenthic community collected at three stations of northern Bingo-Nada

	1986									1987		
	Apr. 9	May. 22	Jun. 30	Jul. 29	Aug. 26	Sep. 2	Oct. 27	Nov. 28	Dec. 24	Jan. 30	Feb. 20	Mar. 6
Polychaeta	191	208	154	153	82	79	211	165	227	165	258	308
Paraprionospio sp. type. B	71	83	72	57	19	21	97	74	93	44	76	100
Prionospio ehlersi	17	21	11	13	6	4	59	38	57	32	53	34
Prionospio cirrifera	—	—	4	13	11	—	—	—	—	—	—	—
Polydora sp.A	29	—	21	2	—	—	—	—	6	2	4	25
Polydora sp.B	4	4	—	—	—	—	—	—	4	2	6	—
Nephtys polybranchia	8	25	4	2	—	11	11	2	15	13	19	21
Nephtys caeca	4	—	6	—	—	—	2	—	—	—	—	—
Lumbrineris longiforia	4	4	2	—	—	2	—	—	4	6	15	9
Sigambra tentaculata	8	17	—	9	6	19	6	15	9	4	11	15
Notomastus latericeus	—	8	4	42	32	9	4	6	9	11	6	9
Others	46	46	30	15	8	13	32	30	30	51	68	95
Mollusca	933	1000	1446	474	11	95	182	201	411	389	470	449
Theora lubrica	867	958	1422	464	2	91	178	193	387	313	334	337
Others	67	42	23	11	9	4	4	9	23	76	135	112
Crustacea	21	—	15	4	13	15	19	6	11	—	17	9
Others	146	13	23	34	19	13	15	2	17	85	93	64
Total	1291	1221	1638	665	125	202	427	374	666	639	838	830

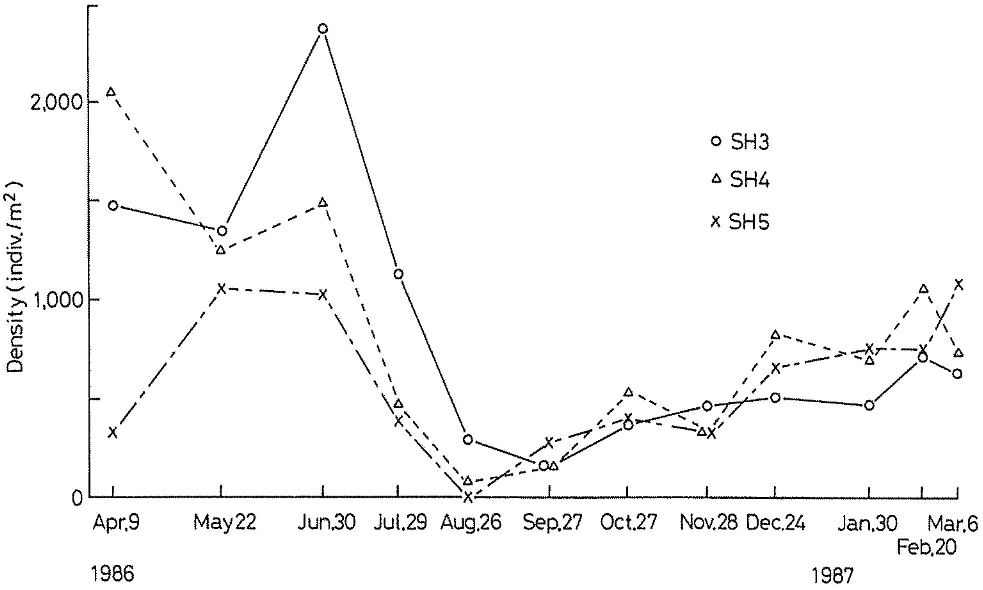

Fig. 3. Seasonal changes in the density of macrobenthic community collected at Stns.SH3, SH4 and SH5 in northern Bingo-Nada.

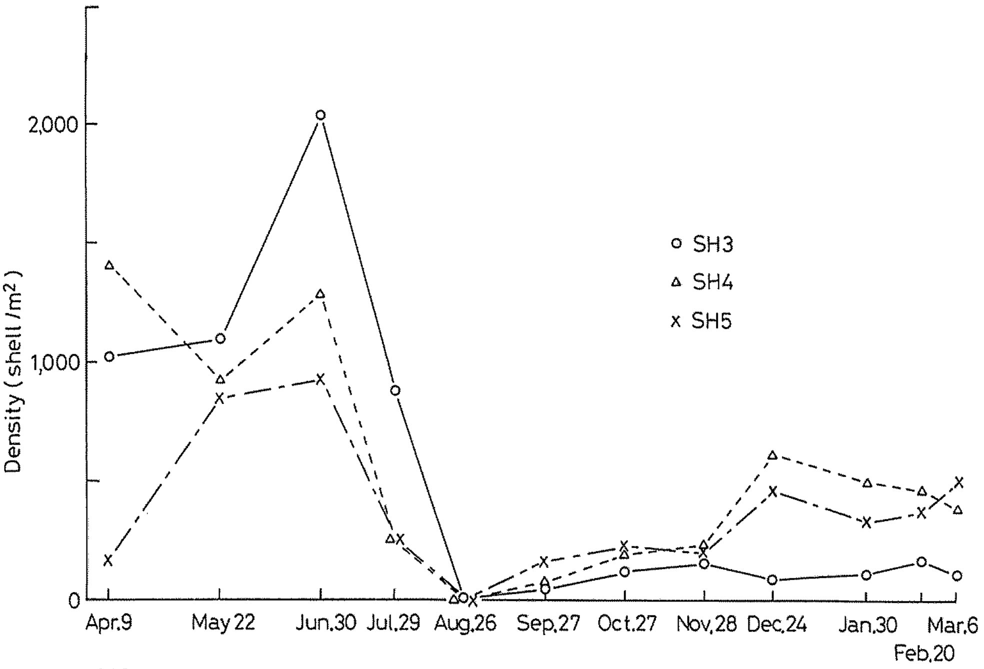

Fig. 4. Seasonal changes in the density of *Theora lubrica* collected at Stns.SH3, SH4 and SH5 in northern Bingo-Nada.

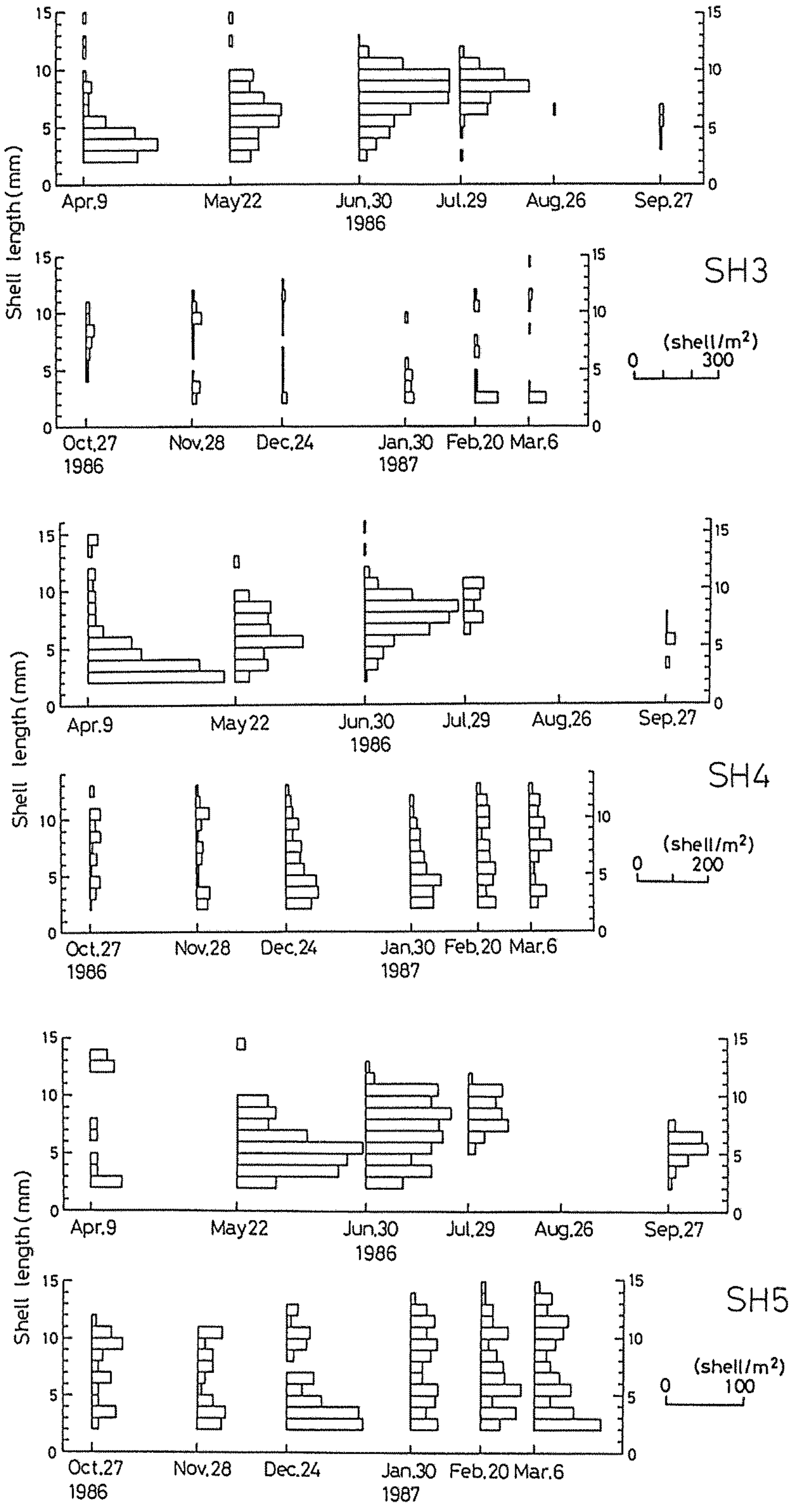

Fig. 5. Seasonal changes in the size composition of *Theora lubrica* collected at Stns.SH3, SH4 and SH5 in northern Bingo-Nada.

winter, the density was recovered to a considerable extent of 39-610 ind./m^2.

Based on the seasonal changes in the size compositions (Fig. 5), a similar population dynamics among three stations was indicated as follows. First, excepting summer the newly settled individuals of 2-3 mm in shell lenght occurred. Secondly, the size compositions at each sampling time was composed of 1-3 cohorts, and their modes corresponded each other. Thirdly, disappearance and recovery of the population during August to September occurred at the same time. Lastly, although the large-sized individuals of 13-16 mm, substantially corresponding to its maximal size, had a slightly higher density at offshore stations, there was no or little difference in the size composition (KIKUCHI and TANAKA, 1976).

The seasonal changes in the density and distribution indicated that the bivalves collected at Stns.SH3, SH4 and SH5 belonged to the same populaltion, and hardly migrated to offshore area.

Production and respiratory energy loss

Seasonal change in the density and size composition in sampling area was shown in Fig. 6. The small-sized individuals of 2-3 mm immediately after settlement were obtained except August, especially abundantly in April (254 ind./m^2). The settlement occurred intermittently and formed several groups of benthic life, whose size compositions were separated each other. Therefore these groups could be referred to as cohorts. Seven cohorts A-G were divided, based on their growth process.

Cohort A was largest in density among seven cohorts, and obviously showed a normal distribution in the size composition. The settling duration ranged from February to April, and the growth rate during April-June was estimated 0.073 mm/day on their increasing

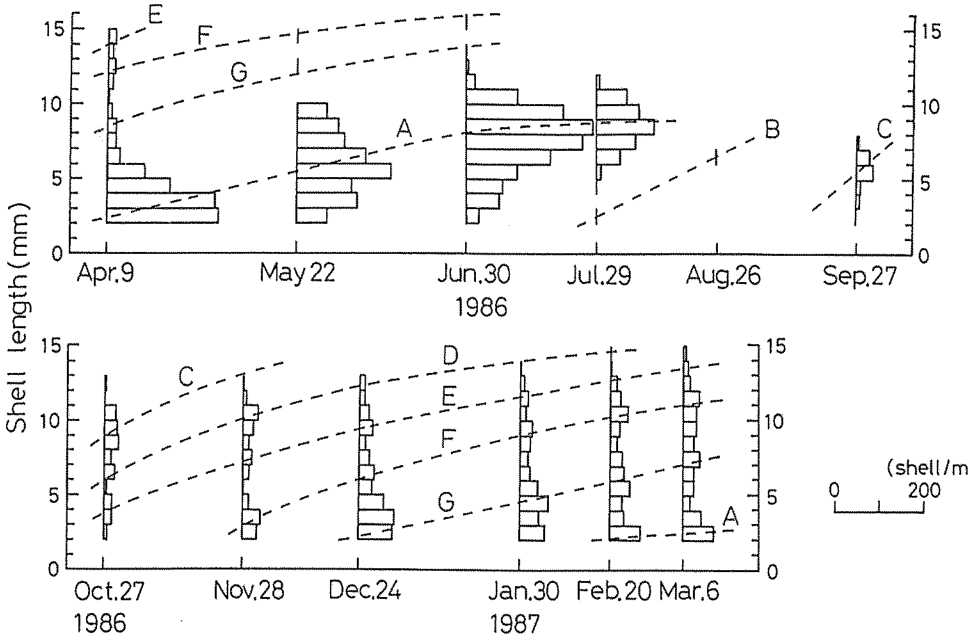

Fig. 6. Seasonal changes of seven settled cohorts (A-G) in the size composition of *Theora lubrica* collected at three stations of northern Bingo-Nada.

modes. In July a large mortality and slow growth were observed in cohort A probably because of an oxygen-deficient condition.

In summer when sediment temperature was highest during a year, the newly settled cohorts C and D had a high growth rate of approximately 6 mm/month. On the contrary, a low rate of growth was seen in cohorts settling in winter, e.g., cohort G.

The densities of seven cohorts were obtained by separating them at a point of lower frequency in the size compositions formed at sampling times. In each cohort, mean weight was calculated from a length-weight relation (Fig. 7). Table 2 showed the production of each cohort. Accordingly their total productions in a year were estimated 21.1 g dry weight/m^2, and the most was composed of cohort A (10.5 g dry weight/m^2/year) with the highest abundance. Cohort B had the smallest production of 8 mg dry weight/m^2/year. In cohorts E and F, whose large-sized individuals above 20 mg dry weight/ind. survived to a higher degree than other cohorts, the production was relatively large (2.4-2.5 g dry weight/m^2/year).

There was not a large difference in the production among three stations (18.1-23.7 g dry weight/m^2/year).

Seasonal change in the total production was depicted in Fig. 8. The maximum and minimum were reached in June and September, respectively. Change of the production was similar to that of biomass. The ratio of production P to annual average biomass B was 6.3/year, while varying with the sampling time. The P/B ratio was the lowest on June 30 (0.01 /day), and the highest on November 28 (0.03 /day).

Respiration of the bivalve population was estimated at regular intervals, as shown in Table 3. The total respiratory energy loss in a year was 80.6 g dry weight/m^2, and concentrated in the period of May to July, especially in June (0.95 g dry weight/m^2/day). Although seasonal change of the respiration was almost similar to that of biomass (Fig. 8), the former was considerably larger than the latter in summer of a high temperature.

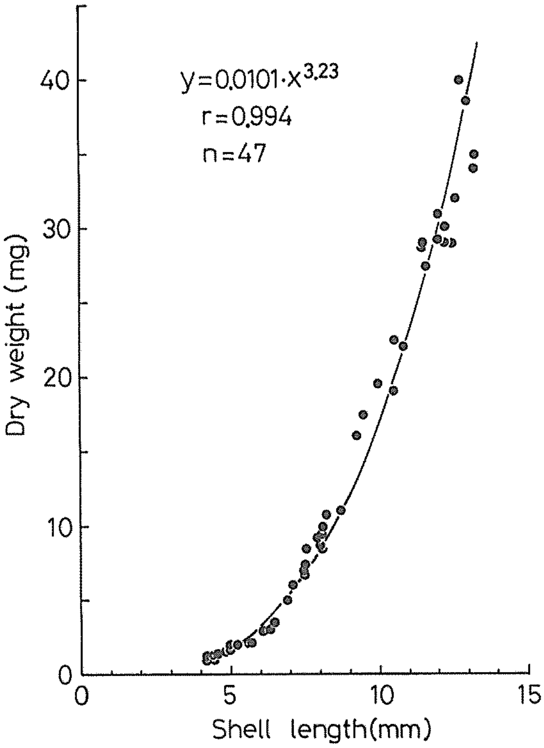

Fig. 7. Relationship between shell length and dry weight, including shell, in *Theora lubrica*.

DISCUSSION

The production of *Theora lubrica* is considered to vary with the time and space, because the population dynamics with a selective deposit-feeder is influenced by its sedimental environment (IMABAYASHI and TSUKUDA, 1984).

TANAKA and KIKUCHI (1970) in-

Table 2. Seasonal changes in the productions of seven cohorts (A-G) in *Theora lubrica* collected at three stations of northern Bingo-Nada from 1986 to 1987

Date	Cohort	Density (ind./m^2)	Mean dry weight (mg/ind.)	Production Increment (mg/m^2)
Feb. 20	A	100	0.314	
Mar. 6		123	0.449	15
Apr. 9		721	0.798	147
May. 22		942	4.22	2,845
Jun. 30		1418	8.56	5,121
Jul. 29		461	11.1	2,386
Total				10,514
Jul. 29	B	2	0.193	
Aug. 26		2	4.22	8
Total				8
Sep. 27	C	91	2.81	
Oct. 27		91	15.6	1,164
Nov. 28		2	34.9	897
Total				2,061
Oct. 27	D	47	4.69	
Nov. 28		62	18.6	758
Dec. 24		25	30.8	531
Jan. 30		2	44.8	189
Feb. 20		2	56.4	23
Total				1,501
Oct. 27	E	40	0.815	
Nov. 28		49	6.55	255
Dec. 24		66	15.4	509
Jan. 30		38	26.3	567
Feb. 20		34	30.4	148
Mar. 6		23	42.4	342
Apr. 9		29	51.4	234
Total				2,055
Nov. 28	F	85	0.537	
Dec. 24		85	4.12	305
Jan. 30		62	10.8	491
Feb. 20		55	18.0	421
Mar. 6		61	23.7	331
Apr. 9		29	31.4	347
May. 22		8	56.4	463
Jun. 30		2	69.9	68
Total				2,426
Dec. 24	G	212	0.629	
Jan. 30		218	1.37	159
Feb. 20		144	4.21	514
Mar. 6		129	7.67	472
Apr. 9		88	8.39	78
May. 22		8	34.9	1,272
Jun. 30		2	44.8	50
Total				2,545

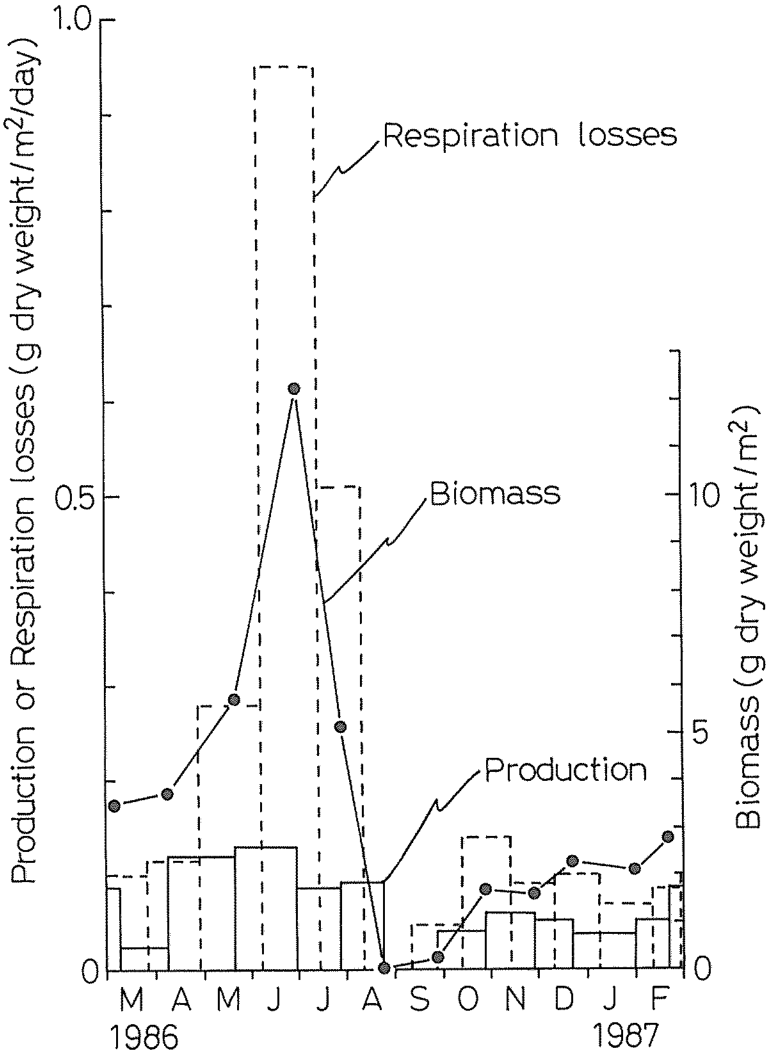

Fig. 8. Seasonal changes in the production, respiratory energy losses and biomass of *Theora lubrica* collected at three stations of northern Bingo-Nada.

vestigated the population dwelling in Tomoe Bay, which formes a semi-enclosed small waters covered with soft-muddy bottom. The production widely ranged from 2.4 to 14.2 g dry weight/m^2/year in only three years (1969-1971), based on the summation of mortality. Moreover, this range was large compared with the variation of annual average biomass (1.2-4.2 g dry weight/m^2). The P/B ratio, turn-over rate per generation, was calculated at 2.0-3.4 /year. In this area recruitment of the cohorts occurred twice a year.

The strait region of Bingo-Nada with a muddy bottom exhibited 3.9 /year in P/B ratio and an annual average biomass of 1.07 g wet weight/m^2 (MUKAI, 1974). Supposing that dry weight is approximately 25 % of wet weight in the bivalve, the production is calculated at 1.04 g dry weight/m^2/year, which is remarkably small compared with that of the present study (21.1 g dry weight /m^2/year). The population was maintained by three cohorts

Table 3. Seasonal change in the respiratory energy losses of *Theora lubrica* collected at three stations of northern Bingo-Nada from 1986 to 1987

Time interval Δt	Δt (hr)	Mean Water Temp. (℃)	Log a	a	$\Sigma f_i \cdot W_i^{0.726}$	Respiration $\Delta t_j \cdot a_j \cdot \Sigma f_i \cdot W_i^{0.726}$ $\times 10^3$ (m$\ell O_2/m^2/\Delta t$)	Respiration (g/m²/day)
Mar. 23～Apr. 29	912	10.2	−0.500	0.316	1835	529	1.2×10^{-1}
Apr. 30～Jun. 9	984	15.0	−0.298	0.504	2715	1346	2.8×10^{-1}
Jun. 10～Jul. 13	816	18.7	−0.142	0.721	6436	3786	9.5×10^{-1}
Jal. 14～Aug. 11	696	21.6	−0.0196	0.956	2588	1722	5.1×10^{-1}
Aug. 12～Sep. 10	720	25.8	0.157	1.44	6	6	1.7×10^{-3}
Sep. 11～Oct. 11	744	24.4	0.0982	1.25	183	170	4.7×10^{-2}
Oct. 12～Nov. 11	744	19.6	−0.104	0.787	835	489	1.4×10^{-1}
Nov. 12～Dec. 10	696	15.9	−0.260	0.550	787	301	8.9×10^{-2}
Dec. 11～Jan. 10	744	13.4	−0.365	0.432	1158	372	1.0×10^{-1}
Jan. 11～Feb. 8	696	10.3	−0.495	0.320	1039	231	6.8×10^{-2}
Feb. 8～Feb. 26	432	9.9	−0.512	0.308	1327	177	8.4×10^{-2}
Feb. 27～Mar. 23	576	9.9	−0.512	0.308	1578	280	1.0×10^{-1}
						9409 (m$\ell O_2/m^2$/year)	80.6 (g/m²/year)

a) Log a$=0.0421 \cdot \theta - 0.929$ ($r=0.999$), resulted from plotting Log a against temperature θ for estimating a at any given temperature where respiration equation is $Q = a \cdot W^b$ (Q: amount of respiration, W: body weight, a, b: coefficients).

b) fi: frequency of size class, W_i: mean dry weight of size class (mg), 0.726: mean exponent b in respiration equations (Imabayashi, 1989).

without large-sized individuals more than 10mm in shell length, whereas hardly decreased to a great extent in summer.

In comparison with the two areas mentioned above, it is suggested from the following characteristics of the pupulation dynamics that the bivalve in northern Bingo-Nada plays a more important role in cycle of eutrophic matters; The number percentage in macrobenthic community (70 %), annual average biomass (3.34 g dry weight/m²), production (21.1 g dry weight/m²/year) and P/B ratio (6.3 /year) were considerably higher. The higher value of P/B ratio was due mainly to the large number of cohorts (7), and high survival and growth rate of large-sized individuals, which generally account for the increased production of organisms. Thus, northern Bingo-Nada seems to be a suitable area both for settlement of the planktonic larvae and for nursery of the benthic bivalve. In summer, however, a severe depletion of ambient oxygen temporarily caused a high mortality and a discontinuance of the recruitment, in addition to an increase in the resiratory energy loss whose peak appeared in June (0.95 g dry weight/m²/day). These environmental and physiological effects are considered to result in decreasing production of the bivalve cohort B settling in summer.

Morisita (1975) emphasizes that the turn-over rate of non-stationary population, whose age composition and biomass are not constant in a year, can be more properly expressed by P/B_{max} ratio than by P/B ratio, where B_{max} is annual maximum biomass. In this case, P/B_{max} ratio are based on an average period of occurrence of the biomass. Therefore, P/B_{max} ratio is calculated at 1.7 /year in northern Bingo-Nada, where 12.37 g dry weight/m² in B_{max}

was observed in June. Similarly Tomoe Bay (TANAKA and KIKUCHI, 1970) indicates 1.8 /year in 1967 (P: 5.8 g dry weight/m^2/year, B_{max}: 3.3 dry weight/m^2), and the strait region of Bingo-Nada (MUKAI, 1974) shows 1.3 /year (P: 4.15 wet weight/m^2/year, B_{max}: 3.25 wet weight/m^2). Thus, the turn-over rate expressed by P/B_{max} hardly differs among three habitats for the bivalve.

In Suo-Nada of the Seto Inland Sea, TAMAI (1985) estimates the production of spionid polychaete *Paraprionospio* sp.type B, which is almost always distributed with the bivalve (IMABAYASHI, 1989) and has the almost same density (annual average: 79.5 ind./m^2) as northern Bingo-Nada. This species had a striking small production (0.178g dry weight/m^2/year) with a similar value of P/B_{max} ratio (1.5 /year), when compared with the bivalve. Therefore, predominancy of the bivalve in eutrophic waters is supported by the amount of production as well as by the biomass.

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瀬戸内海備後灘北部域におけるシズクガイの生産量と呼吸量

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瀬戸内海備後灘北部域の泥質底において，大型底生動物群集内で卓越するシズクガイ（個体数比率：61-67%）の生産量と呼吸量を推定した．シズクガイは，6月に最高密度を示すが（2,038個体／㎡），その後は急減し8月にはほぼ消滅した．着底・加入個体は夏季の一時期を除いて周年存在し，殻長組成より7個の同時出生群が分離された．シズクガイの生産量と呼吸量を同時出生群ごとに求めると，それぞれ21.1g dry weight/m^2/year，80.6g dry weight/m^2/year を示し，後者の季節的変動幅は前者より大きく，また生物量や水温の動きとほぼ対応していた．しかし，水温上昇期の6-7月の生産量は，生物量が最大となるにもかかわらず増加しておらず，これは呼吸量によるエネルギー損失が上昇したためであると推察される．

キーワード：呼吸量，シズクガイ，生産量，同時出生群，二枚貝，富栄養化．