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THE GROWTH AND PRODUCTION OF *GAFRARIUM TUMIDUM* (RODING) (BIVALVE) IN THE LITTORAL ZONE OF CHIANG-MEI, PENGHU[1]

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Hwey-Lian Hsieh, Chang-Po Chen and Kun-Hsiung Chang (1981). The growth and production of *Gafrarium tumidum* (Roding) (Bivalve) in the littoral zone of Chiang-Mei, Penghu. *Bull. Inst. Zool., Academia Sinica* **20**(2): 11-20 (1981). In a flat beach of Penghu, the dominant intertidal bivalve, *Gafrarium tumidum* displayed a discontinous growth pattern, growing in the summer and ceasing in the winter. The growth equation of shell length (L) was expressed in years (t) as:

$$L_t = 37.4\ (1 - e^{-0.443(t+1.2622)}).$$

It was estimated that this species produced 5.57 g (wet weight with shell) $m^{-2}\,yr^{-1}$, with a production to biomass ratio (P:$\bar{B}$) of 0.36 and eliminated 5.92 g $m^{-2}\,yr^{-1}$, with an elimination to biomass ratio (E:$\bar{B}$) of 0.39. Both P:$\bar{B}$ and E:$\bar{B}$ of this species seem to be lower than comparable values for other bivalves.

Gafrarium tumidum (Roding) is the most abundant bivalve in the benthic littoral area of Penghu[3]. Forming up to 90% of the bivalve community, this species could prove useful for understanding secondary production of intertidal communities and for determining the level of productivity when the ratio of production to biomass is compared with that of other areas[1,2,5].

Little attention has been directed to the production of marine benthic macroinvertebrates in the waters surrounding Taiwan. The results of this study on the growth and production of *G. tumidum* could provide basic data for programing mariculture in the shallow waters of Penghu in the near future.

MATERIALS AND METHODS

479 individuals of *Gafrarium tumidum* (Roding) were sampled from the intertidal flat beach of Chiang-Mei, Penghu[3]. All the specimens were fixed in 10% formalin soulution. Antero-posterior shell-length was measured to the nearest 0.1 mm. The total wet weight including shell was weighed to the nearest 0.01 g.

For testing the validity of ring on the shells, 113 individuals collected from the Hsiao-Chih-Kan in May and August 1979 were used. As shown in Fig. 1, the regressive relationship between shell length (L) and ring length (r_i) are significant. Therefore, the growth rings on the shells can be used for determining age.

In addition, 81 individuals bought at a fish market were used to calcuate the relationship between the total wet weight with shell and the dry weight of flesh.

Growth, production and elimination were calculated according to Crisp[4]. For estimating the population density, mean values in each specified age group from different tidal levels

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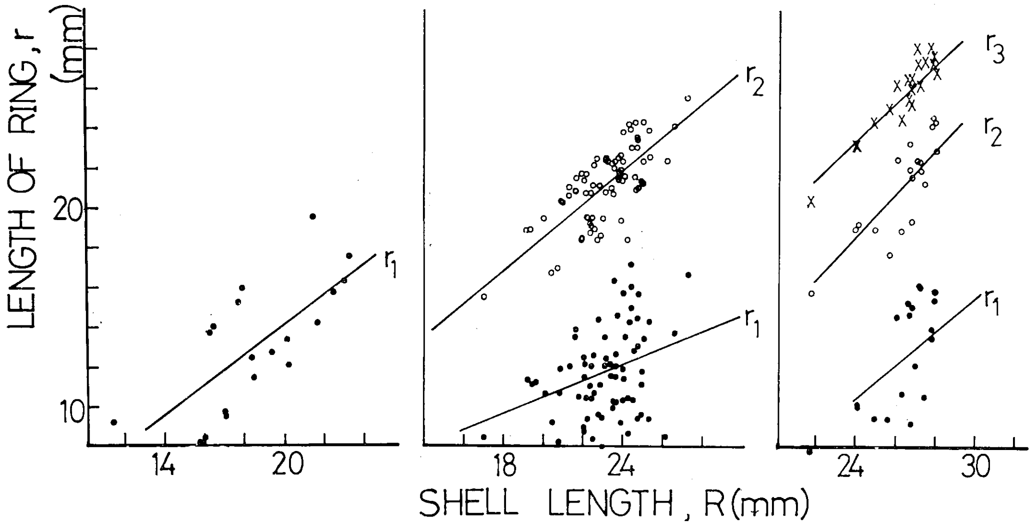

Fig. 1. The linear regression relationships between shell length (R) and ring length (r_i) of *G. tumidum* in

Group I: $r_1 = -1.1441+0.7696\ R,\ r=0.7163$

Group II: $r_1 = 2.1563+0.4208\ R,\ r=0.3478$

$r_2 = 2.0240+0.8320\ R,\ r=0.7486$

Group III: $r_1 = -10.3400+0.8695\ R,\ r=0.5970$

$r_2 = -7.4861+1.0885\ R,\ r=0.8230$

$r_3 = 0.3382+0.9648\ R,\ r=0.9012$

were used to calculate the arithmetical mean of age groups for each sampling date. The body weight of each age group for each sampling date is expressed as the arithmetical mean of all individuals from that specified age group and sampling date.

RESULTS

Age composition

On the basis of their growth rings, *G. tumidum* can be divided into nine age groups (Table 1). 0, I, II, III, and IV were the main age groups, comprising 95% of the total sampling. The seasonal change of size frequency distribution in each of these first five age groups are shown in Fig. 2. The shell-length of each group increased gradually from May, 1979 to February, 1980, but was smaller in May of 1980 within each of the groups. This indicates that a ring had been formed during February to May and spontaneously as all individuals moved into the next age group. The latter are the recruits that shift the range of shell-length

TABLE 1.
The age composition of *G. tumidum*.

Sampling date	Age group 0	I	II	III	IV	V	VI	VII	VIII	Total
May 1979	4	25	9	9	4	1	2	0	1	55
Aug.	5	32	28	14	9	4	0	0	0	92
Nov.	8	44	38	20	8	4	1	0	0	123
Feb. 1980	22	33	27	22	14	0	2	4	0	124
May	8	24	28	16	6	1	2	0	0	85
Total	47	158	130	81	41	10	7	4	1	479
%	9.8	33.0	27.1	16.9	8.5	2.1	1.5	0.8	0.2	

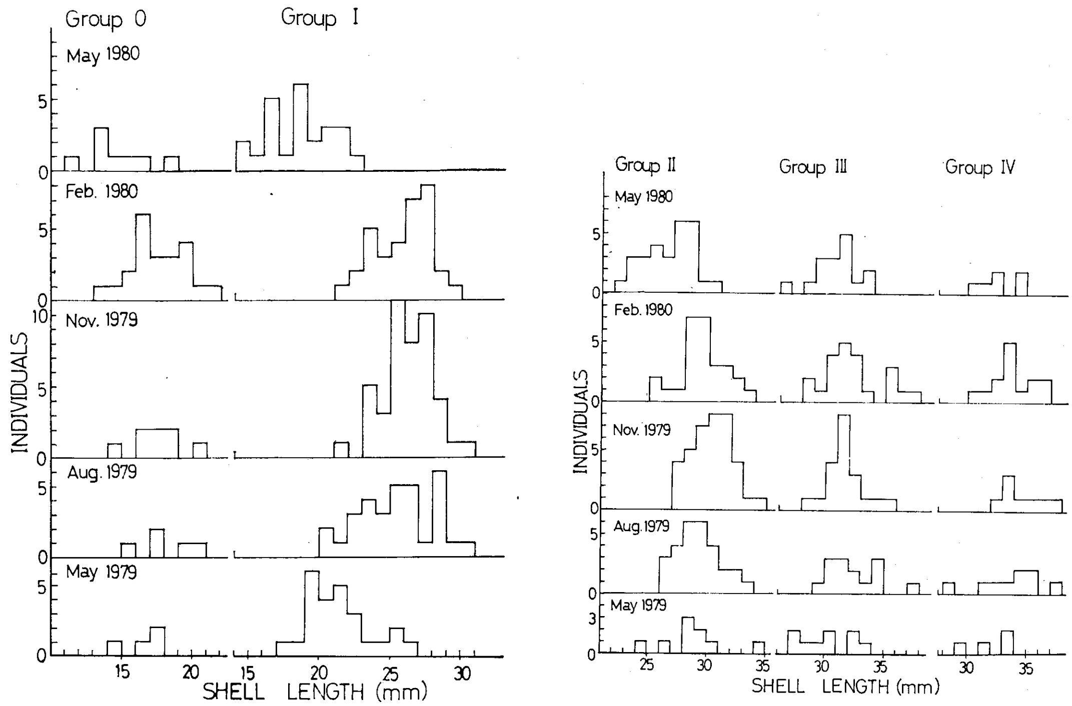

Fig. 2. The seasonal changes of size frequency distribution for five specified age-groups.

of a group to smaller values after a new growth-ring is formed in the period from February to May. Because the length of shell decreased only once a year, ring formation has an annual periodicity. Therefore, it is deduced that the rings on the shell of *G. tumidum* are annual rings.

Growth

The growth pattern in the seasonal variation and the life history for *G. tumidum* are shown in Fig. 3. They reveal an obvious seasonal variation: the animal grew rapidly during the summer from May to August, and markedly more slowly during the winter from November to February. Moreover, the growth trend in the life history also clearly shows that young grew more rapidly than old ones.

The Batterlanffy growth equation was employed to fit the growth curve of *G. tumidum.* Using the Ford-Walford extrapolated method, the maximum shell-length, growth coefficient, and the hypothetical time at which the animal would have been of zero length, were estimated as $L_\infty = 37.4$ mm, $k = 0.443$ and $t_0 = 1.2622$, respectively (Fig. 4). Therefore, the shell growth equation can be expressed as:

$$L_t = 37.4\ (1 - e^{-0.443(t+1.2622)}) \qquad (1)$$

Fig. 5 shows the regressive relationship between length and body weight. The regressive line was obtained as follows:

$$W = 1.5164 \times 10^{-4} L^{3.2463} \qquad (2)$$

Combining equations (1) and (2), the body weight growth equation was:

$$W_t = 19.35\ (1 - e^{-0.443(t+1.2622)})^{3.2463} \qquad (3)$$

As shown in Fig. 6, the growth equations of this species in both shell-length and body weight fit the observed data well.

Mortality

The seasonal changes of age-specified population densities of *G. tumidum* are shown in

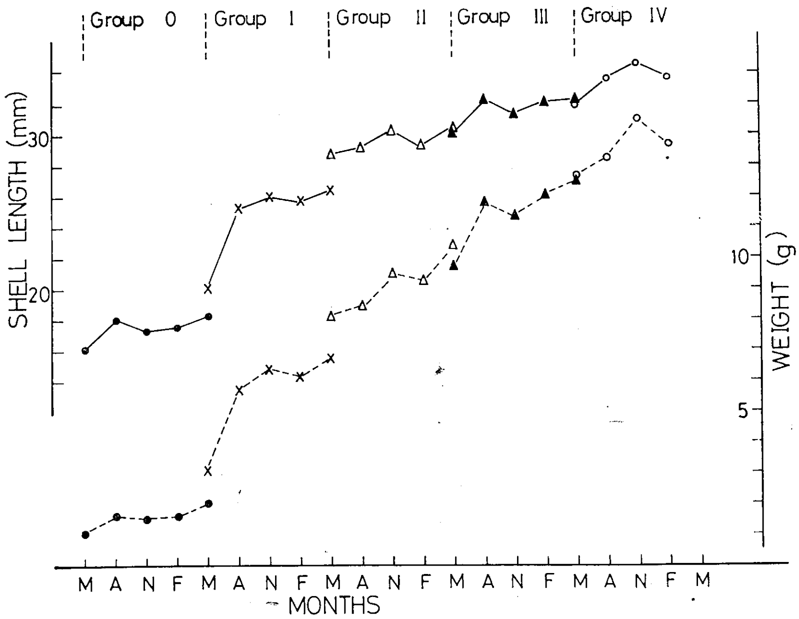

Fig. 3 The growth pattern of shell length and body weight of *G. tumidum.*

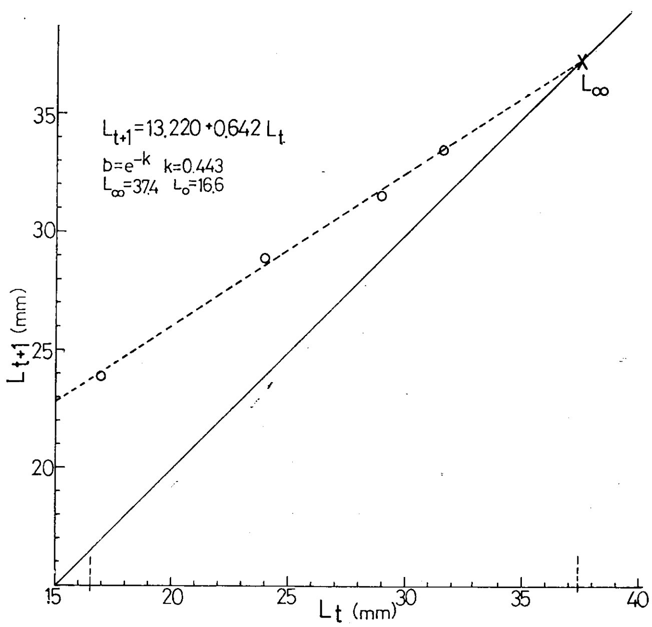

Fig. 4. Ford-Walford plot for the growth equation of shell-length of *G. tumidum.*

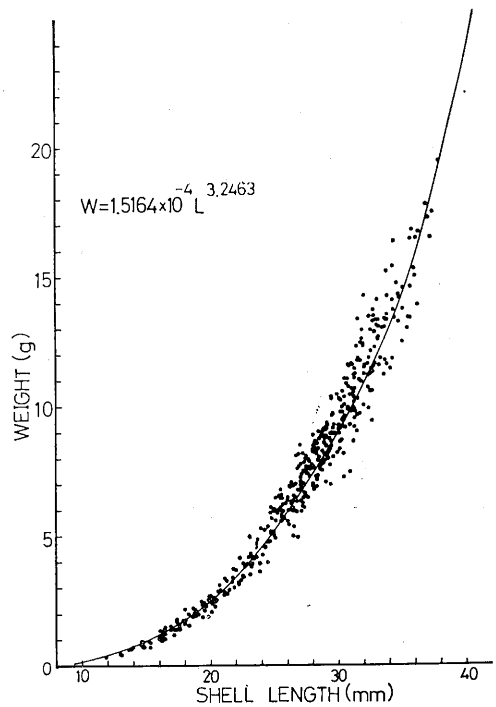

Fig. 5. The regression relationship between length and weight of *G. tumidum.*

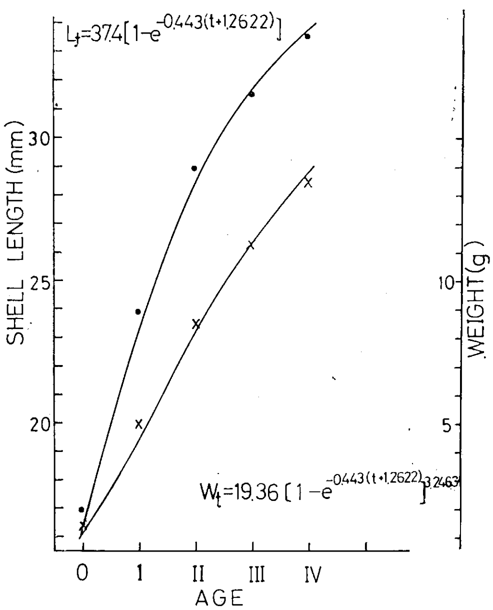

Fig. 6. Growth curves of shell-length and weight of *G. tumidum.*

Fig. 7. Except in May 1979, the age composition had a similar pattern during the period of investigation. By plotting $\ell_n N$ (numbers/m²) against age groups, excluding Group 0, the survival curve of *G. tumidum* was obtained (Fig. 8). This regressive line was fitted as:

$$\ell_n N = -0.03296\, t + 0.2173 \qquad (4)$$

where 0.03296 was the mortality coefficient related to a time interval, t, i. e. months. Therefore, the yearly mortality is obtained as 0.3955 ($=0.03296 \times 12$).

Biomass and production

Because a ring of shell was formed from February to May, each age group advanced to the next age group in May. Therefore, to calculate the production and elimination of Group 0 during 1979–1980, the density and mean weight of Group I in May, 1980 should be substituted for those of Group 0 in May, 1980. The same situation was taken into consideration for other age groups. The values of production, elimination, mean biomass, P:$\bar{B}$ and E:$\bar{B}$ are listed in Table 2. (The detailed calculations for each age group and the regressive line between total wet weight with shell and dry weight of flesh are shown in the Appendix).

Annually, *G. tumidum* had a mean biomass ($\bar{B}$) of 15.2556 g m^{-2} and produced 5.5689 g m^{-2} yr^{-1} (P). So the ratio of production to mean biomass (P:$\bar{B}$), also termed turnover rate, was 0.3650. The P:$\bar{B}$ ratio reached a maximum in the second age group, Group I, and then decreased gradually with age. That is to say, young animals had higher turnover rate than older ones. At the same time, *G. tumidum* eliminated 5.9204 g m^{-2} yr^{-1} with a elimination: mean biomass ratio (E:$\bar{B}$) of 0.3881. Except for both Group 0 and Group II's, that had negative elimination values, the population showed a trend of increasing E:$\bar{B}$ ratios with age.

Group I was the main producer and had the greater turnover rate, with a value of 1.3 to 2.5 times those of other age groups.

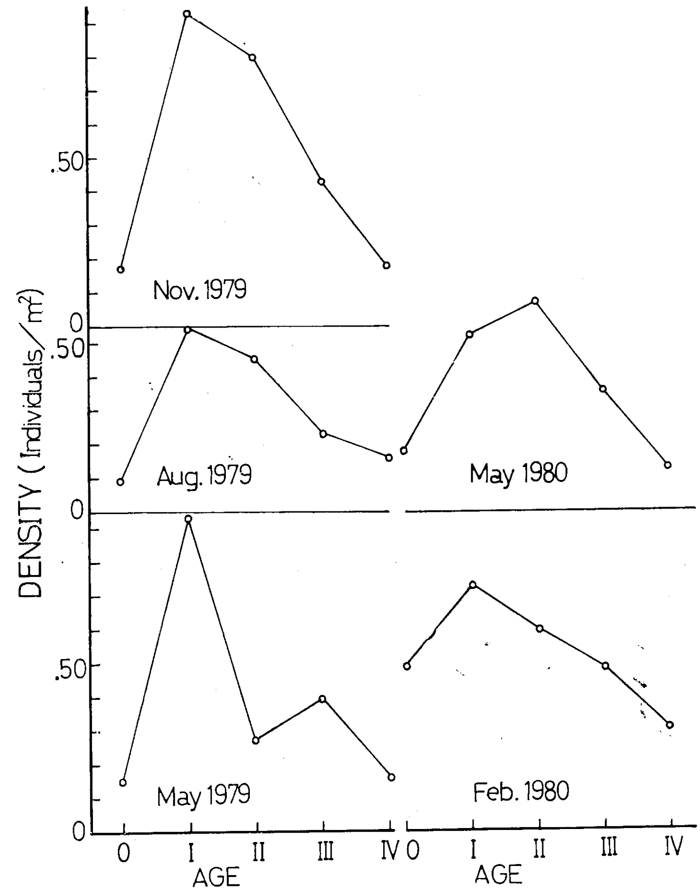

Fig. 7. The seasonal changes of population density in each age group of *G. tumidum*.

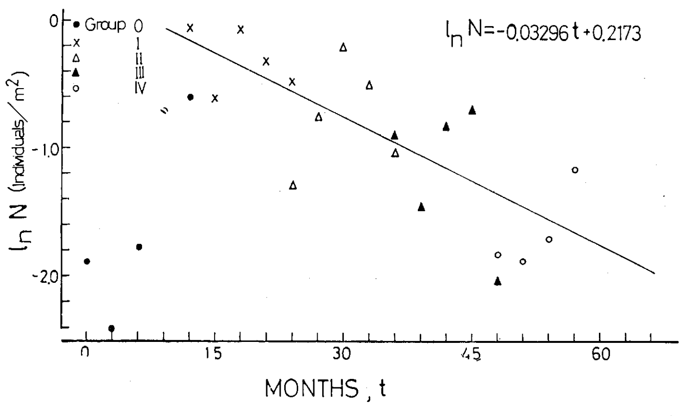

Fig. 8. The survival curve of *G. tumidum* (exclusive of Group 0) (follow Ansell, *et al.*, 1978).

TABLE 2.
Annual production (P), elimination (E), average biomass ($\bar{B}$) (as total wet weight with shell) and ratios between them, for *G. tumidum*.

Age group	P g m^{-2} yr^{-1}	$\bar{B}$ g $m^{-2}$$\pm$SE	E g m^{-2} yr^{-1}	P : $\bar{B}$	E : $\bar{B}$
0	0.2394	0.5022±0.4268	−0.6780	0.4767	−1.3500
I	2.5650	4.1283±1.2315	1.3470	0.6213	0.3263
II	1.2078	4.5746±2.0747	−0.2658	0.2640	−0.0581
III	1.0019	3.8050±1.6928	3.2593	0.2633	0.8566
IV	0.5548	2.2454±1.4105	2.2579	0.2471	1.0056
Total	5.5689	15.2556±3.2952*	5.9204	0.3650	0.3881

* Total SE$=\sqrt{\Sigma(SE_i)^2}$ where SE_i=standard error of the *i*th age group (follow Burke and Mann, 1974).

DISCUSSION

Only when the age of animals is known, can growth and production with time be estimated easily and adequately. The hard parts of animals, such as bivalves' shells with age marks are among the best materials for determining age[4]. For example, Thompson, *et al.*[9] tested the validity of the external and internal growth bands of the shells of *Artica islandica* and showed unequivocally that the rings formed periodically on or in the shell of bivalves can be used as a basis for estimating age.

The rings on the shells of *G. tumidum* in Penghu are adduced as growth marks and are related to cessation of growth in winter: this agree with other bivalves, such as *Scrobicularia plana*[6] and *Cerastoderma edule*[8]. Thompson, *et al.* found out that the growth mark appeared to coincide with spawning in *A. islandica.*[9] Further study, however, is need to related the growth mark of *G. tumidum* to spawning.

The growth pattern of *G. tumidum* shows two annual phases. A growing phase followed by retardation of growth (see Fig. 3). This kind of growth pattern is common among marine invertebrates, e. g. in the bivalves, *Venerupos japonica*[7], *Macoma balthica, Mya arenaria*[2], *Cerastoderma edule*[8], and the polychaete, *Nephtys hombergi*[10]. In *C. edule*, it was found that rapid growth was resumed only when spawning had been completed. Since the energy available to any population is generally limited in some way, there sometimes exists a strategy to utilize energy separately for reproduction and growth.

For estimating production, a reliable determination of population density is necessary. Local fishermen regularly collected *G. tumidum*, and its density varies with tidal level[3]. Consequently, the fluctuations of densities found in this study caused a negative elimination value in Group 0 and II. Nevertheless, the estimated production could still be obtained.

For *G. tumidum*, the P:$\bar{B}$ ratios for all age groups showed a trend decreasing with age, except for Group 0 in which it was smaller. A similar trend also has been found in other bivalves, such as *Cerastoderm edule*, *Mercenaria mercenaria* and *Venerupia aurea*[5]. The phenomenon has been reviewed by Ansell, *et al.*,[1] who concluded that the ratio P:$\bar{B}$ "takes high values for young animals of a species and increasingly smaller values for older animals". Also, Warwick and Price[10] found that in the polychaete *Ampharete acutifrons*, production is greater when growth is fast. In *G. tumidum*, the growth rate is faster in younger groups than old ones (see Fig. 6); therefore, faster growth may be one of factors resulting in higher ratios of P:$\bar{B}$ in younger groups.

The available published data of P: $\bar{B}$ ratios, ranging from 10.29–0.2, for intertidal bivalves is cited in Table 3. The P:$\bar{B}$ ratio of *G.*

TABLE 3.
P:$\bar{B}$ ratios for various intertidal bivalves from published data.

Species	P : $\bar{B}$	Life span	Habitat	Source
Indian tropical				
Donax incarnatus	5.88	1.5-2	exposed sandy beach	Ansell *et al.*, 1978
Donax spiculum	10.29	0.5-0.7	exposed sandy beach	Ansell *et al.*, 1978
Caribbean tropical				
Donax denticulatus	0.47	2	sandy beach	Cited by Ansell *et al.*, 1978
Heterodonax bimaculatus	0.28	2	sandy beach	Cited by Ansell *et al.*, 1978
Subtropical				
Gafrarium tumidum	0.36	9+	sandy flat	This study
Atlantic temperate				
Cerastoderma edule	1.1-2.6	5+	mud-flat	Hibbert, 1976
Mercenaria mercenaria	0.2-0.5	9+	mud-flat	Hibbert, 1976
Macoma balthica	1.53	3	sandy flat	Burke and Mann, 1974
Macoma balthica	0.9	6+	mud-flat	Warwick and Price, 1975
Mya arenaria	2.54	3	sandy flat	Burke and Mann, 1974
Mya arenaria	0.5	8	mud-flat	Warwick and Price, 1975

tumidum for Penghu is 0.36, which lies in the lower range when compared with those of bivalves living in Indian tropics, Carribean tropics and even temperate Atlantic beaches. The relationship between the ratio P:$\bar{B}$, longevity and the temperature have been generalized by Ansell *et al.*,[1] who showed that tropical bivalves having a higher metabolic rate at their normal environmental temperature exhibit a faster growth rate, shorter life span and a great turnover of biomass. Waters[11] has pointed out that freshwater benthic insects with a longer life history tend to have a smaller annual P:$\bar{B}$ ratio. Penghu is subtropical, it is crossed by the tropic of Cancer, and the environmental temperature experienced by *G. tumidum* is lower than most tropical intertidal bivalves. Therefore, it is reasonable to find that *G. tumidum* should possess a small turnover rate per unit biomass.

Ansell *et al.*[1] have pointed out that over the whole life span of a single cohort, production and elimination are identical, and P>E for the earlier part of life span, E>P for the latter part of the life span; but when cohorts are present in different proportions, the values of P and E are different. In the entire population of *G. tumidum*, P>E in the younger stages, E>P in the old ones, and both annual production and elimination also showed nearly equal values (see Table 2). However, elimination was slightly greater than production, which meant there was a net decrease in biomass. This situation leads us to suppose that the population of *G. tumidum* in Penghu may be suffering from overfishing.

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APPENDIX 1

The mean density in age-group (N, numbers/m^2), mean weight per individual (W, g), weight increment since previous sample (ΔW, g), average mean density during period ($\overline{N}$), production increment ($P=\Delta W\times\overline{N}$, g m^{-2} yr^{-1}), average mean weight during period ($\overline{W}$), decrease in population (ΔN), elimination ($M=\overline{W}\times\Delta N$, g m^{-2} yr^{-1}) and biomass ($B=N\times W$, g/m^2) for *G. tumidum*.

Sampling date	Age group	N	W	ΔW	$\overline{N}$	P	$\overline{W}$	ΔN	M	B
May, 1979	0	0.15	1.110	—	—	—	—	—	—	0.1665
Aug.		0.09	1.680	0.570	0.120	0.0684	1.395	0.06	0.0837	0.1512
Nov.		0.17	1.659	−0.021	0.130	−0.0027	1.670	−0.08	−0.1336	0.2820
Feb. 1980		0.49	1.689	0.030	0.330	0.0099	1.674	−0.32	−0.5357	0.8276
May	I	0.54	2.007	0.318	0.515	0.1638	1.848	−0.05	−0.0924	1.0838
						Σ0.2394			Σ−0.6780	
May, 1979	I	0.93	3.164	—	—	—	—	—	—	2.9425
Aug.		0.54	5.628	2.464	0.735	1.8110	4.396	0.39	1.7144	3.0391
Nov.		0.93	6.389	0.761	0.735	0.5593	6.008	−0.39	−2.3431	5.9418
Feb. 1980		0.73	6.243	−0.146	0.830	−0.1212	6.316	0.20	1.2632	4.5574
May	II	0.62	6.711	0.468	0.675	0.3159	6.477	0.11	0.7125	4.1608
						Σ2.5650			Σ1.3470	
May, 1979	II	0.27	8.073	—	—	—	—	—	—	2.1797
Aug.		0.46	8.411	0.338	0.365	0.1234	8.242	−0.19	−1.5660	3.8691
Nov.		0.80	9.497	1.086	0.630	0.6842	8.954	−0.34	−3.0444	7.5976
Feb. 1980		0.60	9.289	−0.208	0.700	−0.1456	9.393	0.20	1.8786	5.5734
May	III	0.35	10.438	1.149	0.475	0.5458	9.864	0.25	2.4660	3.6533
						Σ1.2078			Σ−0.2658	
May, 1979	III	0.40	9.730	—	—	—	—	—	—	3.8920
Aug.		0.23	11.849	2.119	0.315	0.6675	10.790	0.17	1.8343	2.7253
Nov.		0.43	11.279	−0.570	0.330	−0.1881	11.564	−0.20	−2.3128	4.8500
Feb. 1980		0.49	12.088	0.809	0.460	0.3721	11.684	−0.06	−0.7010	5.9231
May	IV	0.13	12.573	0.485	0.310	0.1504	12.330	0.36	4.4388	1.6345
						1.0019			3.2593	
May, 1979	IV	0.16	12.705	—	—	—	—	—	—	2.0328
Aug.		0.15	13.269	0.564	0.155	0.0874	12.987	0.01	0.1299	1.9904
Nov.		0.18	14.548	1.279	0.165	0.2110	13.908	−0.03	−0.4172	2.6186
Feb. 1980		0.31	13.727	−0.821	0.245	−0.2011	14.138	−0.13	−1.8379	4.2554
May		0.02	16.500	2.773	0.165	0.4575	15.114	0.29	4.3831	0.3300
						0.5548			2.2578	

Note: Weight was given as g wet weight with shell. The regressive line between total wet weight with shell and dry weight of flesh is expressed as the equation:

$$W_{(\text{dry weight of flesh})}=-0.0095+0.0177W_{(\text{total wet weight with shell})},\ r=0.98$$

APPENDIX 2
Mean biomass ($\bar{B}$) of *G. tumidum*.

Sampling data	Biomass Age group 0+I+II+III+IV
May, 1979	11.2135
Aug.	11.7751
Nov.	21.2900
Feb. 1980	21.1369
May	10.8624
mean biomass	15.2556

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澎湖講美潮間帶厚殼仔成長及生產量之研究

謝蕙蓮　陳章波　張崑雄

本研究自民國六十八年五月至六十九年五月，每三個月在澎湖講美潮間帶定量採集一次。共計採得厚殼仔 (*Gafrarium tumidum*) 479 個。經殼輪判讀發現二月至五月間成輪，殼輪卽爲年輪。年齡組成共計九個年齡羣，以 0, I, II, III, IV 五個年齡羣爲主。由 0～IV 各年齡羣的平均殼長，求出殼長成長方程式，又由殼長、體重之關係，求出體重成長方程式。成長有隨年齡增加而減慢的趨勢。

參照 Crisp, D. J. 1971 的方法，估算厚殼仔 0～IV 年齡羣的生產量，得年產量 5.57 g/m² (含殼濕重)，年減除量爲 5.92 g/m² (含殼濕重)，年平均生物量 ($\bar{B}$) 爲 15.26 g/m² (含殼濕重)。生產量與生物量的比值 (P : $\bar{B}$) 爲 0.36，減除量與生物量的比值 (E : $\bar{B}$) 爲 0.39。