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Energy Budget for a Japanese Common Scallop, *Patinopecten yessoensis* (Jay), in Mutsu Bay

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Abstract

An energy flow diagram for a scallop, *Patinopecten yessoensis* (Jay), at Moura along the southern coast of Mutsu Bay, Aomori Prefecture, was outlined from August 1970 to August 1971, using estimates of animal growth, observations on defaecation and respiration rates. The total ingested by one individual scallop was computed at 299.8 K-cal per year, 232.4 K-cal per year, and 104.0 K-cal per year in 3-, 2-, and 1-year-old animals, with 70–80% attributable to assimilation and 30–20% to egestion. The production, expressed as body growth and gonad growth, occurred for an energy flux of about 58.7 K-cal per year, 50.8 K-cal per year, and 41.2 K-cal per year in 3-, 2-, and 1-year-old scallops, respectively. Before maturity, most of the energy stored was used for the growth of the non-gonad tissue, while after the arrival to maturity the main part of the energy stored by the individual was utilized not for linear growth but for the development of the gonad. On the other hand, the amounts of energy lost in respiration and in the release of gametes were estimated as about 165.8 K-cal per year for 3-year-old scallops, 111.3 K-cal per year for 2-year-old, and 42.0 K-cal per year for 1-year-old ones. Growth efficiency decreased from about 50% in 1-year-old scallops to 33% in 2-year-old, and 29% in 3-year-old ones.

The biology of the scallop have shown a steady progress and many valuable references have been published, some of which are of much use to promote the advancement of the ecology of the scallop. A number of studies have been published on the distribution,[1-4] growth,[5-8] reproduction,[9-14] feeding,[15-17] and niche relationship of natural population.[18-20] No studies on the scallop, however, have yet been attempted to assess its energy flux and nutrient transfer through its body. In general, the basic functions of the organism, its growth, reproduction, development and so forth, all take place at the expense of the energy which enters the organism in the form of its food. Consequently, to assess the energy budget is one of the important problems in understanding an organism ecology. This study is an attempt to analyse the biological production of the scallop, *Patinopecten yessoensis* (Jay), with the intention of providing some useful knowledge in the ecological field of the scallop biology.

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Materials and Methods

In this study, the 1-, 2-, and 3-year-old animals were collected by means of dragging from Kawauchi, along the northern coast of Mutsu Bay. At the beginning of the experiment, they were grouped into three age categories, and eighteen experimental groups of ten animals each were placed in net cages (40×40 cm in dimension) which were set at a depth of 3 m in the cove of Moura.

Growth during the period of observation could be based only by knowing the size of the experimental scallops at the beginning of the observation. Sample scallops, therefore, were selected to represent each group of the experimental scallops. The sample scallops were approximately the same size as the experimental scallops. They were collected at the same time and were treated in exactly the same way as the experimental scallops, and the shell height was periodically measured during the course of the present observation. Eight to sixteen of the experimental scallops were bimonthly picked up from each group, and their shell height was measured. After this procedure, shell (consisting of test proper and ligament), adductor muscle, digestive diverticula, mantle and gill, and gonad were removed separately. The tissues removed from the body were placed in a drying oven at 60°C, until constant weight was achieved. After drying, the weight was measured. The dry substances were minced by means of a ball mill, and they were stored in a desiccator for the measurement of the calorific value.

The seasonal aspects of biodeposition were bimonthly investigated during August 1970 and August 1971. For collecting the biodeposits, a 60 cm diameter plankton net (GG 54) was set at 10 cm below the bottom of the net cage. Biodeposits from each unit of ten scallops were removed from the net, and were combined into one sample. They were washed with distilled water to remove salts, dried at 60°C and weighed to the nearest 0.1 mg: results were expressed as total deposition in gr/day/individual. The seston settled out by gravity in a control net where ten scallop shells were substituted for living scallops was collected and treated the same as biodeposits. The weight of this seston (control sediment) was subtracted from the biodeposit weight.

Oxygen consumption by scallops of different sizes at various seasons was measured. The scallops were acclimated to each experimental condition for 24 hours, and experiments were run under a constant flow of sea water. It followed that the fluctuations in sea temperature were never more ±2°C any one day. The oxygen uptake of a submerged scallop was calculated by measuring the difference between the oxygen concentration of the incoming water and of the outflowed

water. The oxycalorific coefficient of 4.86 cal/ml–O_2 was used to convert oxygen consumption to the calorific equivalent. The calorific value of the scallop was measured in a Nenken YM-B type adiabatic oxygen bomb calorimeter, and the calorific measurement of the biodeposits was adopted the Karzinkin and Tarkovskaya modification[21] of the Wet combustion method.

Results

Growth rate: For the purpose of estimating the growth rate, the shell height of the experimental animals belonged to three different age-groups being bimonthly measured to the nearest 0.1 mm. A growth pattern in terms of shell height was shown for each age-group (Table 1). The most rapid growth in shell height occured in October until December, and it was less in February until April. From the slopes of the growth curves, it appears that the growth rate is more rapid in small members than in large ones.

The regression formulae showing the relation of dry weight of shell, adductor muscle, digestive diverticula, mantle and gill, and gonad to the shell height were calculated bimonthly. When plotted on logarithmic scales the relationship between shell height and each of body components is linearly (Table 2). From the regression formulae shown in Table 2, it is possible, without killing an animal, to compute an accurate estimate of dry weight of each body component from mean shell height of the sample scallops. Dry weight of body components of an individual belonging to various age-groups was enumerated in Table 3 according to various times of the year. The production amount of body components during a two-month period was computed as the difference between the dry weight of the tissues at the beginning and at the end of each two-months. The result is shown in Table 4.

The duration from December to April is the period of the most rapid shell production for the scallops older than two years, and the months of April through August are the co-ordinate for the young ones (1-year-old). The shell production decreases as the scallops grow larger, it ranges from 45 gr per year per individual

Table 1. *Seasonal increments in shell height (cm) of scallops.*

Months	Age groups		
	I	II	III
Aug.	5.06±0.66	9.63±0.46	11.55±0.56
Oct.	5.70±0.31	9.65±0.44	11.55±0.56
Dec.	6.58±0.42	9.83±0.44	11.63±0.52
Feb.	7.40±0.62	10.73±0.38	12.42±0.44
Apr.	7.62±0.65	11.10±0.39	12.64±0.46
June	8.02±0.38	11.14±0.41	12.68±0.40
Aug.	8.58±0.45	11.29±0.34	12.81±0.37

Table 2. *Regression formulae for computing dry weight of the*

Months	Shell weight—shell height relationship	Gonad weight—shell height relationship	Digestive shell height
Aug.	log W=3.0072 log S−1.1614	log G=2.9496 log S−3.7767	log D=
Oct.	log W=2.9970 log S−1.1414	log G=3.8331 log S−4.5771	log D=
Dec.	log W=3.1542 log S−1.3193	log G=4.1075 log S−4.5022	log D=
Feb.	log W=3.2110 log S−1.4035	log G=5.0367 log S−4.7440	log D=
Apr.	log W=2.8429 log S−0.9840	log G=4.5288 log S−4.6678	log D=
June	log W=2.9123 log S−1.0550	log G=3.2807 log S−3.7815	log D=
Aug.	log W=2.4737 log S−0.5724	log G=3.5474 log S−4.2155	log D=

Table 3. *Dry weight (gr) of each body component of scallops for successive two-month intervals.*

Age group	Month	Shell	Gonad	Digestive diverticula	Adductor muscle	Mantle & gill
I	Aug.	9	0.020	0.071	0.439	0.318
	Oct.	12	0.018	0.114	0.612	0.369
	Dec.	18	0.072	0.181	1.052	0.715
	Feb.	24	0.433	0.469	1.370	1.717
	Apr.	33	0.212	0.786	2.440	1.300
	June	43	0.173	0.797	3.525	1.565
	Aug.	61	0.148	0.807	4.628	1.895
II	Aug.	62	0.133	0.713	4.090	1.874
	Oct.	64	0.157	0.600	3.409	1.885
	Dec.	64	0.376	0.616	3.627	2.063
	Feb.	80	2.798	1.200	4.612	2.600
	Apr.	97	1.165	1.940	6.627	3.519
	June	102	0.450	1.813	8.654	3.752
	Aug.	107	0.330	1.418	8.508	3.289
III	Aug.	108	0.228	1.372	7.686	3.095
	Oct.	110	0.313	1.020	5.912	3.095
	Dec.	110	0.750	1.029	6.090	3.213
	Feb.	128	5.844	1.741	7.435	3.559
	Apr.	140	2.097	2.651	9.356	4.951
	June	147	0.688	2.609	12.883	5.548
	Aug.	147	0.517	1.941	11.937	4.470

for 1-year-old scallops to 39 gr per year per individual for 3-year-old ones. The production of non-gonad tissues, however, appears to increase with the increasing size, it is ranged from 5.98 gr per year per individual in 1-year-old scallops to 14.27 gr per year per individual in 3-year-old ones. The losses in gonad weight during February until April were associated with the spawning period which extends through these months and into June. As spawning takes place between April and May in Mutsu Bay,[9][10] the amount of decrease in the gonad weight from February to June (0.28, 2.35 and 5.15 gr per individual for 1-, 2-, and 3-year-old scallops) is considered to be approximately the weight of the released gametes.

body components (gr) from measurements of shell height (cm).

diverticula weight—relationship	Adductor muscle weight—shell height relationship	Mantle and gill weight—shell height relationship
3.5935 log S−3.6816	log A=3.4676 log S−2.7990	log M=2.7590 log S−2.4410
2.9523 log S−3.1286	log A=3.0551 log S−2.4751	log M=2.4754 log S−2.2662
3.0487 log S−3.2362	log A=3.0832 log S−2.5009	log M=2.6389 log S−2.3051
2.5321 log S−2.5296	log A=3.2661 log S−2.7021	log M=2.1468 log S−1.7975
2.4035 log S−2.2245	log A=2.6571 log S−1.9562	log M=2.6484 log S−2.2220
2.8129 log S−2.6865	log A=3.0760 log S−2.2831	log M=3.0234 log S−2.5910
2.4842 log S−2.4634	log A=2.6842 log S−1.8959	log M=2.4316 log S−2.0427

Table 4. *Amount of absolute growth during two-month periods.*

Age group	Time interval (day)	Amount of growth (g)				
		Shell	Gonad	Digestive diverticula	Adductor muscle	Mantle & gill
I	Aug.—Oct. (72)	3	−0.002	0.043	−0.173	0.051
	Oct.—Dec. (58)	6	0.054	0.067	0.440	0.346
	Dec.—Feb. (62)	6	0.361	0.288	0.318	0.456
	Feb.—Apr. (61)	9	−0.221	0.317	1.070	0.129
	Apr.—June (60)	5	−0.059	−0.067	0.709	0.090
	June—Aug. (62)	16	−0.028	−0.002	0.922	0.298
II	Aug.—Oct. (72)	2	0.024	−0.113	−0.681	0.011
	Oct.—Dec. (58)	0	0.219	0.016	0.218	0.178
	Dec.—Feb. (62)	16	2.422	0.584	0.985	0.537
	Feb.—Apr. (61)	17	−1.633	0.740	2.015	0.919
	Apr.—June (60)	5	−0.715	−0.127	2.027	0.233
	June—Aug. (62)	5	−0.120	−0.395	−0.146	−0.463
III	Aug.—Oct. (72)	2	0.085	−0.352	−1.774	0.000
	Oct.—Dec. (58)	0	0.437	0.009	0.178	0.118
	Dec.—Feb. (62)	18	5.094	0.712	1.345	0.346
	Feb.—Apr. (61)	12	−3.747	0.910	1.921	1.392
	Apr.—June (60)	7	−1.409	−0.042	3.527	0.597
	June—Aug. (62)	0	−0.171	−0.668	−0.946	−1.078

Oxygen metabolism: Successive 3-hour interval measurements of the oxygen consumption rate of the scallops were made throughout a 24-hour period. Figure 1 shows no remarkable divergences among the results of oxygen consumption, which makes it difficult to determine the reality of diurnal trends. In the present study, therefore, the metabolic rate adopted the mean value of oxygen consumption rate over a 24-hour period. Figure 2 shows the oxygen consumption per hour per animal plotted against dry weight on logarithmic scales for different months. It is generally agreed that the logarithm of oxygen consumption, Q, is linearly related to the logarithm of an individual dry-flesh weight, W. The exponential equation is $Q=aW^b$, where a is a constant, and b is the regression coefficient of observation plotted logarithmically. Although the slopes of log Q
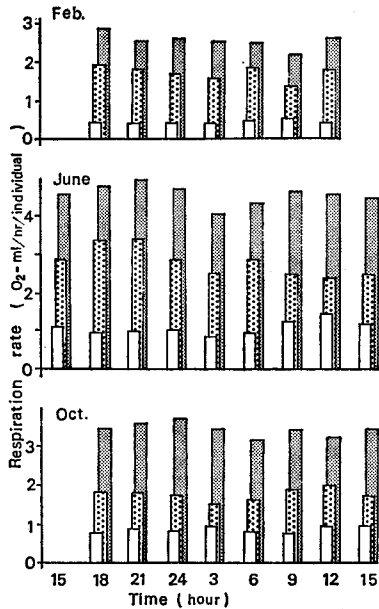
Fig. 1. Variations in oxygen consumption
for the scallops in relation to time
of day.
☐ : 1-year-old individual,
▦ : 2-year-old individual,
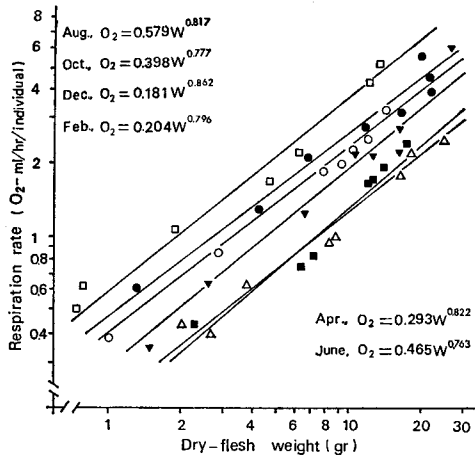▨ : 3-year-old individual.

Fig. 2. Oxygen consumption of scallops in a
continuous-flow procedure at several
months plotted against dry-flesh weight
on logarithmic scales.
☐ : Aug. (22.0–22.8°C),
○ : Oct. (14.3–15.2°C),
■ : Dec. (5.5–6.2°C),
△ : Feb. (4.2–5.0°C),
▼ : Apr. (8.6–9.2°C),
▽ : June (16.4–17.4°C).

versus log W regressions showed no significant difference with seasons, there were
clearly seasonal changes in the respiration rate over the whole range of animal
sizes. In comparison with October and April, for example, despite a 6°C difference
in temperature, there is no remarkable difference between the intercepts of the
two regression lines, while the June rate at 16.9°C was nearly two-thirds of the
August rate at 22.4°C. The parameters a and b of the general equation may be
seen to take various values depending on conditions of both scallops and their
environment on which a metabolic measurement is made.

As the mean dry-flesh weight in the different ages of the scallop is calculated
from the data shown in Table 2, the respiration rate which corresponds to mean
dry-flesh weight is possible to estimate from the above exponential equations.

Defaecation rate: *Patinopecten* feed on suspended matter, which they filter
by means of ciliary mechanisms on gills and labial pulps. Water currents created
by cilia on the gills enter the inhalant chamber, pass through slits in the gills and
proceed posteriorly as exhalant currents. Coarse particles fall out of the stream
to the mantle surface, and they are expelled as pseudofaeces through the exhalant
chamber. Fine particles become entangled in a mucus-sheet covering the gill

Table 5. *Calorific content of egesta voided by individual scallop during two-month periods.*

Time interval	1-year-old			2-year-old			3-year-old		
	Egesta (g)	Calorific value (K-cal/g)	Calorific content (K-cal)	Egesta (g)	Calorific value (K-cal/g)	Calorific content (K-cal)	Egesta (g)	Calorific value (K-cal/g)	Calorific content (K-cal)
Aug.—Oct.	3.53	0.43	1.52	18.63	0.57	10.62	22.69	0.60	13.61
Oct.—Dec.	3.89	0.41	1.59	16.47	0.50	8.23	19.63	0.51	10.01
Dec.—Feb.	7.06	0.50	3.53	32.20	0.44	14.17	34.53	0.45	15.54
Feb.—Apr.	10.06	0.58	5.83	48.72	0.58	28.25	46.49	0.57	26.50
Apr.—June	10.06	0.51	5.13	24.50	0.58	14.21	29.24	0.63	18.42
June—Aug.	8.92	0.49	4.37	10.54	0.48	5.06	21.33	0.63	13.44

surface. The filtered particles are then carried to food grooves at the bases and free margins of the gills and thence towards the mouth. In the present study, it should be noted that the terms of food ingested means the suspended matters taken by the inhalant stream, and that the egesta consists of true-faeces and of pseudofaeces.

The amounts of egesta always greatly exceeded the amount of solids by gravity (control sediments). The amounts of egesta voided during each two-months were computed by averaging the amounts at the beginning and the end of each two-months. The calorific value of the egesta was analyzed for their calorific content using a wet oxidation procedure, and the average calorific value for each two-month period, given in Table 5, was used together with the data on the average defaecation rate to calculate the energy loss for one individual via the egesta for each two-months. The egesta for one individual scallop during a two-month period was characterized by abrupt changes, and nearly all differences were significant.

Energy flux: The energy consumed as food equals to the sum of energy ejected as egesta, energy used for the formation of new tissue, and energy used for muscular works and maintenance which are lost to the surroundings as heat. The first two of these items were open to direct measurement, and the third, metabolic loss, could be estimated indirectly by a respirometory. The bimonthly values for the calorific content of each body components (Table 6) were possible to provide the calorific content of the same for every two-month period. Moreover, the energy lost by metabolic activities for each two-month period was easily estimated from the indirect method of converting respiration rate into heat output by the application of an oxycalorific coefficient (Table 7). The rates of energy flow through an individual scallop, from Tables 4, 5, 6 and 7, may now be calculated in terms of calorific unit. The results are illustrated in Figure 3.

These data suggest that there are some variations in the amount of energy

Table 6. *Calorific value (K-cal/gr) of the body components estimated at different times of the year.*

Age group	Month	Gonad	Digestive diverticula	Adductor muscle	Mantle and gill	Shell
I	Aug.	3.84	6.05	4.52	4.34	0.50
	Oct.	3.94	4.85	4.53	4.21	0.46
	Dec.	3.97	4.72	4.50	3.97	0.41
	Feb.	4.57	4.74	4.55	4.02	0.37
	Apr.	4.36	5.31	4.54	4.00	0.34
	June	3.92	5.74	4.44	3.69	0.33
	Aug.	3.90	6.07	4.48	4.08	0.30
II	Aug.	3.98	6.02	4.54	4.25	0.28
	Oct.	4.05	4.86	4.56	4.16	0.28
	Dec.	4.27	4.31	4.47	3.98	0.28
	Feb.	4.73	4.60	4.55	4.02	0.25
	Apr.	4.28	5.01	4.46	3.87	0.24
	June	3.85	5.90	4.43	3.93	0.24
	Aug.	3.87	6.04	4.57	4.09	0.23
III	Aug.	3.94	6.00	4.53	4.21	0.23
	Oct.	4.14	4.96	4.64	4.06	0.23
	Dec.	4.19	5.07	4.55	4.12	0.23
	Feb.	4.71	4.33	4.44	4.02	0.21
	Apr.	4.51	5.16	4.55	3.93	0.20
	June	3.86	5.82	4.35	3.87	0.20
	Aug.	3.87	5.02	4.57	4.07	0.20

Table 7. *Amount of energy lost in respiration during two-month periods.*

Time interval	1-year-old		2-year-old		3-year-old	
	Respiration rate (ml/day/individual)	Metabolic loss (K-cal)	Respiration rate (ml/day/individual)	Metabolic loss (K-cal)	Respiration rate (ml/day/individual)	Metabolic loss (K-cal)
Aug.—Oct. (72)	11.2	3.94	53.0	18.56	83.6	29.25
Oct.—Dec. (58)	9.2	2.58	30.5	8.60	46.6	13.13
Dec.—Feb. (62)	10.5	3.17	27.9	8.41	42.3	12.75
Feb.—Apr. (61)	19.2	5.68	46.2	13.69	64.7	19.19
Apr.—June (60)	32.9	9.58	72.7	21.21	98.1	28.61
June—Aug. (62)	52.7	15.88	101.7	30.65	135.0	40.68

ingested and in the amount of energy accumulated for the formation of the shell and active tissues, and that they are closely related. The vigorous gonad growth in winter months is followed by a peak of the formation of non-gonad tissue in the seasons covering winter to spring. Since the metabolic loss shows high value during the months of summer, it may be assumed that the energy used for the formation of new tissues is inferior to that in the other seasons. Although the 2-year-old scallops differ in the amount of energy used for the formation of new tissues from 3-year-old ones, the seasonal rhythmicity in the accumulation of

energy tends toward similarity.

Figure 4 indicates schematically the rate of energy flow and the successive transference of the energy through an individual scallop body. A certain amount of energy (about 20–30%) is voided as egesta, while most of the rest is assimilated. During the course of the present observation, about 50% (1-year-old scallops) to 70% (3-year-old scallops) of assimilated energy is lost to the surroundings as heat. The efficiency of growth is expressed as the percentage of energy assimilated gone into new tissues; it is called the net growth efficiency. This efficiency ranged from 50% in 1-year-old scallops to 29% in 3-year-old ones. The rate of energy used for the development of gonad tissue to the energy assimilated increases markedly with increasing age. This ratio is about 2% in 1-year-old scallops, 7% in 2-year-old, and 12% in 3-year-old ones. The energy utilized
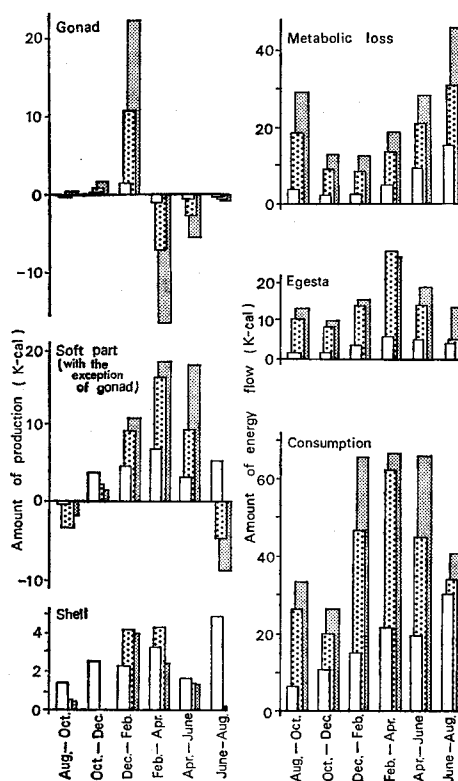

Fig. 3. Components of energy flow for the scallops in relation to time. All symbols are the same as those in Figure 1.
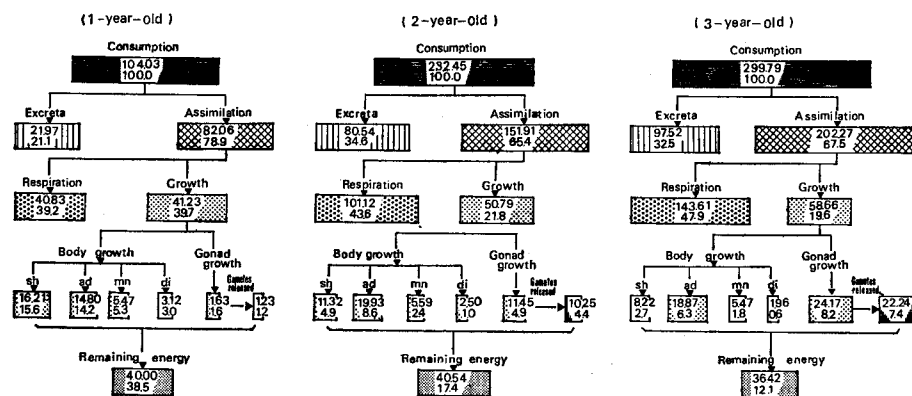

Fig. 4. Scheme showing the rate of energy flow for an individual scallop throughout a year. In each column the figure of top side indicates the amount of calorific content(K-cal/yr/individual), and that of bottom side shows the rate of energy flux (%). sh: Shell, ad: Adductor muscle, mn: Mantle and gill, di: Digestive diverticula.

for shell production, however, decreases with increasing age. Since the energy lost
for gametes liberation has ranged from 1% to 7% of the energy consumed, the
total remaining amount of energy decreases from about 38% of the total consump-
tion in 1-year-old scallops to 17% in 2-year-old, and to 12% in 3-year-old ones.

Discussion

The details of growth profile of the scallop, *Patinopecten yessoensis*, has been
published by several researchers. According to Maru and Obara's recent work[7]
dealing with the growth rate of young and adult scallops in Saroma, Hokkaido,
the adult individual (more than 2 years old) grew vigorously in both spring and
autumn alternating with a stoppage of the shell growth in the rest seasons, where-
as the young scallops (1 year old) elongate steadily through the entire year.
Takahashi and Mori[8] reported that the shell growth of 2-year-old scallops cultivat-
ed in Onagawa Bay, Miyagi Prefecture, was very slow or had stopped in both
seasons of autumn (mid-August to mid-December) and spring (mid-April to mid-
June). Combining the above information, it was pointed out that the months
when the growth ceased almost completely fell within the purview of their pre-
and full-spawning seasons, and that the months when a vigorous shell growth took
place corresponded to the months after the completion of their spawning. In the
present study, the growth profile of the experimental scallops was in agreement
with the above relationship between the shell growth and the gonad growth. The
entire system of our field cages is subject to most of the important environments,
and the production potential of scallops placed in our field cages can be assumed
to reflect that under natural conditions.

Persistence of rhythmicity in oxygen uptake in molluscs under laboratory
conditions was further reported by Gompel[22] and by Sandeen *et al.*[23] However,
van Dam[24] reported that no prolonged interruption of the oxygen uptake of the
deep sea scallop and the bay scallop appeared to be quite uniform. In the present
study, the figures indicate that the oxygen uptake by the Japanese common
scallop are essentially the same as those by the deep sea scallop and the bay
scallop.

The oxygen consumption is a power function (b) of the body weight,[25] and
the biological significance of the value b has been discussed by various authors.[26-28]
Hemmingsen,[34] in a very extensive survey of the literature, found that the b
value of 0.75 could be applied to unicellular organisms, plants, poikilothermal
and homoiothermal animals. For bivalves, Kennedy and Mihursky[29] have
recently summarized values of b recorded in the literatures which range from 0.31
to 0.95, and these authors have recorded the values of b for *Mya arenaria*, *Macoma
balthica* and *Mulinia lateralis* ranging from 0.235 to 0.854. Ansell[30] reported
that a common regression coefficient (b) of 0.865 for *Donax vittatus* could be used

for the regression of oxygen consumption on weight. In the present study, the data from 4.2 to 22.8°C were pooled to give a joint slope of 0.844 which was not significantly different (u (0.05)=1.96>u_0=1.78) from a general value of 0.75 for poikilotherms as suggested by Hemmingsen.[28]

In general, the quantitative assessment of an animal individual is represented by the following relation[31]:

Consumption = Production + Respiration + Egesta + Excreta   where,

Production = Body growth + Gonad growth   In the above equation, (Consumption–Egesta) corresponds to the part of food that is observed into the body through the wall of the alimentary canal. (Consumption–Egesta–Excreta) is the proportion of ingested energy which is assimilated by the animal. Ammonotelic animals, such as bivalves, eliminate ammonia as the major end-product of protein catabolism. This energy loss via nitrogenous excretion and other exudates is assumed to be negligible. So, assimilation and absorption become synonymous in the present paper. In many cases, it has been impossible to estimate every item, especially ingestion, in the above production equation for a single animal species, thus depriving the studies from internal checks on their accuracy.[32-34] The amount of food ingested in our study was estimated by the sum of the items on the right side of the above equation. Although the excreta is usually thought to be negligible, Johannes and Satomi[35] and Hargrane[36] suggested that the imbalance of energy budgets of several benthic filter feeders and detritus feeders have been strongly contributed by this item. Consequently, the value for consumption estimated from the above procedure may be expected to be less than the true value.

As shown in Figure 3, the energy consumed, the energy accumulated as gonad growth, and the energy build up to non-gonad tissues change with the seasons. Before maturity, most of the stored energy is utilized for the growth of non-gonad tissues, while after the arrival to maturity the main part of the energy stored by the scallop is used not for linear growth but for the development of the gonad. The efficiency in converting ingested food into tissue components over the entire period of study was higher for 1-year-old individuals than for either 2- or 3-year-old ones (39.7, 21.8 and 19.6%, respectively). The gross growth efficiencies of 69% for the young mussels, Mytilus edulis, (shell length: 21.0–23.1 mm) to 29% for the adult ones (shell length: 61.0–63.8 mm) were obtained by Jørgensen,[37] who estimated food consumption by converting reported values for oxygen uptake into equivalent weights of combustible organic matter. Similar trends on the growth efficiency for three species of opisthobranch molluscs were pointed out by Carefoot.[38] The growth efficiency for Patinopecten, like other species, decreases as the animals become larger. Thus, the profile of energy flow through the body for the entire life, from birth to death, differs markedly at different seasons, and

at different developmental stages of the scallop.

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