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SEASONAL VARIATIONS IN CONDITION, REPRODUCTIVE ACTIVITY, AND GROSS BIOCHEMICAL COMPOSITION OF TWO SPECIES OF ADULT CLAM REARED IN A COMMON HABITAT: *TAPES DECUSSATUS* L. (Jeffreys) AND *TAPES PHILIPPINARUM* (Adams & Reeve)

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Abstract: The condition, reproductive activity, and gross biochemical composition of an indigenous and an introduced adult clam population raised in a common habitat of the French Atlantic coast were examined over a 74-wk period. The indigenous species, *Tapes decussatus* L. (Jeffreys) and the introduced species, *T. philippinarum* (Adams & Reeve) were raised together on the south Finistère coast of Brittany. The gross biochemical composition of a standard animal of each population was significantly correlated with the population condition indices. During the winter, no reproductive activity was observed in either population, and the contribution of protein, glycogen, and lipids to the maintenance energy was calculated. Protein formed the main reserve, while lipids contributed as much as glycogen in *T. decussatus*, and twice as much in *T. philippinarum*. Although some species differences were noted in the mean levels of biochemical components, the overall seasonal variations were similar in both populations.

INTRODUCTION

Studies of the seasonal changes in the biochemical composition of marine bivalves have been relatively numerous (see, e.g., Ansell & Trevaillion, 1967; Giese, 1969; Ansell, 1972, 1974, 1975; Beukema & De Bruin, 1977; Shafee, 1978, 1981; Mann, 1979; review by Gabbott, 1983); no study to date, however, has compared the seasonal changes in biochemical composition of an indigenous and an introduced species raised in a common habitat. The present work is the first part of a detailed study of the seasonal evolution of the biochemical composition of two such populations: an indigenous French-Atlantic population of the clam *Tapes decussatus* L. (Jeffreys) and an introduced population of the related Indo-Pacific species *T. philippinarum* (Adams & Reeve).

Although much confusion persists concerning the exact taxonomic status of these two species, most authors agree that both belong to the same genus (for review, see Partridge, 1977). In conformity with the majority of the recent literature, especially that of Vilela (1950), Partridge (1977), and Bernard (1983), the two species will be considered to belong to the *Tapes* genus. The exact taxonomic names and authorities used are *Tapes decussatus* L. (Jeffreys, 1863) for the French Atlantic species, and *Tapes philippinarum* (Adams & Reeve, 1850) for the Indo-Pacific species.

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MATERIAL AND METHODS

SAMPLING SITE

The chosen sampling site was the Kermor commercial rearing pond located at Ile Tudy, in the Sud-Finistère region of Brittany. The limits of the two populations were marked using wooden stakes; a distance of ≈ 50 m separated the two populations, which were at equal depths (0.5 to 1 m, depending on the tides). Previous observations had shown a relative homogeneity of substratum granulometry (D. Moranga, unpubl. data). Temperature and salinity measurements were routinely performed each week.

ORIGIN OF THE TWO POPULATIONS

Wild *T. decussatus* were collected in the immediate vicinity of Kermor Pond in October 1978 and those animals of an estimated age of 2 yr were placed in the marked sampling site in the pond. *T. philippinarum* spat were purchased from the SATMAR hatchery in Barfleur, Normandy; the brood-stock originated from natural populations of the Seattle region of Washington State, U.S.A. The spat were transferred to the rearing pond in June 1977 and were ≈ 2 yr old at the beginning of this study (April 1979).

SAMPLING

Twenty to twenty-five individuals of each population were collected at random at ≈ 4-wk intervals beginning in April 1979 and ending in late August 1980. After each collection, the clams were rapidly transported to the laboratory and placed in 0.8-μm Millipore-filtered sea water at 10 °C for 48 h in order to purge their pseudofaeces and stomach contents. Almost no residue was observed in the aquaria at the end of this period, during which the water was changed every 12 h. The animals were then frozen and stored at -80 °C until analysed.

BIOMETRIC MEASUREMENTS

Fifteen randomly-selected individuals were carefully thawed in aluminum foil over crushed ice. The tissue and adductor muscles were separated from the shell and the mantle fluid carefully absorbed using a paper towel. The flesh weight was then recorded. The shells were rinsed with distilled water and placed in a desiccator over activated silica gel for 24 h before weighing.

Measurements of shell length, width, and height were made as recommended by Ohba (1959). Dry tissue weight (DW) and ash-free dry tissue weight (AFDW) were determined using the techniques outlined below.

The fifteen thawed individuals were transferred to a glass container surrounded by crushed ice and homogenized using an Ultra-Turrax tissue homogenizer. The use of pooled tissue for invertebrate biochemical analyses is recommended by Giese (1966) and Giese *et al.* (1967).

WATER

Three to five g of homogenized tissue were carefully weighed and vacuum-dried over freshly-activated silica gel at room temperature for 12 h. The dried tissue was then weighed to a constant weight in the presence of activated silica gel using a Mettler H54 precision balance. This technique was found to produce homogeneous dried tissue, in contrast to oven-drying, in which the lipids tend to separate and adhere to the container walls.

Preliminary tests showed that in comparison with a tissue oven-dried at 100 °C for 24 h, a 12-h vacuum desiccation removed almost 99% of the water present in the tissue. The remaining 1% may in fact represent other volatile products evaporated by the more severe oven-drying method (Ivell, 1983).

ASH

Three to five g of tissue homogenate were placed in a pre-weighed porcelain container and transferred to a muffle furnace at 100 °C. The furnace temperature was progressively raised to 550 °C (to prevent splashing) and the tissue kept at this final temperature for 24 h to ensure complete incineration of all organic matter while minimizing sodium and potassium losses (Grove *et al.*, 1961). All measurements were performed in duplicate, with a range of differences between paired values of only 2%.

FREE GLUCOSE AND GLYCOGEN

Preliminary studies showed that the enzymatic method of glucose and glycogen determination of Murat & Serfaty (1974) was superior to the anthrone, sulphuric acid or phenol-sulphuric acid techniques. This method was followed here with the added precaution of always keeping the tissue and buffer solution at or near 0 °C immediately before the free glucose determination. Preliminary trials demonstrated the effectiveness of this precaution in preventing the auto-glycolysis commonly detected in dead tissue, as reported by Giese (1967) and Heath & Barnes (1970).

Five determinations were made for each sample, and the coefficient of variation was calculated. For the glycogen values, the coefficient of variation did not exceed 5%, while those for the glucose values were extremely variable and often > 5%. This was probably due to the fact that the very low glucose levels were close to the sensitivity limit of the instrument used (Beckman Glucose Analyser).

TOTAL LIPIDS

A modified form of the gravimetric method of Folch *et al.* (1957) was used both to extract quantitatively and measure the total lipids. Three successive extractions using an Ultra-Turrax blender in the presence of 30 ml of chloroform: methanol (2 : 1) were performed on 5 to 10 g of tissue homogenate. As fatty acid analyses were later done on these lipids (to be published), every precaution was taken to minimize potential oxid-

ation of unsaturated acids. The solvents were independently de-oxygenated by bubbling with nitrogen immediately before the extraction. After transfer of the extracts, rinses, and 0.75% NaCl wash to a separating funnel, the air was purged with nitrogen and the solvent system left to separate overnight. The lipid-containing fraction was then collected, along with a chloroform rinse of the aqueous phase, and the solvents evaporated under reduced pressure at 50 °C using a rotary evaporator. Only the chloroform soluble material was then quantitatively collected and weighed after cooling in a desiccator under nitrogen. This purification was necessary due to the occasional presence of traces of non-chloroform-soluble material in the crude extracts.

Four extractions and determinations were made on each sample pool, and the coefficient of variation ranged from 0.3 to 4.8%.

PROTEINS

Nitrogen was determined using a Hewlett-Packard CHN analyser. Protein nitrogen was calculated using the factor 6.25, as recommended by Jones (1931) and Giese (1967). Determinations were performed in duplicate on the powdered dry tissue, with an excellent reliability both for the cystein standards and for the powdered tissue (maximum difference of 2% between replicates).

ENERGY CONVERSION FACTORS

The widely used and generally accepted factor of 4.1 kcal $\cdot g^{-1}$ (17.2 kJ $\cdot g^{-1}$) was chosen for the carbohydrate energy conversion (Paine, 1971; Ansell, 1972, 1974, 1975; Craig *et al.*, 1978). The corrected protein energy conversion factor of 4.3 kcal $\cdot g^{-1}$ (17.9 kJ $\cdot g^{-1}$) suggested by Beukema & De Bruin (1979) was adopted in the present study, as most bivalves are considered to be ammoniotelic (Bayne *et al.*, 1976; Florkin & Bricteux-Gregoire, 1972), including *T. philippinarum* (Mann & Glomb, 1978).

The lipid energy conversion factor has provoked some discussion recently, as the traditional factor of 9.45 kcal $\cdot g^{-1}$ (Paine, 1971) only applies to Soxhlet-extracted lipids, which often do not include most phospholipids. Calorimetric determinations of chloroform-methanol extracted lipids reveal that the factor is actually considerably lower, especially for bivalves (Beukema & De Bruin, 1979: 8.42 kcal $\cdot g^{-1}$). In view of this uncertainty, four calorimetric determinations were performed in duplicate on the lipid extracts of the tissue homogenate samples from January to July. Since the values showed little variation (from 7.74 to 8.18 kcal $\cdot g^{-1}$), it was decided to adopt the calculated mean value of 7.88 kcal $\cdot g^{-1}$ (33 kJ $\cdot g^{-1}$). This factor is in fact close to that obtained by Beukema & De Bruin (1979) for the bivalve *Macoma balthica*.

STANDARD ANIMAL

The mean dry shell weight of each population over the sampling period was chosen as the standard animal reference (*Tapes decussatus*: 7.354 g; *T. philippinarum*: 19.244 g).

For each sampling, log wet tissue wt against log dry shell wt regressions were determined, and the dry wt of a standard animal was calculated using the water content data from the biochemical analysis. The results of the biochemical analysis could then be expressed in mg per standard animal (absolute value).

Caulton & Bursell (1977) and Read & Caulton (1980) demonstrated that proportions of biochemical constituents vary with organism size; this difficulty was avoided in the present study by using a restricted size range for each species (Table I). Despite this restricted size range, all log wet tissue wt to log dry shell wt regressions were statistically significant ($P \leqslant 0.01$).

CONDITION INDEX

Two indices of condition were adopted in the present study. The first was the ratio of dry tissue wt: dry shell wt, previously used both for *T. decussatus* (Walne, 1976) and *T. philippinarum* (Mann & Glomb, 1978). The second was the more meaningful ratio of AFDW: dry shell wt (Walne & Mann, 1975). Mean monthly values for each sampling were calculated using the biometric data and the monthly water and ash determinations of the pooled tissue.

REPRODUCTIVE ACTIVITY

Two indicators of reproductive activity were used. The first was the temporal variation of the standard animal AFDW, which should normally reveal the onset of accumulation of organic matter for reproduction. The second index was the presence or absence of oocytes in the female gonad, which allows a precise determination of the duration and termination of spawning. At each sampling, four to eight individuals were set aside for microscopic examination of gonad contents.

STATISTICAL TREATMENT OF DATA

As no assumptions could be made concerning the normality of the distributions of the variables measured, only non-parametric statistics were employed in the present study. Spearman rank-correlation matrices were calculated for all absolute values of biochemical variables, and these matrices also included the dry weight condition index, the standard animal dry weight, temperature and salinity.

The Wilcoxon rank-sum test was used to test the difference between the two species in mean values for each biochemical variable over the sampling period. These tests were done assuming a theoretical pool of 1 kg of tissue homogenate for each species.

RESULTS

TEMPERATURE AND SALINITY

The results of the weekly temperature and salinity measures are shown in Fig. 1. A pronounced seasonal cycle is evident, with maxima in summer and minima in late

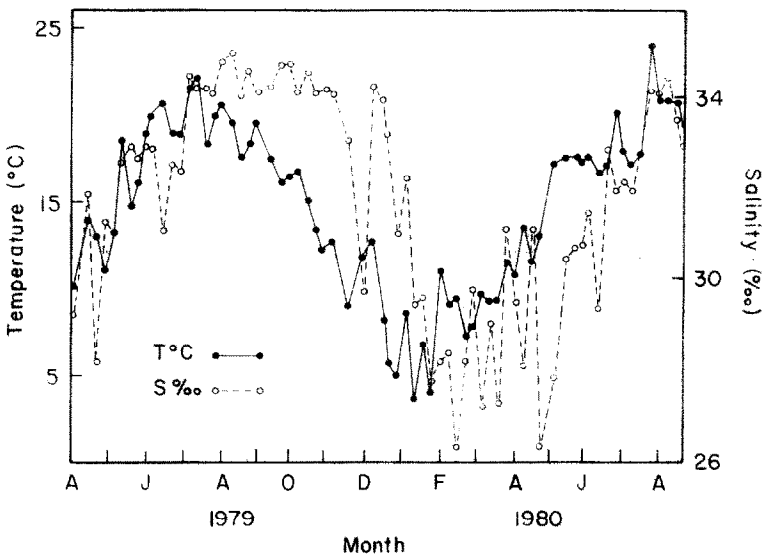

Fig. 1. Weekly variation of temperature and salinity in Kermor rearing pond, April 1979–August 1980.

winter. These cycles are probably due to the shallow depth of the rearing pond. As no temperature measurements were made at night, it was not possible to evaluate any diurnal temperature fluctuations.

GROWTH AND CONDITION INDEX

There was, on the whole, no flesh growth of *T. decussatus* during the sampling period, and very little, if any, shell growth (Table I). The shell and flesh growth of *T. philippinarum* appeared to level off after mid-August 1979, but at much higher values than for *T. decussatus*.

The two types of condition indices followed each other very closely in both populations (Fig. 2). The maxima were in mid-April to mid-June 1979 and mid-April 1980 for *T. decussatus* and in mid-May to mid-June 1979 and mid-April 1980 for *T. philippinarum*. In both cases, the 1980 maxima were much lower than the 1979 maxima.

TABLE I

Biometric measurements of the sampled individuals of the *T. decussatus* and *T. philippinarum* populations: FW, mean flesh weight (g); SW, mean dry shell weight (g); L, mean length (cm); W, mean width (cm); H, mean height (cm); s, ± SD.

Month	FW	s	SW	s	L	s	W	s	H	s
T. decussatus										
1979										
April	4.759	0.621	6.931	0.858	3.83	0.18	2.82	0.42	1.94	0.08
May	3.765	0.955	5.815	1.228	3.61	0.26	2.63	0.16	1.98	0.46
June	4.452	0.917	6.542	1.344	3.73	0.43	2.69	0.19	1.86	0.14
July	3.191	0.504	5.212	0.734	3.63	0.17	2.60	0.13	1.71	0.08
Aug.	4.354	0.855	8.078	1.146	3.96	0.25	2.88	0.16	1.98	0.11
Sept.	3.930	0.569	7.351	0.836	3.80	0.21	2.79	0.16	1.89	0.09
Oct.	3.902	0.575	7.666	0.835	3.91	0.18	2.83	0.12	1.95	0.11
Nov.	4.166	0.611	8.299	1.239	4.02	0.25	2.90	0.12	1.99	0.12
Dec.	3.536	0.562	7.007	1.007	3.82	0.15	2.75	0.13	1.93	0.14
1980										
Jan.	3.194	0.786	5.950	1.783	3.75	0.21	2.68	0.15	1.86	0.15
Feb.	2.925	0.783	6.376	1.589	3.70	0.23	2.67	0.13	1.80	0.14
March	3.668	0.739	7.414	1.165	3.85	0.29	2.77	0.16	1.94	0.21
April	4.539	0.943	8.807	1.544	4.11	0.21	2.89	0.24	2.16	0.50
May	3.849	0.822	8.070	1.057	3.96	0.23	2.85	0.13	1.99	0.13
June	3.474	0.556	8.329	0.943	4.01	0.23	2.88	0.17	1.99	0.7
July	3.630	0.740	8.726	1.839	4.06	0.25	2.92	0.14	2.05	0.11
Aug.	3.865	0.667	8.437	1.227	3.99	0.22	2.98	0.51	2.03	0.10
T. philippinarum										
1979										
April	5.549	0.987	8.437	1.397	3.90	0.22	3.00	0.38	2.02	0.14
May	8.491	1.000	11.594	1.255	4.45	0.21	3.29	0.10	2.28	0.10
June	9.205	1.114	12.071	1.436	4.56	0.24	3.26	0.29	2.35	0.10
July	11.520	2.812	17.377	4.233	5.17	0.43	3.77	0.40	2.62	0.25
Aug.	11.461	2.279	19.223	2.848	5.22	0.26	3.84	0.22	2.74	0.13
Sept.	10.932	1.988	20.794	3.391	5.43	0.35	3.98	0.23	2.76	0.15
Oct.	8.987	1.583	21.066	4.177	5.13	0.34	3.89	0.23	2.80	0.17
Nov.	9.021	2.133	21.186	2.719	5.38	0.26	3.92	0.23	2.78	0.18
Dec.	9.330	1.666	23.717	3.854	5.50	0.47	4.02	0.17	2.91	0.15
1980										
Jan.	7.987	1.843	20.193	3.911	5.19	0.40	3.82	0.27	2.74	0.20
Feb.	9.549	1.592	21.290	3.291	5.35	0.33	3.90	0.21	2.82	0.18
March	9.534	1.317	21.782	3.190	5.58	0.25	3.98	0.18	2.81	0.12
April	11.077	1.670	20.527	6.186	5.44	0.28	3.93	0.17	2.90	0.15
May	8.777	1.386	18.865	3.546	5.19	0.36	3.80	0.23	2.68	0.17
June	10.264	1.724	24.458	3.332	5.38	0.28	4.07	0.18	2.93	0.14
July	9.957	2.669	22.972	2.982	5.56	0.35	4.00	0.20	2.84	0.14
Aug.	8.502	1.485	21.592	3.109	5.34	0.28	3.90	0.19	2.77	0.23

REPRODUCTIVE ACTIVITY

The results of the two measures of reproductive activity are shown in Fig. 2. In both populations, the standard animal AFDW present roughly the same type of variation as

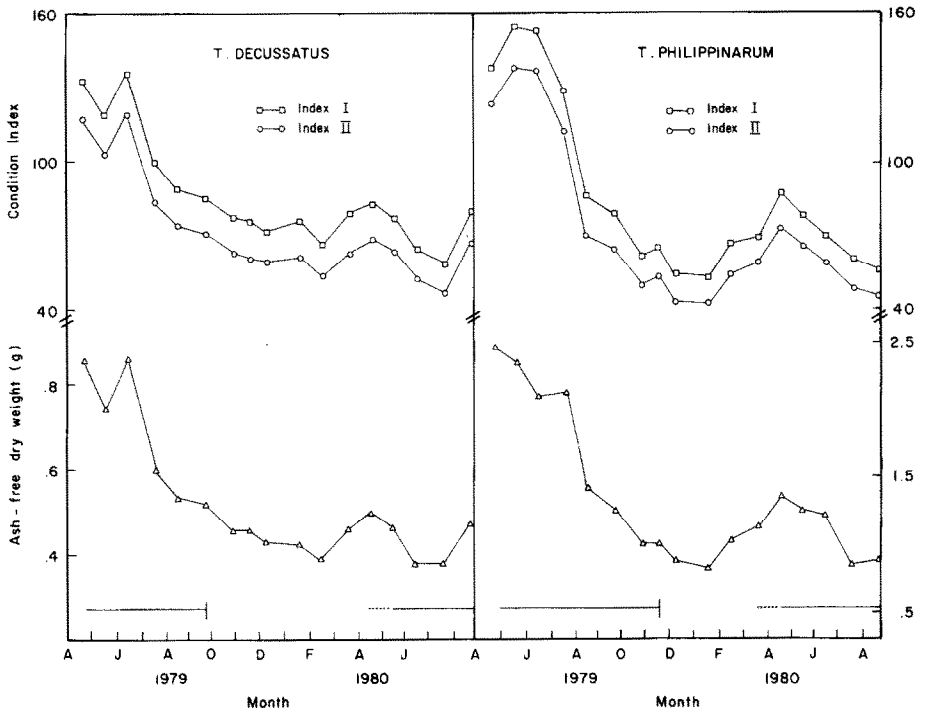

Fig. 2. Condition and reproductive activity in the two populations studied: □, monthly variation of the two condition indices calculated for *T. decussatus* and *T. philippinarum* (for explanation, see p. 23); ○, indices of reproductive activity in the two populations; △, ash-free dry weight of a standard animal; ——, presence of mature oocytes; · · · · ·, presence of immature oocytes.

the mean monthly condition indices. No oocytes were observed in *T. decussatus* after mid-September 1979, and developing gametes were again observed beginning in April 1980, with mature oocytes present up to the end of the sampling period (mid-August 1980). In *T. philippinarum*, mature oocytes persisted until mid-November 1979. Immature oocytes appeared relatively early in mid-March 1980, with mature oocytes present from April to the end of the sampling period in mid-August 1980. In both populations, the oocytes present in the final month of the 1979 spawning period appeared to be undergoing resorption.

GROSS BIOCHEMICAL COMPOSITION

The results of the gross biochemical analysis are presented in Table II and illustrated in Fig. 3. The absolute values of Fig. 3 generally follow those of the standard animal

AFDW for each population (Fig. 2). The significance of the variation of each component relative to the others and to the reproductive cycle is discussed below.

TABLE II

Gross biochemical composition of *Tapes decussatus* (*Td*) and *Tapes philippinarum* (*Tp*): values expressed as per cent wet weight.

	Protein		Free glucose		Glycogen		Lipid		Ash		Water	
Month	*Td*	*Tp*	*Td*	*Tp*	*Td*	*Tp*	*Td*	*Tp*	*Td*	*Tp*	*Td*	*Tp*
1979												
April	10.1	11.4	0.28	0.30	3.78	4.64	1.18	1.34	2.33	2.30	80.7	79.1
May	10.4	11.9	0.18	0.30	2.52	4.59	1.25	1.42	2.45	2.25	81.7	78.9
June	10.9	10.5	0.16	0.25	2.78	4.25	1.61	1.33	2.41	2.23	80.5	80.0
July	10.4	12.0	0.10	0.20	1.16	2.40	1.03	1.30	2.68	2.48	83.7	80.7
Aug.	9.7	8.9	0.04	0.13	0.96	1.53	1.12	0.98	2.71	2.75	83.6	84.9
Sept.	9.2	9.3	0.07	0.08	0.13	1.27	1.07	0.95	2.72	2.73	84.0	85.0
Oct.	8.4	8.4	0.24	0.10	1.00	1.19	1.05	1.08	2.80	2.78	84.9	85.3
Nov.	8.8	10.2	0.08	0.10	1.20	1.27	1.05	1.05	2.82	2.73	85.0	84.7
Dec.	8.5	7.7	0.13	0.09	0.77	1.55	0.99	0.92	2.80	2.79	85.4	86.2
1980												
Jan.	7.7	8.5	0.07	0.14	0.88	1.00	0.89	0.80	2.69	2.74	86.0	86.5
Feb.	8.5	8.4	0.05	0.09	0.69	1.53	0.94	0.93	2.76	2.75	85.6	85.1
March	9.0	9.5	0.22	0.26	1.16	1.60	1.04	0.90	3.11	3.04	84.1	84.2
April	9.6	9.2	0.21	0.42	1.29	2.35	1.05	1.02	2.75	2.59	84.1	83.8
May	9.5	10.0	0.14	0.28	1.07	1.96	1.17	1.13	2.76	2.67	83.9	83.2
June	9.9	10.2	0.08	0.19	0.60	1.51	1.20	1.26	2.75	2.57	84.7	83.3
July	8.7	8.8	0.04	0.07	0.40	0.72	1.15	1.05	2.70	2.76	86.1	86.0
Aug.	10.0	8.5	0.19	0.13	1.66	0.62	1.27	1.14	2.69	2.68	82.7	85.7

Spearman correlation matrices (Table III) show a direct relationship between the absolute values of all biochemical components and both the mean condition index and the standard animal dry weight. Similarly, with the exception of the glucose-lipid pair in *T. decussatus*, the absolute values of all biochemical components are significantly correlated. It should be noted that none of the biochemical variables was significantly correlated with environmental salinity, and with the exception of a weak correlation in the case of the *T. decussatus* lipids, none of the biochemical variables was significantly correlated with environmental temperature over the sampling period.

The Wilcoxon rank-sum test for the significance of the difference in mean values for each biochemical component of homogenized tissue over the sampling interval revealed significant differences for two of these: glycogen (*T. decussatus* mean = 13.0, *T. philippinarum* mean = 20.0; $P < 0.001$) and ash (*T. decussatus* mean = 27.0, *T. philippinarum* mean = 26.3, $P \leqslant 0.01$).

The variation of the total energy content and of the lipid and glycogen energy content over the sampling period are shown in Fig. 4. It should be noted that the lipid energy

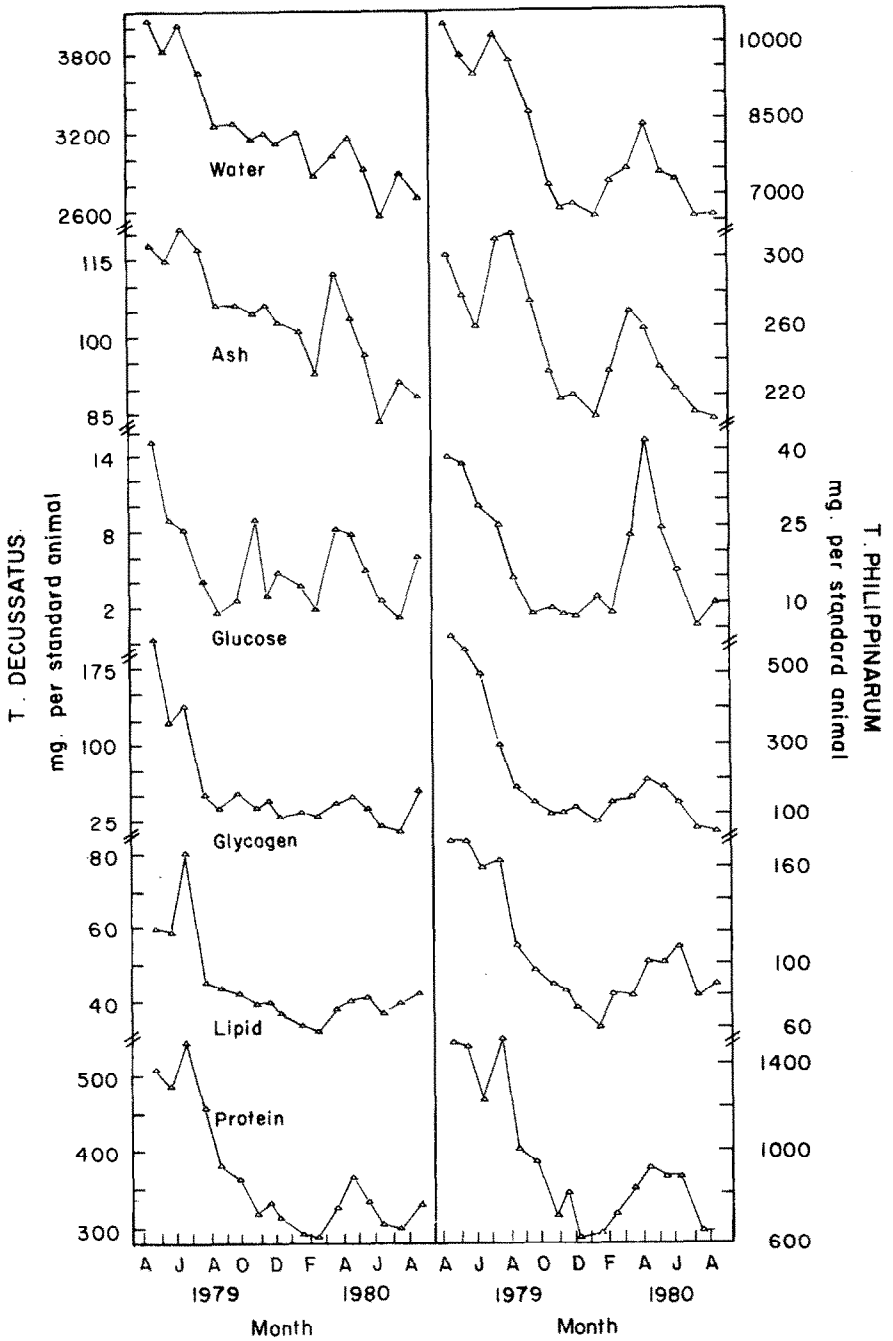

Fig. 3. Monthly variation of the gross biochemical composition of a standard animal of *T. decussatus* and *T. philippinarum*.

TABLE III

Spearman rank-correlation coefficient matrix for gross composition, condition index, standard animal dry weight, temperature and salinity: NS, $P > 0.05$; * $0.05 < P < 0.01$; ** $0.01 < P < 0.001$; *** $P < 0.001$.

		Standard animal dry weight	Condition index I	Glucose	Glycogen	Lipid	Protein	Water	Ash	T °C	S‰	
						T. philippinarum						
Standard animal dry weight			0.975***	0.767***	0.936***	0.933***	0.973***	0.968***	0.892***	NS	NS	
Condition index I		0.984***		0.759***	0.928***	0.907***	0.960***	0.921***	0.840***	NS	NS	
Glucose		0.536*	0.576*		0.828***	0.742***	0.720**	0.718**	0.568*	NS	NS	
Glycogen		0.911***	0.916***	0.627**		0.820***	0.882***	0.931***	0.833***	NS	NS	
Lipid		0.911***	0.913***	NS	0.845***		0.925***	0.841***	0.729***	NS	NS	
Protein		0.950***	0.939***	0.502*	0.848***	0.975***		0.941***	0.870***	NS	NS	
Water		0.825***	0.805***	0.404*	0.703***	0.732***	0.776***		0.953***	NS	NS	
Ash		0.860***	0.810***	0.526*	0.734***	0.699***	0.782***	0.889***		NS	NS	
T °C		NS	NS	NS	NS	NS	NS	NS	NS		0.685**	
S‰		NS	NS	NS	NS	NS	NS	NS	NS	0.685**		
						T. decussatus						

T. decussatus (left) / *T. philippinarum* (right)

content is greater than that for glycogen for most of the period studied. The contributions of protein, lipid, and glycogen to maintenance energy during the winter and in the absence of reproductive activity was calculated as a decrease in biochemical component energy equivalents for the period of absence of oocytes up to the beginning of the spring 1980 standard animal AFDW increase (Table IV).

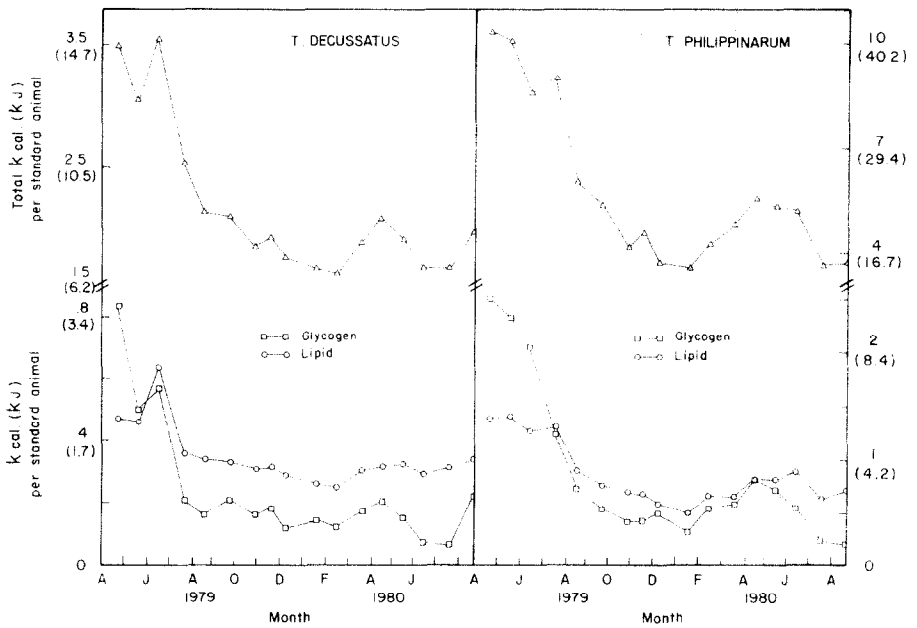

Fig. 4. Monthly variation of the energy content of the standard animal of *T. decussatus* and *T. philippinarum*: Δ, total energy content; energy content of glycogen (□) and lipid (○) components.

TABLE IV

Contribution of protein, lipid, and glycogen to the maintenance energy of a standard animal of *T. decussatus* and *T. philippinarum*, during the absence of oocytes and preceding the spring AFDW increase: ΔE, difference in energy content; % ΔE tot, ΔE as a percentage of the total difference in energy content.

	T. decussatus		*T. philippinarum*	
Component	ΔE (kJ)	(Nov.–Feb.) % ΔE tot	ΔE (kJ)	(Nov.–Jan.) % ΔE tot
Protein	1.34	49.0	3.26	73.6
Lipid	0.33	16.3	0.75	17.0
Glycogen	0.38	18.4	0.42	9.4
Total	2.05		4.43	

DISCUSSION

GROWTH AND CONDITION

The biometric data (Table I) indicate that maximum growth values had been attained in the *T. decussatus* population prior to the present study. Although no published data are available at present, personal observations suggest that these values are typical of Brittany populations of *T. decussatus*. These values are considerably lower than those observed in other regions for the same species (Arnaud & Raimbault, 1963; Walne, 1976).

In contrast, growth in the *T. philippinarum* population continued to maximum values considerably greater than those of the *T. decussatus* population. In both populations, the decrease is characteristic of the diminishing growth rate with size and age observed in marine bivalves (Wilbur & Owen, 1964; Dame, 1972; Seed, 1976). Ohba (1959) reports that the instantaneous growth rate in *T. philippinarum* decreases considerably after 2 yr of age.

The condition indices reveal a good mean condition in both populations in the spring of 1979, followed by an autumn and winter decline, and only a partial recovery in the spring of 1980. A more complete recovery may have been underway for *T. decussatus* in August 1980.

These differences in condition maxima suggest the occurrence of some physiological stress during the autumn and winter, which was not compensated in the spring of 1980. The data from the biochemical analyses presented below indicate a failure to constitute energy reserves in the autumn of 1979 following spawning, and a consequent exhaustion of the energy reserves in the winter. Such winter "degrowth" has been observed in *Chlamys islandica* (Vahl, 1981a, b), corresponding to a negative energy balance in the autumn and winter. In the two populations studied, a more complete recovery may have commenced in late August 1980.

It is interesting to note the very close correspondence between the two condition indices. This suggests that the use of the more easily-measured dry flesh wt condition index is quite adequate for these two species.

The very close correlation of the dry weight condition index with all of the gross biochemical constituents (except for free glucose in *Tapes decussatus*, where the correlation was significant but not strong) is worthy of note. Similar observations have been made independently for several bivalve species, including *T. philippinarum* (Mann, 1978). It is suggested that this type of index is a superior indicator of physiological condition than those based on the ratio of dry flesh wt to internal shell volume, as these have been shown to be poorly correlated with some gross biochemical component levels (Whyte & Englar, 1982).

REPRODUCTIVE ACTIVITY

The reproductive cycle of the two species studied is known to be highly variable, with two possible spawnings in a single season (Vilela, 1950; Ohba, 1959; Adachi, 1979). Certainly the intensity of the spawnings differed for both species in 1979 and 1980 as indicated by the standard animal AFDW values. These values suggest the possibility of a second late-summer spawning in both species. The interval during which no oocytes are present appears much shorter in *T. philippinarum* (mid-November to mid-March) than in *T. decussatus* (mid-September to mid-April). The decrease in standard animal AFDW during this period and before the spring increase indicates a loss of organic matter not associated with spawning, suggesting a period of winter energy imbalance.

GROSS BIOCHEMICAL COMPOSITION

Although the absolute values of water follow those of the standard animal AFDW, it is interesting to note the changes in the proportion of water in the tissue during and after the 1979 spawning (Table II and Fig. 2). In both populations, an increase in the per cent water content is observed during spawning with a high level maintained throughout the winter and even the following summer. Such increases in per cent water content are known in marine organisms subjected to starvation in the laboratory (Wilkins, 1967; Cuzon & Ceccaldi, 1973; Johnston & Goldspink, 1973; Cuzon *et al.*, 1980) as well as in temperate winter waters when food availability is low (Barnes *et al.*, 1963; Ansell, 1975; Taylor & Venn, 1979). The same type of variation occurs in the per cent ash values of both populations (Table II). Mayzaud (1976) associates an increase in per cent water and ash content with a state of starvation in winter zooplankton, and Wilkins (1967) makes the same observation for herring. The water and ash data thus suggest a state of nutritional deficiency in both populations following the 1979 spawning.

Despite the relatively large coefficients of variation previously mentioned, the free glucose absolute values are strongly correlated with those of glycogen in both species. This tends to confirm the hypothesis that free glucose is a glycogenesis regulator (Gabbott, 1975).

Several workers have reported glycogen maxima in bivalves immediately preceding and during gamete maturation (Ansell, 1972, 1974, 1975; Shaffee, 1978; Williams, 1969; Ansell *et al.*, 1980). The increase in glycogen content appears to be related to periods of maximum phytoplankton abundance, even for deep-living bivalves (Ansell & Trevaillion, 1967; Ansell, 1972).

Glycogen has long been considered to be the principal energy reserve of adult marine bivalves (Giese, 1966, 1969) both for the formation of gametes, especially under conditions of nutrient stress (Reid, 1969; Walne, 1970; Gabbott & Stephenson, 1974; Gabbott, 1975; Barber & Blake, 1981), and also in the adult during nutritional stress such as in temperate winter waters (Reid, 1969; De Zwaan & Zandee, 1972; Beukema & De Bruin, 1977). The variation of the glycogen absolute values in both populations tends to support this hypothesis. In particular, the results of the energy study and the

reproductive activity of the two populations reveal a decrease in total energy content during the winter which may not be attributed to spawning. It is thus clear that these two populations were in a state of negative energy balance during this period (Fig. 4). Glycogen served in a limited capacity as an energy reserve during this period, furnishing $\approx 18\%$ of the maintenance energy in *T. decussatus* and 9% in *T. philippinarum*. As neither population consolidated pre-winter energy reserves in 1979, this probably represents the exhaustion of the glycogen remaining after the spawning in 1979.

The pattern of variation of the lipid absolute values corresponds to that previously observed in other marine bivalves (Establier, 1969; Ansell, 1972; Ando *et al.*, 1976; Beukema & De Bruin, 1979; Taylor & Venn, 1979; Ansell *et al.*, 1980). In all the cases cited, maximum levels correspond to the spawning periods, reflecting the fact that lipid is a major component of bivalve oocytes (Holland, 1978; Gabbott, 1983). The temporal separation between the glycogen and lipid variations in the two populations supports the hypothesis that glycogen reserves may be converted to gamete lipids before spawning.

A transfer of lipids from somatic to gonadal tissue may also occur, as suggested by the inverse relationship between somatic and gonadal lipid levels observed in *Chlamys opercularis* (Taylor & Venn, 1979). Walne (1970) suggests that both glycogen and lipids are used in the elaboration of oyster oocytes.

Lipids may also serve as an energy reserve in adult bivalves, especially during periods of nutritional insufficiency, such as in winter conditions in temperate waters (Walne, 1970; Beukema & De Bruin, 1977). In the present study, the lipid contribution to the winter maintenance energy during the non-spawning period was 16% in *Tapes decussatus* and 17% in *T. philippinarum*. These results are comparable with those observed in a group of *Mytilus edulis* starved during the winter, in which the lipids contributed 15% of the maintenance energy and glycogen contributed 10% (Gabbott & Bayne, 1973). Keeping in mind the glycogen contribution previously cited in the two populations studied, it is thus evident that lipid may provide up to twice as much reserve energy as glycogen under prolonged and severe situations of energy imbalance. Holland & Hannant (1976) have noted that the precise rôle of lipids as an energy reserve in adult bivalves remains to be elucidated, particularly that of the large phospholipid fraction. This aspect has been studied in the two *Tapes* populations and will be presented in a later paper.

The maximum observed for the protein absolute values during the spawning period of the two populations studied was to be expected, as protein constitutes the major organic component of bivalve oocytes (Holland, 1978). Similar observations have been made in a number of marine bivalves (Establier, 1969; Williams, 1969; Ansell, 1972, 1974; Beukema & De Bruin, 1977; Nagabhushanam & Talikhedar, 1977; Ansell *et al.*, 1980). Protein may also serve as an energy reserve in adult bivalves, particularly during gametogenesis. As previously mentioned, both glycogen and lipid are mobilized to form oocytes, and oocyte proteins are synthesized de novo (Holland, 1978). Thus, somatic protein becomes the predominant energy substrate during this period. Such a change

in respiratory substrate during gametogenesis has been observed in *T. philippinarum* (Mann & Glomb, 1978), and Adachi (1979) has indeed demonstrated a mobilization of somatic proteins during gonad maturation in this species. A similar observation has been made for *Argopecten irradians concentricus* (Barber & Blake, 1981).

The rôle of somatic proteins as an energy reserve may also extend to situations of nutritional stress and energy imbalance outside the reproductive period, as observed in winter-starved *Mytilus edulis*, where proteins contributed 75% of the maintenance energy (Gabbott & Bayne, 1973). This may be compared with the contribution of 74% in *Tapes philippinarum* and 49% in *T. decussatus* observed in the present study. Such a mobilization of proteins indicates once again that both populations were in a state of energy imbalance during the winter.

To summarize, both the indigenous *T. decussatus* and the introduced *T. philippinarum* showed very similar seasonal variations in condition and gross biochemical composition when raised in a common habitat. This underlines the importance of the environment in determining the physiological responses of marine bivalves. Two basic differences in gross composition, however, seem to prevail. The *T. philippinarum* population is characterized by a higher glycogen level while that of *T. decussatus* is characterized by a slightly greater ash content.

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