Seasonal variation in the relative utilization of carbon and nitrogen by the mussel *Mytilus edulis:* budgets, conversion efficiencies and maintenance requirements

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ABSTRACT: Elemental balances for carbon and nitrogen in an open-shore population of the bivalve mollusc *Mytilus edulis* underwent seasonal changes more characteristic of time-averaged than immediate optimization. Budgets emphasized the significance of shell and byssus towards both the carbon (8 and 44 %, respectively) and nitrogen (8 and 21 %, respectively) within total production, and indicated that between at least 20 and 67 % of the nitrogen in faeces may be of metabolic origin. In addition to differing absorption rates, pronounced seasonal variations of net growth efficiency were effected for each element by changes in metabolic demand that not only reflected requirements *per se,* but also the 'gross efficiencies' with which absorbed nutrients were used to offset net deficits. Changes of 'gross efficiency' were at least partially due to a variable subsidization of maintenance requirements from pre-stored reserves, rather than to possible variations of metabolic efficiency alone. Although net growth efficiencies for nitrogen consistently exceeded those for carbon, the associated seasonal patterns of utilization were different for each element, and are discussed in relation to physiological, storage and reproductive cycles documented elsewhere. Ratios between coincident maintenance requirements for the utilizable carbon and nitrogen in the alga *Phaeodactylum tricornutum* varied from 12 : 1 during summer to as much as 83 : 1 in winter. Further, relative to carbon, mussels regularly absorbed higher proportions of their maintenance requirements for nitrogen. These results, together with known fluctuations of nutrients in the natural environment, imply that there may have been transient limitation of organic processes by the available carbon, and emphasize the need for a multi-elemental approach in future studies of bivalve nutrition.

INTRODUCTION

Filter-feeding bivalves are of widespread significance as biogeochemical agents in nearshore communities (Kuenzler 1961a, b, Kautsky 1981, Jordan & Valiela 1982). There remains, however, little contemporary understanding concerning either the regulation of resource acquisition or the relative utilization of 'essential' elements (Russell-Hunter 1970) absorbed by these or indeed any marine invertebrate. Most previous studies on trophic relations and resource transformations of bivalves have been undertaken in terms of calories (reviewed by Bayne & Newell 1983, see also Winter et al. 1984) or carbon (Kofoed 1975, Gilfillan et al. 1976, Kiorboe et al. 1980, Gallager et al. 1981, Seiderer et al. 1982), when the individual has been assumed to maximize energy/nutrient gain under all

circumstances. In this context, Hawkins et al. (1985) have demonstrated marked seasonal variations of absorption by the blue mussel *Mytilus edulis* which appear endogenously regulated in a manner more indicative of time-averaged than immediate optimization. Further, relative to carbon, nitrogen may better represent one of the specific compounds with potential to limit production (Liebig 1840), being utilized primarily in structural material rather than energy reserves. Flows of carbon/energy within coastal ecosystems are often limited by the availability of nitrogen (reviewed by Mann 1982), and production by many marine invertebrates correlates with the amount of protein ingested (reviewed by Roman 1983). As emphasized by Mann (1982), knowledge of both carbon/energy and nitrogen flows is thus fundamental to any understanding of the fluctuating productivity that

is so often apparent. Nevertheless, few workers have investigated nitrogen/protein balance in bivalves (Bayne & Scullard 1977, Bayne & Widdows 1978, Gallager et al. 1981, Jordan & Valiela 1982), and none has ascertained nitrogen absorption directly. Similarly, little is known concerning the relative maintenance requirements for absorbed nutrients, and nothing of seasonal influences upon those requirements.

This study questions the assumption that nutrient gain and allocation are always maximized in the short-term and compares seasonal variation in the relative utilization of carbon and nitrogen in an open-shore population of *Mytilus edulis* that is naturally subjected to seasonal fluctuation in the supply of food. In addition, we assess the extent to which changing rates of absorption, varying requirements for exogenous nutrients, and the associated degree to which both the carbon and nitrogen absorbed were utilized to offset net deficits affected the net growth efficiencies for each element. Simultaneous nitrogen and carbon budgets are discussed in relation to physiological, reproductive and storage cycles documented previously (Hawkins et al. 1983, 1985, Hawkins & Bayne 1984, Hawkins 1985), and with particular respect to the potential limitation of production by exogenous availability of either element.

MATERIAL AND METHODS

Collection and maintenance. Mytilus edulis L. of 45 to 57 mm shell length were gathered at about low water tide level from Whitsand Bay, southwest England, in March, June and October 1981. Subsequent conditions of feeding and starvation throughout 5 to 6 wk periods of laboratory acclimation, together with methods of culturing $^{15}N : ^{14}C$-labelled *Phaeodactylum tricornutum*, administering this alga to acclimated mussels, and determining isotopic enrichments within samples are described by Hawkins & Bayne (1984) and Hawkins et al. (1983, 1985). These authors have also described methods for estimation of elemental composition, ingestion rate, 'net' and 'gross' absorption efficiencies, oxygen consumption and excretion that are used here to compute elemental fluxes of both carbon and nitrogen.

Carbon balance. The quantity of carbon consumed by mussels was calculated as the product of ingestion (μg dry wt h^{-1}) and mean organic carbon content of *Phaeodactylum tricornutum* (42.78 $\pm$ 0.09 %, 2 SE, $n = 5$). This value, when multiplied by the net absorption efficiency, yields net carbon absorption (μg C h^{-1}). Net absorption efficiencies for carbon were assumed equivalent to those derived using the Conover (1966) ratio, as has been verified for the mussel *Aulacomya*

ater (Stuart et al. 1982). Carbon respired (μg C h^{-1}; mean $\pm$ range) was calculated from rates of oxygen consumption (ml O_2 h^{-1}) (cf. methods of Gilfillan et al. 1976, Rodriguez-Ortega & Day 1978, Gallager et al. 1981) assuming a range of respiratory quotients between 0.71 (1 ml O_2 = 0.38 mg C) and 1.0 (1 ml O_2 = 0.53 mg C). This range accounted for the catabolism of carbohydrate, lipid or protein, including any mixture thereof (Schmidt-Nielsen 1977). Net carbon balance (mean $\pm$ range) was then computed as net carbon absorption minus carbon respired.

Nitrogen balance. Net balances of nitrogen were derived in a manner essentially similar to those for carbon. The mean organic nitrogen content for *Phaeodactylum tricornutum* was 6.64 $\pm$ 0.66 % ($\pm$ 2 SE, $n = 12$). Both net absorption efficiencies and losses of nitrogen within excreted ammonia were determined directly. Net nitrogen balance was computed as net nitrogen absorption minus nitrogen excreted. In addition, differences between coincident measures of the 'net' and 'gross' efficiencies of nitrogen absorption were calculated to enable estimations of the 'metabolic faecal nitrogen' (μg N h^{-1}) (cf. Calow & Fletcher 1972), representing nitrogen of endogenous origin that is lost from the individual as faeces.

Byssus threads. The production of byssal threads was measured as both μg C and μg N $mussel^{-1}$ h^{-1} during March and June 1981. All byssus was cut from mussels ($n = 6$ to 8), and the secreted threads collected from individuals 36 d later. Immediately following collection, threads were freeze-dried and weighed before determining the carbon and nitrogen contents within replicated subsamples using a Carlo Erba elemental analyser with acetanilide as a standard.

^{15}N and ^{14}C incorporation. The relative incorporation of ^{15}N and ^{14}C within tissues and shells of fed mussels ($n = 3$ to 5) was measured at intervals up to 23 d after the ingestion of labelled *Phaeodactylum tricornutum* in March and June 1981. Following excision, the total soft tissues were subdivided into digestive gland, mantle and 'remainder', and the shells thoroughly washed with distilled water. Samples were subsequently freeze-dried, weighed, ground to a homogeneous powder and stored within airtight glass vials at $-90\,°C$ prior to isotopic analyses (Hawkins 1983).

Seasonal elemental budgets. The results were used to construct seasonal budgets for nitrogen and carbon. Each component was computed as a percentage of ingestion rate and expressed in terms of (i) net growth efficiency (the net balance, expressed as a proportion of the coincident ration absorbed), (ii) 'gross efficiency' (the increment in net balance between starved and fed individuals, expressed as a proportion of the associated ration absorbed by fed individuals) and (iii) 'instantaneous maintenance requirements' (the ration neces-

sary to sustain zero net balance at a given moment in time, estimated by computing ration-specific increments of net balance between starved and fed individuals).

RESULTS

The estimated net balances, net growth efficiencies, 'gross efficiencies' and 'instantaneous maintenance requirements' for both carbon and nitrogen are shown in Tables 1 and 2, respectively. Negative elemental balances were recorded in winter (March; $-15.5\,\mu g$ C h^{-1} and $-0.58\,\mu g$ N h^{-1}) and autumn (October;

$-2.8\,\mu g$ C h^{-1}) and positive balances in summer (June; $+36.4\,\mu g$ C h^{-1} and $+9.5\,\mu g$ N h^{-1}). It is, however, notable that the net balance of nitrogen remained positive during autumn ($+8.09\,\mu g$ N h^{-1}).

Seasonal net growth efficiencies for nitrogen consistently exceeded those for carbon; the efficiencies for each element varied over wide ranges, and were lowest during winter (Table 1 & 2). Quite apart from the influence of differing absorption rates, these variations of net growth efficiency were clearly effected by seasonal changes of metabolic demand and the associated gross efficiency with which each element was utilized from the available ration to offset net deficits. The

Table 1. *Mytilus edulis.* Computation of net balances, net growth efficiencies, gross efficiencies and maintenance requirements for carbon among 45 to 57 mm shell-length mussels either fed or starved during acclimation in March, June and October 1981

Date and nutritional status	Ingested ration	Net C absorption	CO_2 equivalents of oxygen consumed[a]	Net C balance[a]	Change in body-C	Net growth efficiency	Gross efficiency[b]	Maintenance requirements Ingested	Absorbed
	(μg C h^{-1})	(μg C h^{-1})	(μg C h^{-1})	(μg C h^{-1})	(% d^{-1})	(%)	(%)	(μg C h^{-1})	(μg C h^{-1})
March									
Fed	72.7	27.3	42.8± 6.9	−15.5± 6.9	−0.15	−56.8	+ 4.0	1097.1	412.0
Starved	–	–	16.6± 2.7	−16.6± 2.7	−0.17	–	–		
June									
Fed	231.0	120.6	84.2±13.7	+36.4±13.7	+0.23	+30.2	+82.5	146.5	76.5
Starved	–	–	63.1±10.2	−63.1±10.2	−0.38	–	–		
October									
Fed	132.6	72.7	75.5±14.9	− 2.8±14.9	−0.02	− 3.8	+89.3	138.3	75.8
Starved	–	–	67.7±11.0	−67.7±11.0	−0.52	–	–		

[a] Values presented ± the range computed assuming respiratory quotients between 0.72 and 1.00
[b] Note a distinction here from the 'gross growth efficiency' of Thompson & Bayne (1974) and others. The present estimates of gross efficiency were derived by computing increments in carbon balance between fed and starved conditions and expressing these as fractions of the associated net carbon absorption for fed individuals; thus, for March, gross efficiency = [(− 15.5)–(− 16.6)]/27.3 = 0.04

Table 2. *Mytilus edulis.* Computation of net balances, net growth efficiencies, gross efficiencies and maintenance requirements for nitrogen among 45 to 57 mm shell-length mussels either fed or starved during acclimation in March, June and October 1981

Date and nutritional status	Ingested ration	Gross N absorption	Metabolic faecal N	Net N absorption	Ammonia-N excretion	Net N balance	Change in body-N	Net growth efficiency	Gross efficiency[b]	Maintenance requirements Ingested	Absorbed
	(μg N h^{-1})	(μg N h^{-1})	(μg N h^{-1})	(μg N h^{-1})	(μg N h^{-1})	(μg N h^{-1})	(% d^{-1})	(%)	(%)	(μg N h^{-1})	(μg N h^{-1})
March											
Fed	11.29	9.16	4.32	4.84	5.42	− 0.58	− 0.03	− 12.0	+ 71.5	13.2	5.6
Starved	–	–	–	–	4.04	− 4.04	− 0.20	–	–		
June											
Fed	35.86	19.69	3.95	15.74	6.24	+ 9.50	+ 0.35	+ 60.3	+ 90.7	12.0	5.3
Starved	–	–	–	–	4.77	− 4.77	− 0.17	–	–		
October											
Fed	20.58	15.48	4.16	11.32	3.23	+ 8.09	+ 0.37	+ 71.5	+ 86.5	3.6	2.0
Starved	–	–	–	–	1.70	− 1.70	− 0.08	–	–		

[b] See footnote *b* in Table 1

Table 3. *Mytilus edulis*. Secretion of byssal threads by 45 to 57 mm shell-length mussels in March and June 1981. Values are means ± 2 SE for *n* mussels, where dry weights of byssal threads were converted to units of nitrogen and carbon using measured elemental contents of 14.38 % (2 SE = 0.52, *n* = 8) and 54.71 % (2 SE = 0.95, *n* = 8), respectively

Month	*n*	Byssal thread secretion (μg h⁻¹ mussel⁻¹)		
		Dry weight	Nitrogen	Carbon
March	6	5.15 ± 1.79	0.74 ± 0.30	2.82 ± 1.04
June	7	5.29 ± 2.06	0.76 ± 0.32	2.89 ± 1.21

pattern of such changes was different for each element, and appeared more extreme for carbon than nitrogen. Indeed, whereas ingested maintenance requirements for carbon were 7.5 to 7.9 times higher during winter than in summer or autumn, demands for nitrogen were recorded during both winter and summer at levels which were only 3.3 to 3.7 times greater than in autumn. Coincident gross efficiencies for each element were roughly equivalent during summer and autumn (82 to 90 %), but displayed winter minima of 71 % for nitrogen and as little as 4 % for carbon (Table 1 & 2).

There was no evidence for seasonal variation between rates of byssal thread production (Table 3) (*t*-test value t_s = 0.0115 for 11 DF, $P > 0.05$). These rates, measured using mussels of 0.33 to 0.71 g dry tissue weight, compare favourably with those of 2.5 to 5.8 μg dry byssus h⁻¹ recorded for smaller *Mytilus edulis* of 0.20 to 0.27 g tissue weight by Kiorboe et al. (1981).

Percentages of the isotopes ingested that were incorporated within shells are presented in Table 4. The relative incorporations of carbon and nitrogen appeared similar. Greater proportional uptake of each element into the shell of mussels during summer, when feeding was maximal (Table 1 & 2), is consistent with there being a positive correlation between gain in shell weight and the amount of food ingested by *Mytilus edulis* (Winter 1974, 1976).

Time-series for the percentage contributions from each tissue division towards isotopic excesses within the total soft tissues are shown in Fig. 1. Significant

Table 4. *Mytilus edulis*. Percentages of ingested isotopes that were incorporated within shell matrices of 45 to 57 mm shell-length mussels in March and June 1982. Values are means ± range for *n* mussels

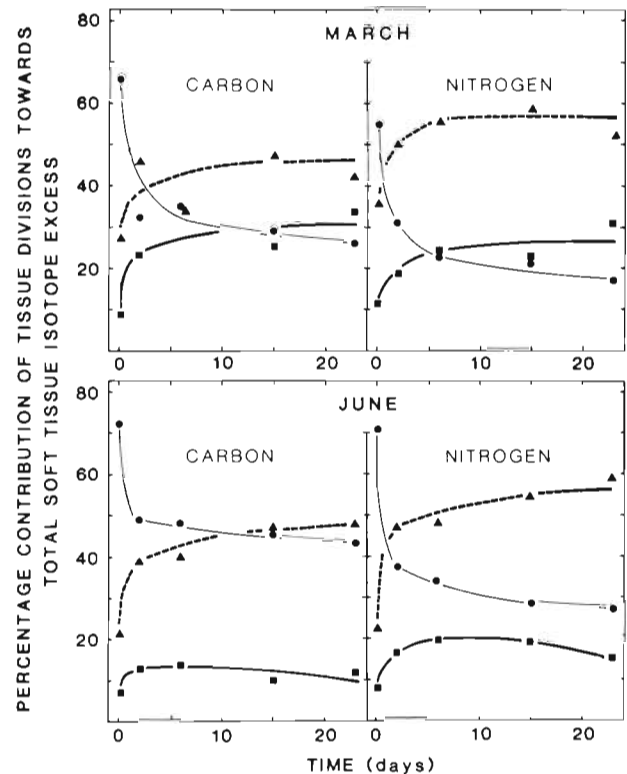| Month	*n*	Percentage incorporation	
		¹⁵N	¹⁴C
March	3	3.49 ± 0.11	2.86 ± 0.53
June	4	5.47 ± 0.79	6.97 ± 0.27

Fig. 1. *Mytilus edulis*. Percentage contributions of digestive gland (●), mantle (■) and remainder (▲) tissue divisions towards both the atom excess ¹⁵N (μg) and ¹⁴C (DPM) within total soft tissues of 45 to 57 mm shell-length mussels at intervals up to 23 d after ingesting labelled alga in March and June, 1981. Curves fitted by eye

differences were apparent between the internal translocation of each element. In particular, relative to ¹⁵N, a consistently higher percentage of ¹⁴C was incorporated within the digestive gland, and vice versa for the remainder tissue division (Table 5, Fig. 1). This clearly reflects the role played by digestive tissues in the storage of lipid and carbohydrate reserves (Gabbott & Bayne 1973, Hawkins et al. 1985). Further, compared with ¹⁴C, greater proportional allocation of ¹⁵N to the

Table 5. *Mytilus edulis*. Results of *t*-tests for paired comparisons (Sokal & Rohlf 1969) between coincident time-series for the percentage contributions of digestive gland, mantle and remainder tissue divisions towards the atom excess ¹⁵N and ¹⁴C within total soft tissues after ingesting labelled alga in March and June, 1981 Data are illustrated in Fig. 1 t_s: Students *t*-value; *P*: the probability that the mean of differences between pairs of data is different from zero at *n* −1 = 4 DF

Tissue division	March		June	
	t_s	*P*	t_s	*P*
Digestive gland	4.031	< 0.02	4.462	< 0.02
Mantle	1.539	NS	3.199	< 0.05
Remainder	3.739	< 0.05	4.397	< 0.02

mantle in summer, but not winter (Table 5, Fig. 1), was probably associated with the seasonal deposition of protein within adipogranular cells (Hawkins et al. 1985, cf. Houteville 1974, Mathieu 1979). Although not showing clear differences in the flow of each element, gametogenic demands were evidenced during winter when, relative to summer, a higher percentage of absorbed ^{14}C (t-test value for paired comparisons $t_s = 3.732$, DF = 4, $P < 0.05$; equivalent t_s value for nitrogen = 2.210, DF = 4, $P < 0.10 > 0.05$) was transferred to the mantle (Fig. 1).

MARCH

INGESTION

	BIODEPOSITION	RESPIRATION	NON-FAECAL EXCRETION	BYSSUS	SHELL
CARBON	62.4	58.9	ND	3.9	2.9
NITROGEN	57.1	NA	48.0	6.6	3.5

NET SOFT

TISSUE BALANCE

CARBON - 28.1

NITROGEN - 15.2

JUNE

INGESTION

	BIODEPOSITION	RESPIRATION	NON-FAECAL EXCRETION	BYSSUS	SHELL
CARBON	47.8	36.5	ND	1.1	7.0
NITROGEN	56.1	NA	17.4	2.1	5.5

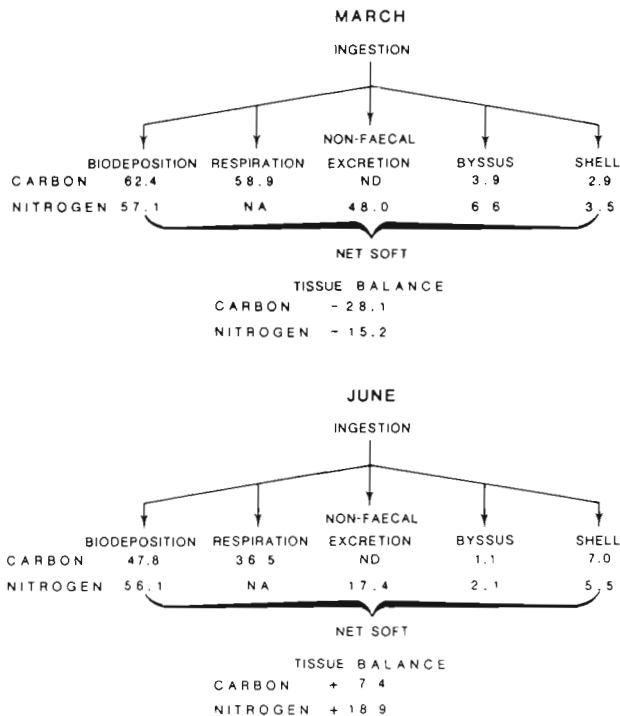NET SOFT

TISSUE BALANCE

CARBON + 7.4

NITROGEN + 18.9

Fig. 2. *Mytilus edulis.* Carbon and nitrogen budgets for 45 to 57 mm shell-length mussels in March and June, 1981. NA: not applicable; ND: not determined

Major components of the seasonal nitrogen and carbon budgets are shown in Fig. 2. More than 48 % of each element consumed was voided as faeces. Within these faeces, however, 'metabolic faecal nitrogen' ranged between 731 and 2,451 mg nitrogen per 100 g of dry diet ingested. These values are substantially higher than those of < 215 mg 100 g^{-1} diet reported for other species that include prawns (Forster & Gabbott 1971), fish (Nose 1967, Jauncey 1982), rats (Williams & Senior, 1981) and man (Maynard & Loosli 1969). Complementary evidence for the significant presence of metabolic material within faeces has stemmed from patterns of isotope defecation, from which Hawkins & Bayne (1984) estimated that the excretion of metabolised isotope constituted about 15 % of all faecal ^{15}N in summer. An equivalent calculation, based upon

data for net and gross absorption during summer (Table 2), is consistent with this estimate, indicating that metabolic excretion contributed $(3.95/[35.86 - 15.74]) \times 100 = 20$ % towards faecal nitrogen. This contribution increased to as much as $(4.32/(11.29 - 4.84)) \times 100 = 67$ % of faecal nitrogen during winter.

Percentages of both the ingested carbon respired and the ingested nitrogen excreted were also considerably higher in winter (59 and 48 %, respectively) than in summer (36 and 17 %, respectively). Associated with such changes, gross production efficiencies ([byssus + shell + soft tissue]/ingestion) for carbon and nitrogen alternated from negative values during winter (-16 and -32 %, respectively) to become positive in summer (19 and 32 %, respectively). Byssus and shell each accounted for substantial proportions of both the carbon (8 and 44 %, respectively) and nitrogen (8 and 21 %, respectively) within total production (byssus + shell + soft tissue) during the summer period of net soft tissue growth (Table 1 & 2, Fig. 2).

DISCUSSION

Perhaps because it is not generally appreciated that byssal threads are comprised largely of proteins (Waite 1983), and because organic matter in most bivalve shells amounts to less than 5 % by weight (Price et al. 1976, Cameron et al. 1979), these materials have often been ignored in production studies. Our findings for *Mytilus edulis,* however, together with those for the mussels *Geukensia demissa* (Kuenzler 1961a, Jordan & Valiela 1982) and *Perna perna* (Berry 1978), have shown that both shell and byssus may represent substantial fractions of annual production. Accordingly, just as these materials should not be underestimated in studies of standing stock biomass (Price et al. 1976, Paterson 1982), they clearly warrant consideration as significant components of production.

Estimates that more than 48 % of both the carbon and nitrogen consumed were expelled as faeces reflect the potential role of mussels as biogeochemical agents. At least 20 % of the nitrogen within these faeces was shown to be of metabolic origin, rather than being the unabsorbed remnants of ingestion alone; we are not aware that this phenomenon has previously been quantified for any bivalve. Among gastropods, the faecal mucous envelope may account for 9 to 10 % of both the carbon and nitrogen within faeces (Edwards & Welsh 1982). *Mytilus edulis* not only produces mucous-bound faecal ribbons (Dinamani 1969, Arakawa 1970), but may 'incubate' bacteria within the digestive system (Prieur 1981), and reject the undigested remnants of intracellular lysosomal activity within residual

bodies from the digestive cells (Platt 1971). In addition, periods of net nitrogen loss to the faeces during winter coincided with elevated rates of ammonia excretion, suggesting that metabolic end-products may be secreted directly into the alimentary canal (Hawkins et al. 1983).

Our observations of negative elemental fluxing from *Mytilus edulis* in March and October are reminiscent of measurements by Gilfillan et al. (1976). These authors documented net losses of carbon from 2 populations of the bivalve *Mya arenaria* during 7 mo of the year, including the spring phytoplankton bloom. It is significant that such pronounced seasonal variations of net elemental flux, due to both varying rates of absorption and changing maintenance requirements, were apparent here despite the experimental standardization of nutrient availability and the close similarity between ambient and experimental water temperatures. Whereas conventional ideas assume a 'maximal' retention of nutrients under all circumstances, this finding suggests an endogenous influence concerning the long-term balance between aquisition and utilization of both carbon and nitrogen, as has previously been discussed for energy by Hawkins et al. (1985).

Although net fluxes of carbon and nitrogen showed the same seasonal pattern of changes, significant differences were apparent between the overall flow of each element. In particular, and regardless of season, net growth efficiencies for nitrogen regularly exceeded those for carbon. Such a conservation of nitrogen undoubtedly reflected the pronounced 'protein sparing' behaviour effected both by recycling of breakdown products to synthesis and a progressive reduction in fractional protein degradation with elevated net protein balance (Hawkins 1985). This behaviour was most obvious during autumn, when a positive net balance for nitrogen coincided with net losses of carbon.

Further differences between the relative utilization of nutrients were illustrated by elemental maintenance requirements. The seasonal increase in requirements during winter was more pronounced for carbon than nitrogen. For each element, these increased requirements derived from reduced gross efficiencies (i.e. the efficiency with which absorbed nutrients were used to offset net deficits), together with the concurrent demands of gametogenesis. Quite apart from possible changes in metabolic efficiency *per se*, the low gross efficiencies computed for mussels in winter must at least partially reflect a reduced subsidization of maintenance requirements from pre-stored reserves by starved individuals (cf. Hawkins et al. 1985). The coincident seasonal depletion of carbohydrate and lipid reserves signifies that the gross efficiency for carbon was substantially lower than for nitrogen, leading to a relatively more pronounced increase in the maintenance requirement for carbon. Such variable subsidization, which is a feature of protein sparing behaviour, represents a major influence upon changing elemental requirements. Requirements for exogenous nitrogen remained high during summer, when carbon requirements had fallen to levels equivalent to those recorded in autumn. This was in agreement with concurrent measurements showing maximum observed rates of protein synthesis (Hawkins 1985) and the deposition of that protein within adipogranular cells (Hawkins et al. 1985). A subsequent reduction in measured nitrogen requirements between summer and autumn reflected the preferential respiratory catabolism of carbon-rich reserves abundant at that time. Indeed, only 10 % of total catabolic substrates were comprised of protein during autumn, relative to about 35 % in March.

These findings, then, illustrate a varying balance between the elemental demands stemming from seasonal cycles of substrate storage, gametogenesis and somatic development. Assuming that all organic matter is derived from protein, Russell-Hunter (1970) calculated that the required C : N ratio for adequate animal food intake is about 17 : 1. Results presented here indicate ingested maintenance requirements for *Mytilus edulis* feeding upon *Phaeodactylum tricornutum* that varied in C : N ratio from at least 83 : 1 in winter to 12 : 1 during summer. Maintenance requirements computed in elemental terms will change according to the digestibility, biochemical composition and total energy content of food available. Nevertheless, it is clear that the pronounced variation of demands evidenced here, contrasted with known seasonal fluctuations in exogenous resources, may result in transient nutritional limitation of organic processes. Phytoplankton with mean C : N ratios of 5 to 8 : 1 (Fenchel & Jorgensen 1976, Cullen & Horrigan 1981) are abundant during spring and autumn blooms within the English Channel (Maddock et al. 1981), whereas ratios of up to 10 to 35 : 1 may be obtained in the senescent organic tissues available in winter (Russell-Hunter 1970, Sakshaug & Holm-Hansen 1977). Although C : N ratios calculated on the basis of both protein and non-protein nitrogen within decomposing algae and detritus may have been higher still (Rice & Tenore 1981), our data suggest that *M. edulis* from this open shore population feeding primarily upon phytoplankton were more likely to have been limited by utilizable carbon than by nitrogen. Such limitation seems especially probable during winter, when overall maintenance requirements are maximal and nutrient reserves exhausted.

Complementary evidence suggesting that growth was more likely to have been limited by available carbon than nitrogen was apparent from the relative

degrees to which elemental maintenance require-
ments were satisfied. Compared with carbon, consis-
tently greater percentages of the maintenance require-
ments for nitrogen were absorbed in winter (7 and
86 %, respectively), summer (158 and 297 %, respec-
tively) and autumn (96 and 566 %, respectively). These
results were unexpected, for it is generally assumed
that production by marine herbivores may be limited
by nitrogen (references reviewed by Mann 1982), with
little documented evidence for similar limitation by
carbon. In this context, it is interesting that elemental
balances recently computed by Newell & Field (1983)
have indicated that available carbon may also limit
production at the community level, in this instance
among the predominantly filter feeding consumers
within a kelp bed ecosystem.

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