CARBON AND NITROGEN SCOPE FOR GROWTH AS A FUNCTION OF DIET IN THE SEA SCALLOP *PLACOPECTEN MAGELLANICUS*

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Laboratory feeding experiments with the sea scallop *Placopecten magellanicus* were carried out to compare scope for growth (SFG) to measured growth and determine the effect of diet on carbon and nitrogen SFG. Diets consisting of cultured phytoplankton, kelp detritus, and resuspended sediment were provided daily for 52 days (October-December). Measurements of clearance rate, absorption efficiency, respiration, O/N ratio, and carbon and nitrogen content of diets and scallop tissue were used to construct carbon and nitrogen budgets for each diet. Growth coefficients were calculated from change in tissue weight during the study period.

Scope for growth tended to overestimate actual growth for phytoplankton diets, but assessment of variance in energy budget terms suggested closer agreement between observed and predicted growth. Individuals fed kelp and sediment diets showed depressed respiration rates and greatly reduced growth compared to phytoplankton, a result verified by SFG estimates. Phytoplankton provided at least six times greater carbon and nitrogen balance than detrital sources. Sediment allowed a relatively favourable nitrogen balance due to low C/N, but unfavourable carbon balance due to high inorganic content. In contrast, kelp provided comparatively better carbon than nitrogen nutrition. Tissue C/N did not differ between scallops fed kelp and microalgal diets. Depending on the nutritional state of *Placopecten magellanicus* and its subsequent O/N ratio, sediment and kelp could enhance phytoplankton diets, but could not act as sole food sources. These results indicate that carbon or energy based scope for growth measurements may overestimate secondary production under nitrogen-limited conditions.

INTRODUCTION

The measurement of energy budget parameters to predict residual energy which is potentially available for growth and reproduction (scope for growth, SFG) has been widely applied to invertebrates, particularly marine bivalves (Bayne *et al.*, 1985). Scope for growth has proved to be a useful concept in assessing the effects of environmental stress, the relative importance of energy terms (*e.g.* growth efficiency), and differences in physiological traits between populations (Bayne *et al.*, 1985; Widdows & Johnson, 1988). A major advantage of this calculation is that bivalve growth responses which would require long-term studies can be estimated in short-term experiments.

An important assumption in some uses of SFG is that it corresponds to actual growth. Considering the wide application of SFG, it is surprising that few studies have specifically measured actual and potential growth on the same animals. Using flow-through laboratory systems, Riisgård & Randløv (1981) and Poulsen et al. (1982) found that growth closely matched SFG in *Mytilus edulis* fed with algal monoculture. Other workers have compared SFG to rates estimated from growth curves (*e.g.* von Bertalanffy) using age, length, and tissue-shell allometry in field animals (Bayne & Worrall, 1980; Gilfillan et al., 1976; MacDonald & Thompson, 1986). While these studies have generally found agreement between measured and predicted growth, rates are usually annual estimates because age/length relationships are based on shell annuli. Thus, short-term changes in growth caused by environmental fluctuations or reproductive cycles may be detectable by sensitive SFG measurements, but are seldom verified by actual growth rates.

Variation in growth rates within the course of a year may be substantial (Bayne & Widdows, 1978) because some of the factors which affect net energy balance and thus growth and reproduction (food and temperature) vary on sub-annual time scales from hours to months. Types of food particles such as phytoplankton, macrophyte detritus, and organic matter resuspended from sediments will be a major component of the variance in food quality. Scope for growth measurements have been useful in detecting nutritionally poor conditions as reflected in low food concentration, reduced ingestion, and/or assimilation rates as well as lowered metabolism (Bayne & Newell, 1983; Hawkins & Bayne, 1985; Bayne et al., 1987; Griffiths & Griffiths, 1987).

In the laboratory, SFG has similarly been applied to a variety of controlled diets to assess the utilization of particles by bivalve populations (Griffiths & Griffiths, 1987; Bayne et al., 1989). A number of related studies of digestion and enzyme activity have specifically sought to assess the role of macrophyte detritus in bivalve trophic ecology (Seiderer et al., 1982; Langdon & Newell, 1990). In attempting to determine the proportion of carbon requirements that can be met by detrital food, much of this work is dependent on SFG being realized as actual growth. However, invertebrate production may be limited by factors other than carbon (Mann, 1988). The coherence between scope for growth and actual growth is thus a function of which elemental budget is studied, as well as the changing nutritional demands of growth and reproduction throughout the year.

In the present study, we have maintained adult sea scallops (*Placopecten magellanicus* Gmelin) on various laboratory diets, measuring energy budget parameters in order to predict scope for growth. This species occurs in both coastal and shelf environments, and is thus exposed to a wide spectrum of particle sources. In previous reports on these experiments we examined changes in somatic and gonad tissue weight (Grant & Cranford, 1989), clearance rates, and various measures of absorption efficiency (Cranford & Grant, 1990) in relation to diet. In the present paper we incorporate measures of respiration and excretion to calculate scope for growth and compare these values to actual growth measured in the same animals. In addition, specific measurements from this study and previous work are used to derive carbon and nitrogen budgets for different diets. We utilize this information (a) to assess the agreement between scope for growth and actual growth for both optimal and suboptimal diets, and (b) to compare SFG predicted by both carbon and nitrogen budgets, and the effect of diet on this comparison.

MATERIALS AND METHODS

Details of the feeding experiments, growth studies, clearance rates, and absorption efficiencies have been presented in Grant & Cranford (1989) and Cranford & Grant (1990). Only relevant information and results from those studies will be reported here. The initial set-up and maintenance of feeding experiments required that energy budget measurements be made during the latter part of the study. It was thus necessary to incorporate some coefficients from the literature to allow for variation in temperature and allometry during the course of the experiment.

Post-spawn scallops collected from Georges Bank (off Nova Scotia) were maintained in fibreglass tanks (25 scallops per tank) and drip-fed six diets: *Chaetoceros gracilis* and *T-Isochrysis* aff. *galbana* (both cultured on-site), powdered kelp *Laminaria longicruris*, either fresh or aged four days in bubbling sea water, resuspended sediment eluted from intertidal sand, and a control diet receiving only filtered sea water (5 μm). The kelp and sediment diets were sieved to <106 μm. The duration of the experiment was 52 days, but scallops were fed six days per week (11 hours drip day^{-1}) for a total of 45 feeding days. Carbon, nitrogen, and concentration of the diets are given in Table 1.

Table 1. *Clearance rate (CR, three temperatures), ingestion (Ing), and absorption (Absorpt) of carbon and nitrogen by* Placopecten magellanicus *fed various diets*

Diet	Chaetoceros	T-Isochrysis	Sediment	Aged Kelp
CR-6°C (l h^{-1})	16.0	11.2	6.4	4.1**
CR-8.5°C (l h^{-1})	19.0	13.3	7.6	4.9
CR-12°C (l h^{-1})	24.2	17.0	9.7	6.2
SPM (mg l^{-1})	1.94	1.97	0.97	1.59
%C	34.7	47.9	13.1	29.0
Carbon Ing (mg C ind^{-1} t^{-1})	6485.5	6379.6	489.7	1140.4
AE-C (%)	84.6*	69.4	28.9*	87.4
Carbon Absorpt (mg C ind^{-1} t^{-1})	5486.7	4427.5	141.5	996.7
C:N	5.2	6.0	6.0	18.2
Nitrogen Ing (mg N ind^{-1} t^{-1})	1247.2	1063.3	81.6	62.7
AE-N %	91.6*	69.4	49.5*	87.4
Nitrogen Absorpt (mg N ind^{-1} t^{-1})	1142.4	737.9	40.4	54.8

*Determined specifically for C or N, otherwise for total organic matter; see text. **Includes determinations for both fresh and aged kelp diets. Rate functions are normalized to a standard animal (6·3 g dry tissue weight). SPM = mean suspended particulate matter concentration entering holding tanks; same concentrations used at the start of clearance measurements. SPM values differ slightly from similar data given in Cranford and Grant (1990) because additional data on SPM in holding tanks were used further to characterize food levels in scope for growth estimates. Ingestion and absorption are expressed for t=52 day growth trials assuming 45 days of actual feeding. AE=absorption efficiency.

Scallops were sampled for body component measurements four times during the study period (Grant & Cranford, 1989), but only initial and final tissue weight is considered here. Because the fresh kelp diet yielded highly variable assimilation efficiencies (probably due to settled food mixed with faecal samples; Cranford & Grant, 1990), we exclude this diet from calculations of carbon and nitrogen budgets. Data from this diet however, were used in the respiration/tissue-weight regression.

Clearance rates of individual scallops were measured as depletion of particles from each diet (N=4-5, CV=11-48%) in closed stirred chambers (4·25 l) at 5-8°C. Particle concentrations were measured with a Coulter Counter and clearance rate calculated as in Marin *et al.* (1986). Retention efficiency of *P. magellanicus* is 70-95% over the size range of most of the diet particles (5-30 μm) such that particle size was not considered limiting for ingestion (Cranford & Grant, 1990). Net absorption efficiency (AE) was measured weekly (N=8) by comparing food and faeces samples with the ash ratio method for total organic matter (Conover, 1966), and with biogenic silica as an inert tracer for carbon and nitrogen specific AE (diatom and sediment diets). Comparisons of these methodologies are discussed fully in Cranford & Grant (1990).

Respiration was measured as oxygen depletion in stirred 1·5 l chambers, darkened and incubated in a water bath at 6°C. Individual scallops were randomly chosen from the feeding tanks and placed into respiration chambers with flowing filtered sea water until the shell was open with tentacles extended. An initial water sample was taken and the chamber sealed. Oxygen in initial and final samples was measured with a Radiometer blood-gas analyzer. Reduction in oxygen from initial values was <20% over the 1·5-h incubations. Rates were corrected with control chambers containing 5 μm filtered sea water.

Scallops used in the laboratory population spanned a narrow range of shell height (mean=102 mm ±4·7 SD), but due to positive and negative tissue growth during the study period, shell-height/dry-tissue-weight regressions changed for each diet. In order to maintain the experimental population for growth measurements, tissue weights of scallops used in respiration experiments were predicted from length/weight regressions determined periodically during the study by sampling animals from each diet. Due to the small range in shell height, the mean of predicted weights differed by <9% from the measured mean weights within diet and date. An exception was the T-*Iso* diet where randomly-selected scallops for respiration measurements had greater shell height and estimated tissue weight (mean=8·8 g) than the mean tissue weights for that sampling period (mean=5·9 g). Estimated dry tissue weights were plotted *vs* individual respiration rates to create an overall regression for all diets.

In order to compensate for declining ambient temperature during the study, three median temperature periods were defined: days 0-15, 12°C (range 11-13·5°C); days 16-35, 8·5°C (range 7-10°C); and days 36-52, 6°C (range 5-7°C). A Q_{10} of 2·0 was applied to the respiration rates measured at 6°C. This value was based on calculation of a Q_{10} ~2 (0-12°C) from data on *Placopecten* respiration in Newfoundland waters (MacDonald & Thompson, 1986) and a Q_{10} ~2·4 (5-15°C) for this species on the coast of Maine (Shumway *et al.*, 1988).

Clearance rates could not simply be correlated with individual tissue weight for the overall data set because clearance rates were so strongly affected by diet. Even for the combined phytoplankton diets, we found no significant relationship between clearance and weight, but this included a very small weight range of animals (~7-9 g dry wt). Mean clearance rates were instead matched with contemporaneous mean dry weight of

scallops for that period sampled from a given diet. Rates were scaled to a scallop of standard weight:

$$R_{std} = (W_{std} / W_{obs})^b \cdot R_{obs} \tag{1}$$

where R_{std} is the clearance rate of a standard scallop ($1 \, h^{-1}$), W_{std} and W_{obs} are the dry tissue weights (g) of a standard and observed scallop respectively, and R_{obs} is the observed clearance rate. MacDonald & Thompson (1986) determined a consistent weight exponent of b=0·7 for clearance in *Placopecten*, and we have applied this value to Eq. 1. Their data suggest a Q_{10} of ~2·0 for clearance rate, also used in our calculations.

Ingestion rates were calculated as the product of clearance and initial concentration. A Perkin-Elmer 240B CHN analyzer was used to measure elemental content of the diets to derive carbon and nitrogen specific ingestion rates, and analyze carbon and nitrogen content of adductor muscle tissue. Carbon loss due to respiration was calculated with RQ=0·8 characteristic of post-spawn scallops (*Argopecten*) with protein-based metabolism (Barber & Blake, 1985). Following Seiderer & Newell (1985), we have estimated ammonia excretion using the known range of O/N for *Placopecten*. Volckaert (1988) determined an O/N=31·2±12·0 SD for juvenile Placopecten fed on a *Chaetoceros* and *Isochrysis* diet, and O/N=12·7±2·9 SD for starved scallops. In summer shipboard experiments with thermally-stressed sea scallops from Georges Bank (Grant & Cranford, in preparation), we determined an O/N=8·9±2·0 SD. The range of O/N used in our calculations (9-31) is close to the range determined for *Argopecten irradians concentricus* (Barber & Blake, 1985).

RESULTS

Scope for growth was calculated as the difference between carbon absorption and respiration (SFG_C), and nitrogen absorption and excretion (SFG_N). We have neglected other energy pathways in our calculations including excretion of amino acids and urea, and input of energy into shell growth, but these deletions are likely to be a small source of error (MacDonald, 1986; Griffiths & Griffiths, 1987). We first consider respiration and excretion for the various diets.

Carbon and nitrogen loss

A plot of respiration and estimated weight indicated that to some extent, rates of O_2 uptake differed simply due to change in weight of scallops under the different nutritional regimes (Figure 1). Compared to a linear model, a traditional log-log model of the data provided a substantially reduced fit with r^2=0·61 between respiration (mg O_2 ind^{-1} h^{-1}) and dry tissue weight W (g):

$$R=0·04 \, W^{1·64} \tag{2}$$

While the small size range of animals would influence the respiration-weight equation, the exceptionally high exponent relative to the average value of ~0·7 (Bayne & Newell, 1983) suggested that poor diets were causing reduced respiration beyond the effect of

weight alone. Weight-adjusted respiration rates (mg O_2 (g dry wt)$^{-1}$ h^{-1}) were significantly higher for scallops fed phytoplankton diets (0·15±0·02 SD, N=6) than in other diets, including the starved control (0·11±0·04 SD, N=12; Wilcoxon rank sum test, $P<0·05$).
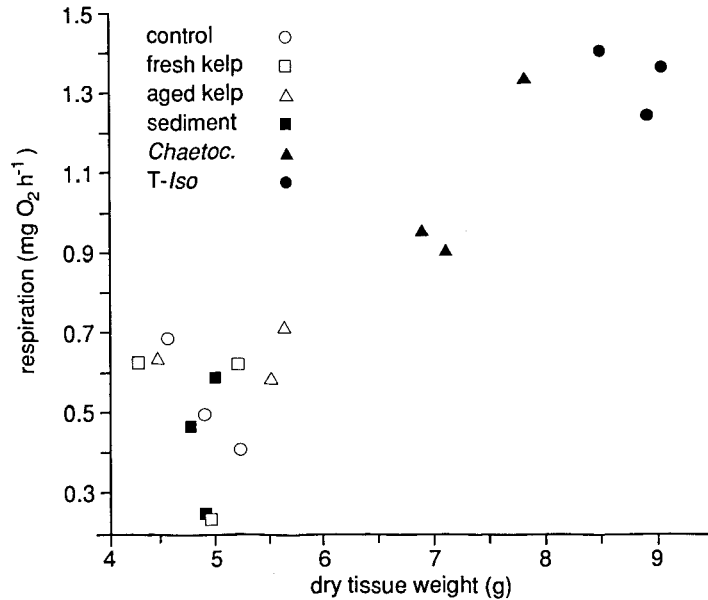

Figure 1. Respiration rate of individual *Placopecten magellanicus* vs estimated dry tissue weight for various laboratory diets.The regression equation is respiration = 0·21 (weight) - 0·50; r^2=0·81, $P<0·05$.

The linear regression equation for Figure 1 was used to estimate respiratory carbon loss in SFG calculations. Mean initial dry tissue weight of scallops was 6·30 g ±1·15 SD. With a carbon content of 40% dry tissue weight and C/N=3·5 (see below), the initial values for a standard scallop were 2·52 g C and 0·72 g N. At 6°C, respiration from the equation in Figure 1 was 0·82 mg O_2 ind^{-1} h^{-1}. Summing temperature-specific respiration rates over the three temperature periods and converting to carbon equivalents yielded a respiratory loss of 377 mg C ind^{-1} for a standard scallop during the study period.

Nitrogen loss was assumed to be due only to ammonia excretion (Bayne & Newell, 1983). For an O/N=9, a standard scallop lost 1·7 mg N d^{-1} at 6°C. Applying a Q_{10}=2·0 to maintain O/N, and summing over the temperature intervals, resulted in an ammonia excretion rate of 107·9 mg N for a standard scallop over the study period. For O/N=31, the corresponding value was 32·5 mg N.

Carbon and nitrogen intake

Multiplying standard clearance at each temperature by measured particle concentration, carbon content, and time for each temperature interval (11 h feeding d^{-1}, allowing seven unfed days) gave total carbon ingestion for the study period (Table 1). Sedimentation of the sediment and kelp diets made it difficult to maintain weight rations equivalent to

those supplied with phytoplankton diets. Because we were comparing SFG to actual growth, we have not normalized concentration to a standard value. In any event, the combination of high clearance and high carbon content resulted in much greater ingestion rates for individuals fed phytoplankton diets (Table 1). Increased concentration and carbon content of *Laminaria* detritus relative to resuspended sediment produced a twofold greater ingestion for kelp. Application of the absorption efficiency allowed calculation of the absorbed ration for each diet. Absorbed rations reflect the relative patterns of ingestion except for sediment, where a comparatively low AE for carbon caused this diet to lag further behind.

Similar calculations were applied to nitrogen intake using the C/N ratio to determine nitrogen ingestion for the study period (Table 1). Despite lower seston concentration in the sediment diet, its high nitrogen content and slightly higher clearance values allowed more nitrogen ingestion than in the kelp diet. The differential between phytoplankton and other diets was higher for nitrogen ingestion than for carbon ingestion (Table 1). In contrast to carbon absorption, the nitrogen richness and high AE of the sediment diet resulted in an absorbed nitrogen ration similar to the kelp diet.

Scope for growth and measured growth

Calculation of SFG produced a single value per diet for carbon (SFG_C) and two values for the nitrogen budget based on minimum and maximum O/N (SFG_{N9}, SFG_{N31}; Table 2). As expected, phytoplankton diets always displayed a positive SFG for both carbon and nitrogen. Net production efficiency for carbon ($NPE_C=SFG_C/$ Absorption; Tables 1 & 2) was usually >90%, among the highest values determined for suspension-feeding bivalves, including pectinids (Bayne & Newell, 1983; Griffiths & Griffiths, 1987; Thompson & MacDonald, in press). Sediment SFG_C was negative, but still less severe than the carbon loss associated with starvation in the unfed control. Aged kelp had a positive SFG_C ($NPE_C=62\%$), albeit 6-8 times less than the T-*Iso* and *Chaetoceros* diets.

For scallops fed phytoplankton, nitrogen excretion was small compared to absorption, and the range of the O/N ratio did not affect the high SFG_N. For sediment and kelp diets, animals with an O/N=31, indicative of non-stressful conditions, showed a positive

Table 2. *Scallop carbon and nitrogen scope for growth (SFG) based on the balance of measurements in Table 1*

Diet	SFG (mg C or mg N ind⁻¹ t⁻¹)			Growth Coefficient			
	C	N9	N31	G_C	G_{N9}	G_{N31}	G_{obs}
Chaetoceros	5109.3	1034.5	1109.9	0.63	0.51	0.54	0.12
T-Isochrysis	4050.0	630.0	705.4	0.54	0.36	0.39	0.15
Sediment	-235.9	-67.5	7.9	-0.08	-0.06	0.01	-0.11
Aged Kelp	619.3	-53.1	22.3	0.11	-0.04	0.02	-0.20
Control	-471.8	-107.9	-32.5	-0.12	-0.09	-0.03	-0.06

SFG was used to calculate monthly growth coefficients, specific to carbon (G_C), or nitrogen with O:N ratios of 9 (G_{N9}) and 31 (G_{N31}). Tissue growth measurements were used to calculate an observed growth coefficient (G_{obs}). Control diets of filtered sea water include only carbon and nitrogen loss terms. t = 52 days.

SFG_{N31}, with kelp (NPE_{N31}=41%) being superior to sediment (NPE_{N31}=20%). In contrast, an O/N=9, indicative of starvation, demonstrated a similar negative SFG_{N9} for both sediment and kelp diets. These results indicate that kelp and resuspended sediment could provide adequate supplemental nutrition for adult *Placopecten* which are not under previous nutritive stress. However, these foods do not seem adequate as sole dietary sources, as they did not show a positive SFG_{N9} in an animal which was previously nutrient-deprived.

In a comparison of carbon *vs* nitrogen scope for growth (Table 2), the kelp SFG_C was positive and relatively large next to SFG_{N31}, as expected of this high-carbon, readily-assimilated food source. In contrast, sediment SFG_C showed a carbon deficit while SFG_{N31} allowed a small but positive energy balance. We stress the difference between lack of growth in sediment and kelp diets: sediment was insufficient in carbon content and ration supplied, and thus indicated a negative balance in the carbon budget; kelp was adequate in carbon nutrition, but relatively deficient in nitrogen nutrition.

For comparisons with observed scallop growth, SFG was used to calculate a monthly carbon- or nitrogen-specific growth coefficient (G_C, G_N) using initial carbon or nitrogen weight (W_o=2·52 g C and 0·72 g N) and predicted carbon or nitrogen weight based on SFG (W_t=W_o+SFG) over t=52 days:

$$G_C, G_N = 30 \,/\, 52 \ln (W_t/W_o) \qquad\qquad (3)$$

Growth coefficients were also calculated from observed weight changes in scallops sampled from each diet (G_{obs}). Because shell height did not change significantly throughout the study, the initial shell height/weight relationship for scallops (all diets combined; Grant & Cranford, 1989) was used to back-calculate an initial weight for each scallop whose shell height and final weight were measured directly. The mean initial and final weights (N=5 for each, CV<20%) for each diet were used to derive G_{obs}. The use of growth coefficients allowed non-dimensional comparisons between growth rates estimated for carbon and nitrogen balance and change in weight (Table 2).

In most cases, the G_{obs} was less than the G_C and G_N's determined from scope for growth calculations (Table 2). Control values showed the closest agreement between observed and calculated results, but there is no variance arising from an ingestion term in this treatment. Discrepancies were greatest in the phytoplankton diets where G_{obs} was ~20-40% of those predicted from SFG_C and SFG_N. There was a reasonable correspondence between observed and predicted G_C and G_N for the kelp and sediment diets. The extent of deprivation in these detrital diets is apparent in comparing their growth coefficients with that of the starved control.

Within the G_C values (Table 2), individuals fed the kelp diet had a growth rate equal to 17% of the highest G_C (*Chaetoceros*). The G_{N31} for kelp was smaller but also positive. In contrast, the G_{N9} for kelp was negative, reflecting the negative SFG and reiterating that an animal under nutritive stress will not recover with this detrital diet. The sediment diet had a negative carbon growth coefficient, but displayed balanced nitrogen growth (G_{N31}=0·01). A closer correspondence between G_{N9} and G_{obs} than occurred with G_{N31} suggested that the lower O/N was probably a more realistic value for the detrital diets.

Tissue carbon and nitrogen

Adductor tissue had a carbon content of ~40% and a nitrogen content of ~13% (Table 3) agreeing closely with values found by Ansell (1974) for *Chlamys septemradiata*. In this species and *Placopecten*, the high nitrogen content of adductor tissue resulted in a C/N ratio of 3·0-3·2. In post-spawn scallops, gonad tissue had a similar carbon content to adductor tissue, but a lower C/N ratio due to higher nitrogen content (Ansell, 1974; Grant & Cranford, 1989). The other tissues (mantle, gills, etc.) have a C/N ratio of 4 or greater, elevating the C/N ratio of the whole animal (Ansell, 1974), and justifying our value of 3·5 as an average for *Placopecten magellanicus*.

Diet seemed to have little effect on *Placopecten* tissue composition (Table 3). Changes in bivalve C/N ratio are expected during starvation (Ansell & Sivadas, 1973) as reflected in utilization of protein reserves and decreasing O/N ratios, especially in reproductively spent animals (Bayne, 1973; Gabbott & Bayne, 1973; Bayne & Scullard, 1977). The range of C/N ratios for pectinids appears less than for *Donax vittatus* and *Mytilus edulis* (Ansell & Sivadas, 1973; Hawkins *et al.*, 1985), such that C/N may be a less suitable indicator of stress in this group.

Table 3. *Mean carbon and nitrogen content (%) of dry tissue weight (±SD) of scallop adductor muscle tissue at beginning and end of feeding trials for two diets, N=3*

Diet	20 October			11 December		
	C	N	C/N	C	N	C/N
Chaetoceros	40.3	12.7	3.2	40.0	13	3.1
	(3.2)	(0.6)	(0.2)	(1.0)	(1.7)	(0.3)
Aged Kelp	40.3	12.7	3.2	37.7	13.3	2.9
	(3.2)	(0.6)	(0.2)	(3.2)	(2.5)	(0.4)

DISCUSSION

Our results showed that scope for growth was an accurate predictor of actual growth for detrital diets in which animals were under nutritive stress. With such low growth efficiencies, SFG was predicting the rate of starvation; errors in ingestion were not critical. Potentially optimum diets of phytoplankton did not produce the growth predicted by the scallop energy budget. These results are opposite those of Riisgård & Randløv (1981) who found that SFG and growth agreed well in *Mytilus edulis* fed algal monoculture. In food-limited mussels, SFG produced an over-estimate of weight loss because their calculations incorporated respiration rates extrapolated from healthy individuals.

Our respiration values were in general agreement with those obtained previously for *Placopecten magellanicus* (MacDonald & Thompson, 1986; Shumway *et al.*, 1988). Figure 1 allowed for the dietary source of variance in our estimates of respiratory loss, such that sediment and kelp diets were probably between basal (starving) and standard (quiescent) metabolic rates (Hawkins *et al.*, 1985). Similarly, MacDonald & Thompson (1986) found higher weight-adjusted respiration in a shallower (10 m) *P. magellanicus* population than

in a 31-m food-poor population. Depression of weight-specific respiration rate due to nutritive stress has also been observed in *Mytilus edulis* (Bayne, 1973).

Scallops fed on phytoplankton diets were noticeably more active than those receiving detrital diets. The oxygen consumption rates for the *Chaetoceros* and T-*Iso* rations were probably closer to a routine rate (*sensu* Bayne *et al.*, 1985) reflecting the extra activity associated with feeding, digestion (Bayne & Scullard, 1977), and growth (Hawkins, 1985). The occasionally-observed swimming activity would periodically add to these respiratory costs (Thompson *et al.*, 1980). Our measurements indicate an increase in weight-adjusted metabolism of 36% in the phytoplankton *vs* other diets. Hawkins *et al.* (1985) determined an increase of 38% for a similar comparison between fed and starved *Mytilus edulis*.

Variance in carbon and nitrogen SFG arises from estimates of ingestion rates because particle depletion in the feeding tanks was greater with phytoplankton than with detritus diets (Cranford & Grant, 1990). Scallops fed phytoplankton would thus be exposed to a more variable food supply such that average incoming food concentrations used in SFG calculations might over-estimate ingestion. In addition, filtration rates based on short-term measurements (necessitated by diet supply) may not be constant during the day (Mathers, 1976).

Errors associated with the carbon budget including both estimated (Q_{10}, weight exponents) and measured (*e.g.* clearance) components add considerable variance to SFG calculations, if ingestion is over-estimated and metabolic cost is under-estimated (Bayne & Widdows, 1978). We thus depict a 'worst case' carbon budget for the *Chaetoceros* diet in which clearance rate was given its 6°C value and assumed not to increase with temperature. In addition, respiration rate was doubled to account for active metabolism including swimming (Thompson *et al.*, 1980). The results are expressed using eq. 3 to solve for final weight (W_t) after 52 d (Table 4). This crude sensitivity analysis indicated that there was a greater than two-fold difference in final weight in comparing the G_C to G_{obs}. However, a minimum G_C incorporating the above corrections provided much closer agreement with G_{obs}. A comparison of SFG to observed growth in *P. magellanicus* and *Mytilus edulis* (Bayne *et al.*, 1979; Thompson & MacDonald, in press) suggests that the range of differences in Table 4 are not exceptional, especially after spawning.

Although SFG is not necessarily a measure of short-term production, it remains an invaluable tool for comparison of populations, sources of stress, etc. (Bayne *et al.*, 1985; Widdows & Johnson, 1988). For example, SFG enabled us to determine the different

Table 4. *Prediction of final dry tissue weight (W_t) of standard scallops (initial dry weight=6.3 g) at the end of feeding experiments (t=52 days)*

Source	G	W_t(g)
Observed	0.12	7.8
SFG_C	0.63	18.8
SFG_C(Min)	0.35	11.6

Monthly growth coefficients (G) used in eq. 3 to calculate W_t (specific to a *Chaetoceros gracilis* diet) are derived from measured tissue weight (observed), or estimated from carbon scope for growth (SFG_C; Table 2), and a minimum SFG_C which incorporates the simplifying assumptions specified in the text.

reasons why both resuspended sediment and kelp detritus failed to produce tissue growth. A more important result of our study than an absolute SFG/measured growth comparison is the contrast in carbon and nitrogen scope for growth and its relationship to diet.

The animals used in the feeding experiments were presumably in the resting stage of gametogenesis wherein tissue weight components and indices are at an annual low (Thompson, 1977; Robinson *et al.*, 1981; Grant & Cranford, 1989). Energy reserves of adductor muscle carbohydrate and lipid used in gametogenesis are depleted, and adductor protein becomes the major energy reserve (Barber & Blake, 1985). Protein, a primary component of tissue, is less often considered in bivalve growth and reproduction (Hawkins, 1985) compared to the emphasis on carbohydrates and lipid storage cycles (Gabbott, 1975; Bayne *et al.*, 1982). In *P. magellanicus* from Georges Bank, protein content of all tissue is high enough that tissue nitrogen content remains >8% (Cranford, unpublished).

In order for the nitrogen content of tissue to be conserved, adequate nitrogen must be present in the diet. Bayne & Widdows (1978) found positive nitrogen balance in *Mytilus edulis* for most of the year, while Hawkins & Bayne (1985) calculated a minimum diet C/N requirement of 12 (summer) to 83 (winter) for this species (culture fed) and suggested that carbon limitation may be significant in a phytoplankton-based mussel population. Using the clearance rate, concentration, and AE of the *Chaetoceros* diet, *Placopecten* could balance nitrogen excretion (O/N=9) with a diet C/N ratio as high as 65. Phytoplankton diets can clearly allow favourable nitrogen balance (Table 2), even with a post-spawning shift toward increased nitrogen utilization.

Despite the nutritive importance of phytoplankton, the high primary production of macrophytes in coastal ecosystems points to the trophic significance of material such as kelp detritus (Branch & Griffiths, 1988; Mann, 1988). For inshore sea scallop populations, non-phytoplankton food sources may be a substantial portion of the suspended particle load. Recent field studies in the Aleutian Islands suggest that growth in *Mytilus edulis* is 2-4 times greater in a kelp-rich environment (Duggins *et al.*, 1989). Some kelp bed suspension feeders can take advantage of intermittently high concentrations of suspended detritus (Fielding & Davis, 1989) which offsets the poor quality of these diets. *Placopecten* increases its ingestion rate with higher concentrations of resuspended sediment, even over a range of several mg l^{-1} (Cranford & Grant, unpublished data), but the functional response of scallops to seaweed detritus is unknown. Nonetheless, sea scallops have a low clearance rate for kelp detritus relative to phytoplankton at a similar concentration (Table 1), limiting the contribution of kelp to the ingested ration.

For an aged kelp diet (concentration, clearance, AE as in Table 1), a C/N food ratio of ~11 would be required to balance nitrogen demand (O/N=9) in *Placopecten magellanicus*. The lowest value recorded in our kelp incubations (maximum ageing=6 days) was ~14, although Stuart *et al.* (1982) found C/N as low as ~6 for *Laminaria pallida*. Further work on functional aspects of feeding are clearly necessary (Bayne *et al.*, 1989), but our SFG results (O/N=31) support the role of seaweed detritus as a food supplement (Seiderer & Newell, 1985; Fielding & Davis, 1989) if not a sole diet. Carbon-rich substrates such as

macrophyte detritus may be suitable for the rebuilding of carbohydrate or lipid reserves in the depleted, low C/N adductor tissue of post-spawn inshore scallops.

Recent studies have emphasized the extent to which carbon requirements of invertebrates can be met by detrital food sources including macrophyte debris (Mann, 1988; Fielding & Davis, 1989). Stuart (1982) predicted a large positive scope for growth and NGE up to 87% for the mussel *Aulacomya* on a diet of kelp detritus. Our results indicate that caloric or carbon budgets may overestimate scope for growth when inadequate nitrogen is available. The same conclusion is supported for *Aulacomya* in that ~70% of nitrogen requirements but 142-165% of carbon requirements are met from seston above a kelp bed (Fielding & Davis, 1989). In our work, nitrogen limitation provides a satisfactory explanation for the inadequacy of the macroalgal diet and supports the classical paradigm of detrital-based food webs: despite abundant particulate organic carbon, particulate nitrogen can impose limits on secondary production (Mann, 1989). Carbon and nitrogen needs of bivalves relative to temporal changes in food quantity, somatic growth, and gonad growth (Hawkins & Bayne, 1985; Hawkins *et al.*, 1985), will determine the suitability of carbon budgets alone as measures of scope for growth.

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PERMISSIONS

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