INFLUENCE OF THE NATURAL FOOD SUPPLY ON THE PHYSIOLOGICAL ENERGETICS AND BIOCHEMICAL STORAGE CYCLES OF THE HORSE MUSSEL, Modiolus modiolus (Linnaeus)

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Influence of the Natural Food Supply on the Physiological Energetics and Biochemical Storage Cycles of the Horse Mussel, *Modiolus modiolus* (Linnaeus)

by

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ABSTRACT

A population of *Modiolus modiolus* (horse mussel) inhabiting a sub-arctic environment in Logy Bay, Newfoundland, was studied for a period of two years. The main objective was to gain insight into the relationship between environmental factors (temperature and components of the seston) and the physiological response of this species. Measurements of the biochemical composition of the gonad, digestive gland and remaining tissue were made over the same period to support the physiological and environmental data. All the variables determined for the suspended particulate matter (seston), i.e. organic matter, chlorophyll *a*, organic carbon and nitrogen, lipid, carbohydrate and protein, and the number and volume of the particles, showed a clear seasonal pattern, with higher values during the spring and summer of each year of study.

The highest values for energy acquisition (ingestion and absorption rates) by *Modiolus modiolus* coincided with the spring phytoplankton bloom occurring during April-May in Logy Bay, whereas energy expenditure (oxygen uptake and ammonia excretion rates) was greatest during the summer (July and August). The result was a clear seasonal fluctuation in the two physiological integrations, scope for growth (SFG) and net growth efficiency (K_2), for which lower values were associated with a high metabolic rate, high temperature and low quality of the food supply. Conversely, higher values of SFG and K_2 were associated with a low metabolic rate, low temperature and an energy-rich food supply provided by the phytoplankton bloom.

The ash-ratio technique (Conover, 1966) was compared with other techniques for measuring absorption efficiency, and found to be a valid as well as a convenient method for use with horse mussels feeding on natural seston.

Proximate biochemical analysis of the gonad, digestive gland and remaining tissue suggested that in Logy Bay *Modiolus modiolus* may compensate for the nutritive stress induced by poor food conditions for much of the year by prolonging the period over which energy reserves are accumulated, rather than by a reduction in fecundity or egg quality.

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CONTENTS

ABSTRACT ii
ACKNOWLEDGMENTS iii
LIST OF ABBREVIATIONS viii
LIST OF TABLES ix
LIST OF FIGURES xii

I. INTRODUCTION 1

I.1. GENERAL 1
I.2. ENVIRONMENTAL VARIABLES 1
I.3. PHYSIOLOGICAL PROCESSES 2
I.4. ENERGY STORAGE CYCLES 4
I.5. OBJECTIVES 5

II. MATERIAL AND METHODS 6

II.1. ENVIRONMENTAL VARIABLES 6

II.1.1. Study Site 6
II.1.2. Collection of Water Samples 6
II.1.3. Suspended Particulate Matter (Seston) 6
II.1.4. Chlorophyll *a* and Phaeopigments 7
II.1.5. Particulate Organic Carbon (POC) and Nitrogen (PON) 7
II.1.6. Particulate Carbohydrate 7
II.1.7. Particulate Lipid 8
II.1.8. Food Index 8
II.1.9. Particle Size Distribution 8

II.2. PHYSIOLOGICAL EXPERIMENTS 9

II.2.1. Experimental Animals 9
II.2.2. Clearance Rate 10
II.2.3. Ingestion Rate 12
II.2.4. Absorption Efficiency 12
II.2.5. Oxygen Uptake 12
II.2.6. Ammonia Excretion 13
II.2.7. Scope for Growth 13

II.2.8. Net Growth Efficiency (K_2) 15

II.3. COMPARISON OF METHODS FOR ABSORPTION EFFICIENCY 15

II.3.1. General 15
II.3.2. Ash 16
II.3.3. Silicate 16
II.3.4. Chloropigments 17
II.3.5. Carbon 17

II.4. FAECES AND PSEUDOFAECES PRODUCTION 18

II.4.1. Biodeposition 18
II.4.2. Microscopic Analysis 18
II.4.3. Chlorophyll *a*, Carbon, Nitrogen and Silicate Content 18

II.5. ENERGY STORAGE CYCLES 18

II.5.1. General 18
II.5.2. Lipid 19
II.5.3. Carbohydrate 19
II.5.4. Protein 19

II.6. STATISTICAL ANALYSIS 19

III. RESULTS 21

III.1. ENVIRONMENTAL VARIABLES 21

III.1.1. Temperature and Suspended Particulate Matter 21
III.1.2. Chlorophyll *a* and Phaeopigments 21
III.1.3. Particulate Organic Carbon (POC) and Nitrogen (PON) 27
III.1.4. Biochemical Composition of the Seston 27
III.1.5. Food Index 30
III.1.6. Particle Size Distribution 30
III.1.7. Correlation Analysis 33

III.2. PHYSIOLOGICAL PROCESSES 33

III.2.1. Clearance Rate 33
III.2.2. Ingestion Rate 38
III.2.3. Absorption Efficiency 44
III.2.4. Oxygen Uptake 44

III.2.5. Ammonia Excretion 44
III.2.6. Scope for Growth 51
III.2.7. Net Growth Efficiency 51
III.2.8. Correlation Analysis and Multiple Regression 57
III.2.9. Nitrogen Balance 57

III.3. ABSORPTION EFFICIENCY: COMPARISON AND EVALUATION OF DIFFERENT TECHNIQUES 60

III.4. FAECES AND PSEUDOFAECES PRODUCTION 63

III.4.1. Biodeposition 63
III.4.2. Microscopic Analysis of the Biodeposits; Microalgae Composition 70
III.4.3. Chlorophyll *a*, POC, PON and Silicate Content in Food, Faeces and Pseudofaeces 71

III.5. WEIGHT AND ENERGY STORAGE CYCLES 76

III.5.1. Seasonal Changes in Tissue Weight 76
III.5.2. Seasonal Synthesis and Utilization of Biochemical Energy Reserves 80

III.5.2.1. Introduction 80
III.5.2.2. Somatic tissue 80
III.5.2.3. Gonad tissue 82
III.5.2.4. Digestive gland 85

III.5.3. Seasonal cycle in energy content 89

IV. DISCUSSION 91

IV.1. QUANTITY, BIOCHEMICAL COMPOSITION AND SIZE SPECTRA OF THE SESTON 91

IV.2. PHYSIOLOGICAL PROCESSES 97

IV.3. TECHNIQUES FOR THE MEASUREMENT OF ABSORPTION EFFICIENCY 104

IV.4. BIODEPOSITS 105

IV.5. TISSUE WEIGHT CYCLES 107

IV.6. SYNTHESIS AND UTILIZATION OF BIOCHEMICAL ENERGY RESERVES 109

V. CONCLUSIONS 111

VI. REFERENCES 114

VII. APPENDICES 128

VII.1. RATE OF AMMONIA EXCRETION AS A FUNCTION OF INCUBATION TIME 129

VII.2. HYDROLYSIS CONDITIONS FOR SILICATE ANALYSIS 130

VII.3. ENERGY CONTENT OF THE SESTON 131

LIST OF ABBREVIATIONS

AE = Absorption Efficiency

AR = Absorption Rate

CHLA = Chlorophyll *a*

CHO = Particulate Carbohydrate

CR = Clearance Rate

DTW = Dry Tissue Weight

FIDX = Food Index

FM = Food Material

IR = Ingestion Rate

K_2 = Net Growth Efficiency

LIP = Particulate Lipid

PARTN = Particle Number

PARTV = Particle Volume

PIM = Particulate Inorganic Matter

POC = Particulate Organic Carbon

POM = Particulate Organic Matter

PON = Particulate Organic Nitrogen

SFG = Scope For Growth

SPM = Suspended Particulate Matter

TCA = Trichloroacetic Acid

TEMP = Temperature

TPM = Total Particulate Matter

TIR = Total Ingestion Rate

VNH_4-N = Ammonia Excretion Rate

VO_2 = Oxygen Uptake Rate

LIST OF TABLES

Table 1. Comparison of TPM and POM between samples collected and pumped from Logy Bay. Significance was measured by a t-test of paired comparisons. 25

Table 2. Gravimetric, electronic and chemical analyses of suspended particulate matter in Logy Bay (Monthly means). 26

Table 3. Pearson product-moment correlation coefficients between environmental variables. $P \leq 0.05$ (*); $P \leq 0.01$ (**). Number of cases in parentheses. 37

Table 4. *Modiolus modiolus*. Regressions of clearance rate ($l.h^{-1}$) against dry weight (g) for different dates. Regression equations are of the form $Y = aW^b$, where Y = clearance rate and W = dry weight. The statistic F tests the significance of the difference between the slope b and zero. 42

Table 5. *Modiolus modiolus*. Regressions of absorption efficiency (%) against dry weight (g) for different dates. Regression equations are of the form $Y = aW^b$, where Y = absorption efficiency and W = dry weight. The statistic F tests the significance of the difference between the slope b and zero. 46

Table 6. *Modiolus modiolus*. Regressions of oxygen uptake (ml $O_2.h^{-1}$) against dry weight (g) for different dates. Regression equations are of the form $Y = aW^b$, where Y = oxygen uptake and W = dry weight. The statistic F tests the significance of the difference between the slope b and zero. 49

Table 7. *Modiolus modiolus*. Regressions of ammonia excretion (μg NH_4-N. h^{-1}) against dry weight (g) for different dates. Regression equations are of the form $Y = aW^b$, where Y = ammonia excretion and W = dry weight. The statistic F tests the significance of the difference between the slope b and zero. 52

Table 8. *Modiolus modiolus*. Scope for growth for a "standard" horse mussel of 2.0 g dry weight. See "Material and Methods" for details of calculations. 54

Table 9. Pearson product-moment correlation coefficients between physiological and environmental variables. $P \leq 0.05$ (*); $P \leq 0.01$(**). Number of cases in parentheses. 58

Table 10. *Modiolus modiolus*. Multiple regression statistics for several physiological variables vs. subsets of independent variables. * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$. 59

Table 11. *Modiolus modiolus*. Absorption efficiency (%) of horse mussels feeding on natural seston, measured in terms of dry weight of organic matter (ash-ratio and silicate-ratio), organic carbon and chloropigments. 65

Table 12. *Modiolus modiolus*. Comparison of absorption efficiency values from different methods. Significance was measured by the Tukey-Kramer test. 67

Table 13. *Modiolus modiolus*. Biodeposition rate (faeces and pseudofaeces) during and after the phytoplankton bloom of 1988. SE is expressed in parentheses. 68

Table 14. *Modiolus modiolus*. Chemical composition of the food supply and of biodeposits (faeces and pseudofaces) produced during the phytoplankton bloom of 1988. SE is expressed in parentheses. 69

Table 15. *Modiolus modiolus*. Relative content of chlorophyll *a* (by weight) in faeces and pseudofaeces. SE is expressed in parentheses. 74

Table 16. *Modiolus modiolus*. Pigment budget for a "standard" mussel of 2.0 g dry weight during the phytoplankton bloom of 1988. 75

Table 17. *Modiolus modiolus*. Comparison by ANOVA of the biogenic silica content in food, faeces and pseudofaeces followed by a multiple range test (NS, not significant at $P \geq 0.05$). 77

Table 18. *Modiolus modiolus*. Regressions of shell length (cm) against dry tissue weight (g) for different dates. Regression equations are of the form $Y = aX^b$, where Y = dry tissue weight and X = shell length. The statistic F tests the significance of the difference between the slope b and zero. 78

Table 19. Total particulate matter (TPM) and particulate organic matter (POM) concentrations reported at different sites. 92

Appendix III. Conversion of protein, lipid and carbohydrate in the seston to energy equivalents. 131

LIST OF FIGURES

Fig. 1. Apparatus used to measure clearance rates in horse mussels. 11

Fig. 2. Apparatus used to measure oxygen uptake in horse mussels. 14

Fig. 3. Seasonal temperature cycle in Logy Bay. 22

Fig. 4. Seasonal cycles of suspended particulate matter (SPM) in Logy Bay. (A) Total particulate matter (TPM); (B) particulate organic matter (POM); (C) monthly means (± S.E.) for TPM and POM. For clarity only plus S.E. bars are shown. When no S.E. bars are shown they were smaller than the symbols. 23

Fig. 5. Seasonal cycles of chlorophyll *a* (A), phaeopigments as chlorophyll *a* equivalents (B) and chlorophyll *a* : phaeopigments ratio (C) in Logy Bay. 24

Fig. 6. Seasonal variation in (A) particulate organic carbon (POC); (B) particulate organic nitrogen (PON); (C) POC : chlorophyll *a* ratio; (D) C:N ratio in Logy Bay. 28

Fig. 7. Seasonal cycle in particulate carbohydrate (A), lipid (B) and protein (C) in Logy Bay. 29

Fig. 8. Seasonal fluctuation in the concentration of food material (FM) and the food index (FIDX). 31

Fig. 9. Seasonal variation in the size frequency distribution of the SPM in Logy Bay, expressed as total particles per ml (A) and total volume (B). 32

Fig. 10. Size frequency distribution of the SPM in Logy Bay (March-Aug. 1987). 34

Fig. 11. Size frequency distribution of the SPM in Logy Bay (Sept. 1987-Feb. 1988). 35

Fig. 12. Size frequency distribution of the SPM in Logy Bay (March-June 1988). 36

Fig. 13. Representative short-term patterns of clearance rates for individual horse mussels during early summer 1987 (A,B) and spring 1988 (C,D). DTW=Dry tissue weight. 39

Fig. 14. Representative short-term patterns of clearance rates for individual horse mussels during fall 1986 (A,B) and winter 1988 (C,D). DTW=Dry tissue weight. 40

Fig. 15. Clearance rates in three size classes of *Modiolus modiolus*. Values are monthly means ± S.E. When no S.E. bars are shown they were smaller than the symbols. 41

Fig. 16. Ingestion rate (TPM and POM) for a mussel of 2g dry tissue weight. 43

Fig. 17. Absorption efficiency in *Modiolus modiolus*. Values are monthly means ± S.E. When no S.E. bars are shown they were smaller than the symbols. 45

Fig. 18. Oxygen uptake (VO_2) in three size classes of *Modiolus modiolus*. Values are monthly means ± S.E. When no S.E. bars are shown they were smaller than the symbols. 47

Fig. 19. Regressions of oxygen uptake ($ml.h^{-1}$; circles) and ammonia excretion ($\mu g\ NH_4\text{-}N.h^{-1}$; triangles) against temperature for a 5 g dry tissue weight *Modiolus modiolus*. 48

Fig. 20. Ammonia excretion (VNH_4-N) in three size classes of *Modiolus modiolus*. Values are monthly means ± S.E. When no S.E. bars are shown they were smaller than the symbols. 50

Fig. 21. Seasonal variation in the atomic ratio of oxygen consumed to the ammonia-nitrogen excreted in a horse mussel of 5g dry tissue weight. 53

Fig. 22. Seasonal cycle in the scope for growth (SFG) for three size classes of *Modiolus modiolus*. 55

Fig. 23. Net growth efficiency (K_2) (based on regressions of pooled data of each physiological variable) vs. dry tissue weight for *Modiolus modiolus*. 56

Fig. 24. Seasonal variation in the nitrogen balance (as % of body nitrogen) of a horse mussel of 2g dry tissue weight. 61

Fig. 25. Comparison of absorption efficiency values for *Modiolus modiolus* using the ash ratio and the silicate ratio methods. Horse mussels were feeding on natural seston from Logy Bay. (A) Absorption efficiency at different silica concentrations; (B) ratio of values from the ash method to those from the silicate method. 62

Fig. 26. Comparison of absorption efficiency values for *Modiolus modiolus* using the ash ratio and the silicate ratio methods. Horse mussels were feeding on cultured microalgae. (A) Absorption efficiency at different silicate concentrations; (B) ratio of values from the ash method to those from the silicate method. 64

Fig. 27. Comparison of absorption efficiency values from four different methods for *Modiolus modiolus* feeding on natural seston during the phytoplankton bloom. 66

Fig. 28. Organic carbon (A) and nitrogen (B) content of the food, faeces and pseudofaeces during the phytoplankton bloom. 72

Fig. 29. Chlorophyll *a* (A) and biogenic silica content (B) of the food, faeces and pseudofaeces during the phytoplankton bloom. 73

Fig. 30. Seasonal fluctuation in the dry tissue weight for total (A), somatic (B), gonad (C) and digestive gland (D) of a horse mussel of shell length 10 cm. 79

Fig. 31. Seasonal fluctuation in the proximate biochemical composition of the somatic tissue of *Modiolus modiolus*. Biochemical constituents are expressed as percentages of dry weight (monthly means ± S.E., n=5). 81

Fig. 32. Seasonal variation in the weights of the biochemical constituents of the somatic tissue in *Modiolus modiolus* ("standard" animal of length 10 cm). Values are monthly means ± S.E., n=5. 83

Fig. 33. Seasonal fluctuation in the proximate biochemical composition of the gonad in *Modiolus modiolus*. Biochemical constituents are expressed as percentages of dry tissue weight (monthly means ± S.E., n=5)84

Fig. 34. Seasonal changes in the weights of the biochemical constituents of the gonad in *Modiolus modiolus* ("standard" animal of length 10 cm). Values are monthly means ± S.E., n=5. 86

Fig. 35. Seasonal variation in the proximate biochemical composition of the digestive gland in *Modiolus modiolus*. Biochemical constituents are expressed as percentages of dry weight (monthly means ± S.E., n=5). 87

Fig. 36. Seasonal fluctuation in the weight of the biochemical constituents of the digestive gland of *Modiolus modiolus* ("standard" animal of length 10 cm). Values are monthly means ± S.E., n=5. 88

Fig. 37. Seasonal changes in the energy content of the somatic tissue, gonad and digestive gland of *Modiolus modiolus* ("standard" animal of length 10 cm). Values are monthly means ± S.E., n=5. 90

Appendix I. Evidence that the NH_4-N excretion rate in *Modiolus modiolus* is independent of the ammonia concentration in the experimental chambers for at least 20 hours. 129

Appendix II. Time course for the extraction of silica under the conditions described in the text (Material and Methods). Hydrolysis is complete within three hours. 130

I. INTRODUCTION

I.1. GENERAL

Whereas the blue mussel *Mytilus edulis* has been studied extensively, little is known about the closely-related mytilid *Modiolus modiolus*, especially regarding its physiology under natural conditions. One of the more comprehensive studies on this species was that by Rowell (1967), in which he considered aspects of its ecology, growth and reproduction. Apart from this work, some studies have been done on the ecology (Roberts, 1975; Seed and Brown, 1975; Brown et al., 1976), physiology (Schlieper et al., 1958; Winter, 1970; Coleman, 1976; Coleman and Trueman, 1971) reproduction (Brown and Seed, 1976; Seed and Brown, 1977; Comely, 1978, 1981; Jasim and Brand, 1989) and larval development (Schweinitz and Lutz, 1976) of *Modiolus modiolus* (horse mussel).

Modiolus modiolus is a relatively abundant species along the Atlantic coasts of North America and northern Europe and it is of interest to establish the physiological response of this filter-feeding species to changing environmental conditions in order to gain insight into trophic interactions in the ecosystem. A detailed analysis of the energy budget of *Modiolus modiolus* may provide a means of understanding the effects of seasonal environmental changes (mainly seston) on the degree of physiological plasticity and adaptation of this species to its environment.

I.2. ENVIRONMENTAL VARIABLES

Sessile suspension-feeding organisms can experience short-term and long-term changes in environmental conditions (e.g. temperature, salinity and suspended particulate matter or seston). One of the most important environmental variables is the seston, which includes living plankton, organic detritus and inorganic particles. The quantity of suspended particulate matter (SPM) and its quality as food for filter-feeders varies both temporally and spatially in response to physical and biological factors (Armstrong, 1958; Berg and Newell, 1986). Among the principal factors that can influence the quantity and quality of the SPM are biological production (Anderson, 1970; Widdows et al., 1979), aperiodic storms (Ward, 1981; Gordon, 1983), wind-wave resuspension (Soniat et al., 1984; Berg and Newell, 1986) and tidal resuspension (Anderson and Meyer, 1986; Incze and Roman, 1983). A knowledge of the variation in the quality as well as the quantity of the natural diet available for suspension feeding organisms is an important component of any study of feeding behaviour. In this context, Bayne et al. (1987) have reported that at least three features of dietary quality should be considered: a) the size of the suspended

particles; b) the balance in the diet between biologically inert and metabolizable fractions and c) the biochemical composition of this metabolizable fraction.

Many studies have been done on the seston of marine environments, but the majority have been concerned with quantifying either the total suspended organic matter or the concentration and size of the particles. Only a few recent studies (Mayzaud and Taguchi, 1979; Widdows et al., 1979; Kranck, 1980; Mayzaud et al., 1984; Poulet et al., 1986; Mayzaud et al., 1989) have considered the biochemical composition of the SPM, despite its potential value as an indicator of the nutritional value of the seston (Myklestad and Haug, 1972). Healey (1973) suggested that the ratio of protein to carbohydrate may be used as an indicator of nutrient deficiency both for cultured and natural populations of algae. Zeitzschel (1970) assumed that values of 100 or less for the ratio carbon:chlorophyll *a* indicate that the carbon originates mainly from living phytoplankton, suggesting a rich food supply. According to Russell-Hunter (1970), animals have nutritional requirements for proteins which correspond to C:N ratios lower than 17. The nutritive value of the SPM has also been related to the protein to carbohydrate to lipid ratio; Parsons et al. (1961) and Scott (1980) reported that for phytoplankton cultures the required ratios are 4:3:1 or 1:1:1 in order to satisfy the food requirements of filter-feeders. Thus the natural diets of suspension-feeding organisms can fluctuate in time and space, consisting of assemblages of mixed particles having different nutritive values depending on their biochemical composition (Conover, 1978; Mayzaud et al., 1984; Poulet et al., 1986).

According to Worrall et al. (1983), factors such as the quality and quantity of particulate material in suspension are known to alter the physiological responses of bivalves to seasonal environmental changes. The organisms must be able to respond efficiently to these nutritional changes to make maximum use of the environment. It is therefore essential to determine the effects of seasonal fluctuations in the food supply on the physiological adaptability of individuals and the overall physiological plasticity of a species.

I.3. PHYSIOLOGICAL PROCESSES

Suspension feeding bivalves are of considerable importance as primary consumers in many marine systems, and they can play a significant role in energy transfer between trophic levels. These organisms frequently occur at high densities and can therefore remove and store large amounts of organic matter in the form of body tissue. Furthermore, they possess highly efficient filtering mechanisms, which enable them to concentrate large amounts of suspended particles from the pelagic system and reject some of this energy-rich material as faeces or

pseudofaeces, which reach the bottom, where they can be utilized as food by other organisms.

Several workers have determined individual physiological functions and the integrated responses of many species of marine bivalves. Bayne et al. (1976) and Bayne and Newell (1983) have reviewed this literature, which is mostly concerned with measurements made under laboratory conditions, often with algal monocultures as food. Results from such studies may not be truly representative of the natural situation, and more emphasis is now being placed on measurements of physiological rates under more natural conditions, preferably in the field (Bayne et al., 1977; Widdows, 1978; Bayne and Widdows, 1978; Newell and Bayne, 1980; Vahl, 1980; Thompson, 1984a; MacDonald and Thompson, 1986).

Clearance rate is often strongly associated with food availability, and recent theoretical explanations of feeding by suspension and deposit feeders have suggested that the organisms can optimize energy yields when food varies both in quality and quantity (Taghon et al., 1978; Cammen, 1980; Taghon, 1981; Bayne et al., 1988). Thus the optimal response is to increase the feeding rate (or ingestion rate) when an increase in food quality occurs, even when this results in a reduced gut retention time with a consequent decline in absorption efficiency. Thompson and Bayne (1972, 1974), Calow (1975), Widdows (1978a) and Navarro and Winter (1982) have also suggested that ingestion rate and absorption efficiency may indeed be inversely related. Bayne et al. (1985) reported that individuals of *Perna perna* from South Africa feeding on low-quality diets show reduced clearance rates, slower gut passage rates and higher absorption efficiencies. Conversely, this species shows higher clearance rates, rapid passage of food through the gut and reduced absorption efficiencies in higher food concentrations. However, when calculated on a daily basis the absorbed ration is very similar under the two different diets, showing that the physiological flexibility to maximise scope for growth is mainly based on balances between clearance rates, residence time in the gut, and absorption efficiency.

Oxygen uptake also plays a significant role in the calculation of two integrated physiological indices, scope for growth (SFG) and net growth efficiency (K_2). Changes in oxygen uptake are often difficult to interpret when this variable is measured in isolation, but when it is integrated with the other physiological processes it contributes to an understanding of the response of the whole organism to environmental change. According to Widdows (1985), an increase in metabolic rate may represent an adaptive response when it is associated with a higher level of food acquisition, which will result in a higher scope for growth.

The components of the energy budget of an organism (ingestion, absorption, excretion, respiration, growth and gamete production) are functionally coupled, and

changes in any one of these processes have consequences for some or all of the others (Bayne, 1985). The basic physiological rates converted into energy equivalents ($J.h^{-1}$) can be used in the balanced energy equation to calculate SFG and net growth efficiency (K_2). Scope for growth is a physiological index which represents the energy available for somatic growth and gamete production after subtracting the energy losses due to respiration and excretion from the energy absorbed from the food. Scope for growth has the advantage of defining the growth process in terms of individual physiological mechanisms, elucidating the physiological compensations which comprise the response to the environmental change (Bayne, 1985).

The net growth efficiency or K_2 represents the scope for growth per unit of absorbed ration, and is a measure of the efficiency with which food is converted into body tissues. Some of this "food conversion" may be channelled into gonad production rather than somatic growth, depending on the size of the animal and its physiological condition.

Like SFG, values of zero for K_2 indicate that metabolic requirements are just balanced by food intake, and therefore no tissue growth takes place. A value greater than zero indicates a state of positive energy balance and its magnitude is an indicator of the potential for tissue growth. Conversely, a value less than zero reflects a state of negative energy balance, indicating that the organism is using its energy reserves to meet the metabolic demand.

I.4. ENERGY STORAGE CYCLES

There is an extensive literature on seasonal cycles in tissue weight and biochemical composition associated with growth and reproduction in bivalve molluscs from the northern hemisphere (Ansell, 1974; Comely, 1974; Gabbott, 1976, 1983; Thompson, 1977, 1984a; Sastry, 1979; Zandee et al., 1980; Barber and Blake, 1981; Emmett et al., 1987). Most of these studies have been done on commercially important species, especially *Mytilus edulis* and various pectinids and ostreids.

Seasonal variation in the flesh weight and biochemical composition of bivalve molluscs is a function of the complex interactions of food availability and temperature with the processes of growth and reproduction (Ansell and Trevallion, 1967). Despite this consideration there is little information relating the changes in biochemical composition directly to these environmental factors (Thompson and MacDonald, 1990). These authors found that in poor food conditions scallops (*Placopecten magellanicus*) maintained the normal concentration of lipid in the gonad but did not accumulate somatic energy reserves, especially carbohydrate, to the same extent as did scallops under better conditions.

Bayne (1976) described different strategies in the use of energy reserves by temperate bivalves. Some species can accumulate energy reserves in one year to support gametogenesis in the next, whereas in others the synthesis of reserves occurs immediately before gametogenesis. Gabbott (1983) and Thompson (1984a) have shown that *Mytilus edulis* displays both of these strategies, depending on the population. Seed and Brown (1977a) and Comely (1978, 1981) found that the reproductive cycle of *Modiolus modiolus* can be different in populations from different locations, even those which are very close together, suggesting that the energy storage and reproductive cycles are able to respond to changes in environmental conditions.

I.5. OBJECTIVES

The approach to measuring the food supply of filter-feeding organisms was to evaluate the concentration and nutritional quality of the suspended particles throughout the year. One of the objectives of the present study was to quantify these components of the SPM (seston) in order to determine the seasonal changes in the nutritional value of the diet available to *Modiolus modiolus*.

In order to obtain an insight into the relationship between environmental factors (temperature and food supply) and the physiological response of *Modiolus modiolus*, a detailed analysis of size-related rates of oxygen uptake, clearance rate, excretion rate and absorption efficiency under these natural conditions was carried out in Logy Bay during the years 1986-1988. Measurements of the proximate biochemical composition of the gonad, digestive gland and remaining tissue were made at the same time, to provide a framework within which the physiological and environmental data could be interpreted.

The hypothesis of the present study postulates that the physiological response and the biochemical storage cycle of *Modiolus modiolus* in Logy Bay are determined more by the food availability than by the pronounced seasonal temperature cycle in this sub-arctic environment.

II. MATERIAL AND METHODS

II.1. ENVIRONMENTAL VARIABLES

II.1.1. Study Site

The population of *Modiolus modiolus* (horse mussel) used in this study is located at about 15-20 m depth in Logy Bay, southeast Newfoundland (47° 38'N, 52° 40'W), adjacent to the Marine Sciences Research Laboratory. Logy Bay is typical of the shoreline in this region, having precipitous cliffs, access to the sea being limited to coves and a few beaches composed of pebbles or large rocks, with a few areas of coarse sand. The ocean water is clear, with good visibility to a depth of about 20-25 m, except during the spring runoff and phytoplankton bloom. The horse mussels occur in small clumps on rock faces below the kelp zone, and are often associated with the encrusting red alga *Lithothamnion*.

II.1.2. Collection of Water Samples

Water samples were obtained from August 1986 to August 1988 on a monthly, weekly or daily basis, depending on the time of the year. Unfiltered seawater was pumped from about 6 m depth into clean buckets. This water was filtered through a 275 μm nitex mesh to eliminate large zooplankton and debris for immediate analysis of the major components of the suspended particulate matter (total, organic and inorganic particulate matter; chlorophyll *a*; particulate organic carbon and nitrogen; particulate carbohydrate and lipid; total particle counts and size frequency distribution). At each of these sampling times, water temperature was recorded to the nearest 0.1°C. Samples for chemical determinations (e.g. lipid, carbohydrate, particulate organic carbon) were stored at -20°C to await analysis. Blank filters for all the seston analyses were run at each date of collection and treated in the same manner as the samples.

II.1.3. Suspended Particulate Matter (Seston)

Total dry weight of particulate matter (SPM) was determined by filtering a known volume of water (3-4 l) under vacuum through a washed, preignited and preweighed Whatman GF/C filter (4.7 cm diameter) which has a nominal pore size of 1.2 μm and a median retention size of 0.7 μm (Sheldon, 1972). Filters with retained SPM were rinsed with 10 ml of isotonic ammonium formate to remove salt and prevent cell lysing. The amounts of particulate organic matter (POM) and inorganic matter (PIM) in the samples were determined according to Strickland and

Parsons (1972); the filters were dried at 80°C for 24 hours, weighed, combusted at 450°C for 3 hours and reweighed after cooling in a desiccator. A Cahn microbalance was used throughout.

II.1.4. Chlorophyll *a* and Phaeopigments

Chlorophyll *a* and phaeopigments (degradation products) were determined by filtering 0.5 l of the water sample through a GF/C filter (2.5 cm) and following the fluorometric analysis described by Yentsch and Menzel (1963) as modified by Parsons et al. (1984). The pigments were extracted from the filters with 90% acetone for 20 hours at 5°C in darkness. After this period, samples were centrifuged to remove glass fibres, and chloropigments then determined in the supernatant with a Turner Designs Fluorometer (Model 10). Pure chlorophyll *a* (SIGMA) was used as standard for the calibration of the instrument.

II.1.5. Particulate Organic Carbon (POC) and Nitrogen (PON)

Particulate organic carbon (POC) and nitrogen (PON) were measured by filtering 2 l of seawater through a GF/C filter (4.7 cm diameter). All filters were combusted at 450°C for 3 hours in a furnace before use, to remove organic contaminants. Organic carbon and nitrogen were determined by combustion in an oxygen atmosphere using a Perkin-Elmer CHN Elemental Analyzer (Model 240 A). Carbon and nitrogen values were standardized using acetanilide and their concentrations were expressed as $\mu g.l^{-1}$.

Particulate protein was determined by multiplying the nitrogen content of the particulate organic matter by the factor 5.8 (Gnaiger and Bitterlich, 1984).

II.1.6. Particulate Carbohydrate

Suspended particulate matter was concentrated by filtering 3-4 l of seawater through a pre-combusted GF/C filter (4.7 cm diameter) for the determination of carbohydrate by the phenol-sulphuric acid method of Dubois et al. (1956), after extraction in hot 5% trichloroacetic acid (TCA) containing 0.1% silver sulphate (Barnes and Heath, 1966).

Samples and filter blanks were cut into small pieces and homogenized for 1 min in 4 ml 5% TCA with a POLYTRON homogeniser. The homogenate was boiled for 30 min to hydrolyse the complex sugars and centrifuged at RCF=3000

for 20 min. The precipitate was washed with 2 ml distilled water and the sample recentrifuged. The supernatant and washings were made up to 10 ml with distilled water. The concentration of carbohydrate in the supernatant was estimated in triplicate using glucose as a standard. Absorbance was read at 490 nm wavelength with a spectrophotometer (GILFORD 240) and carbohydrate expressed as $\mu g.l^{-1}$ of glucose equivalents.

II.1.7. Particulate Lipid

The concentration of particulate lipid was determined by filtering a known volume of water (3-4 l) through a pre-combusted GF/C filter (4.7 cm diameter). The samples and filter blanks were cut into small pieces and homogenized for 1 min in 2 ml chloroform:methanol (2:1) with a POLYTRON homogeniser. After centrifugation at RCF=1000, the chloroform:methanol extract was dried at 50°C for 5 hours and the lipid residue charred at 200°C after the addition of 0.5 ml concentrated sulphuric acid. Lipid was then estimated spectrophotometrically by the method of Marsh and Weinstein (1966) using tripalmitin as a standard. Absorbance was measured at 375 nm and lipid in the seston expressed as $\mu g.l^{-1}$.

II.1.8. Food Index

The determination of the biochemical components of the suspended particulate matter (protein, carbohydrate and lipid) provides an estimate of the food quality and quantity available to filter-feeding organisms. An evaluation of the nutritional value of the seston through the year in Logy Bay was done using the values of these three biochemical components of the suspended particulate matter. Thus food quantity was defined as the sum of the concentrations of protein, carbohydrate and lipid, and a food index was calculated [(Food/Total Seston) x 100] as the percentage of food in the seston (Widdows et al., 1979). Protein, carbohydrate and lipid were converted into energy equivalents using the factors 24.0, 17.5 and 39.5 J. mg^{-1}, respectively (Gnaiger, 1983).

II.1.9. Particle Size Distribution

The size frequency distribution of particles above 2.0 μm equivalent spherical diameter (ESD) was analyzed with a Coulter Counter Model TAII. According to Bayne et al. (1977), many filter-feeding bivalves are able to retain particles above 2.0 μm with 100% efficiency, and Winter (1969) concluded that *Modiolus modiolus* can efficiently retain *Dunaliella* sp. (5 μm). Since the Coulter Counter can detect particles between 2% and 40% of the orifice diameter of the tube, 100 μm and 280

μm orifice tubes were most appropriate and were used in the present study to examine the distribution of natural particle assemblages. Eighteen size categories representing diameters from 2 to 112 μm were measured and size distributions were expressed as volume versus log particle size (Sheldon and Parsons, 1967). Latex spheres (9.8 μm) and ragweed pollen (19-20 μm) were used to calibrate the 100 and 280 μm tubes respectively. For feeding rate determinations, only the 100μm tube was used.

II.2. PHYSIOLOGICAL EXPERIMENTS

II.2.1. Experimental Animals

Specimens of the horse mussel *Modiolus modiolus* were collected approximately every month by SCUBA diving at 15-20 m depth from a rock face in Logy Bay, near the sea-water intake of the Marine Sciences Research Laboratory. The mussels were immediately transported to the laboratory, where they were cleaned of any epibiota. Mussels were held in flowing unfiltered seawater under ambient conditions of temperature, salinity and seston.

For each collection, fifteen mussels covering a wide size range (≈ 3.0 - 12.0 cm shell length) were selected for physiological experiments and biochemical analyses. After all the measurements were carried out, the soft parts were removed from the shell, and the gonads and digestive glands of eight mussels were dissected from the rest of the tissue and treated separately. Gonad, digestive gland and somatic tissue were weighed after drying at 85°C for 24 hours, to estimate the variation throughout the year in the relation between shell length and weight of the soft tissues.

For comparisons between experiments and to calculate scope for growth for mussels of standard sizes, the physiological rates were standardized to 1, 2 and 5 g dry tissue weight using the following formula :

$$Y_s = (W_s / W_e)^b \cdot Y_e$$

where: Y_s = the physiological rate for an animal of standard weight
W_s = the standard weight of the animal
W_e = the observed weight of the animal
Y_e = the uncorrected (measured) physiological rate
b = the weight exponent for the physiological rate function

II.2.2. Clearance Rate

Clearance rate (CR) is a measure of the feeding activity of the mussel and is defined as the volume of water cleared of suspended particles ≥2 μm diameter per unit of time (Bayne et al., 1977). Clearance rate was measured for 10-15 mussels approximately every month between August 1986 and August 1988. Seawater was pumped directly from the ocean into a mixing chamber of constant volume (15 l) with a flow rate high enough to maintain a well-mixed suspension of particulate matter (Fig. 1). The experimental mussels were placed in plastic containers (0.8 l capacity) and flow rates of 60 to 200 $ml.min^{-1}$ were supplied from the mixing chamber, depending on the size of the mussel. Thus the reduction in particle concentration between inflow and outflow was held between 20-40%, eliminating the possibility of recirculation through the mantle cavity of the mussels. One additional container with the same flow rate, but with no animal, served as a control. The experimental mussels were left undisturbed for at least 12 h before the CR measurements were begun, and the removal of suspended particles was monitored with a Coulter Counter as the water flowed through the experimental chambers containing individual mussels. Measured volumes of water were simultaneously collected from each overflow in a given period of time to determine the flow rate, and a Coulter Counter Model Z_B fitted with a 100 μm orifice tube was used to determine the difference between the particle concentration in the inflow (control value) and the outflow from each container.

Clearance rate was calculated according to Bayne et al. (1977) using the formula:

$$CR = \frac{C_1 - C_2}{C_1} \times F$$

where: CR = Clearance rate ($l.h^{-1}$)
C_1 = inflow particle concentration (particles ml^{-1})
C_2 = outflow particle concentration (particles ml^{-1})
F = flow rate through the chamber ($l.h^{-1}$)

Clearance rate experiments were run for 12 - 24 hours and mean values of several measurements (8-15) calculated, including zero values when the mussel was not feeding.

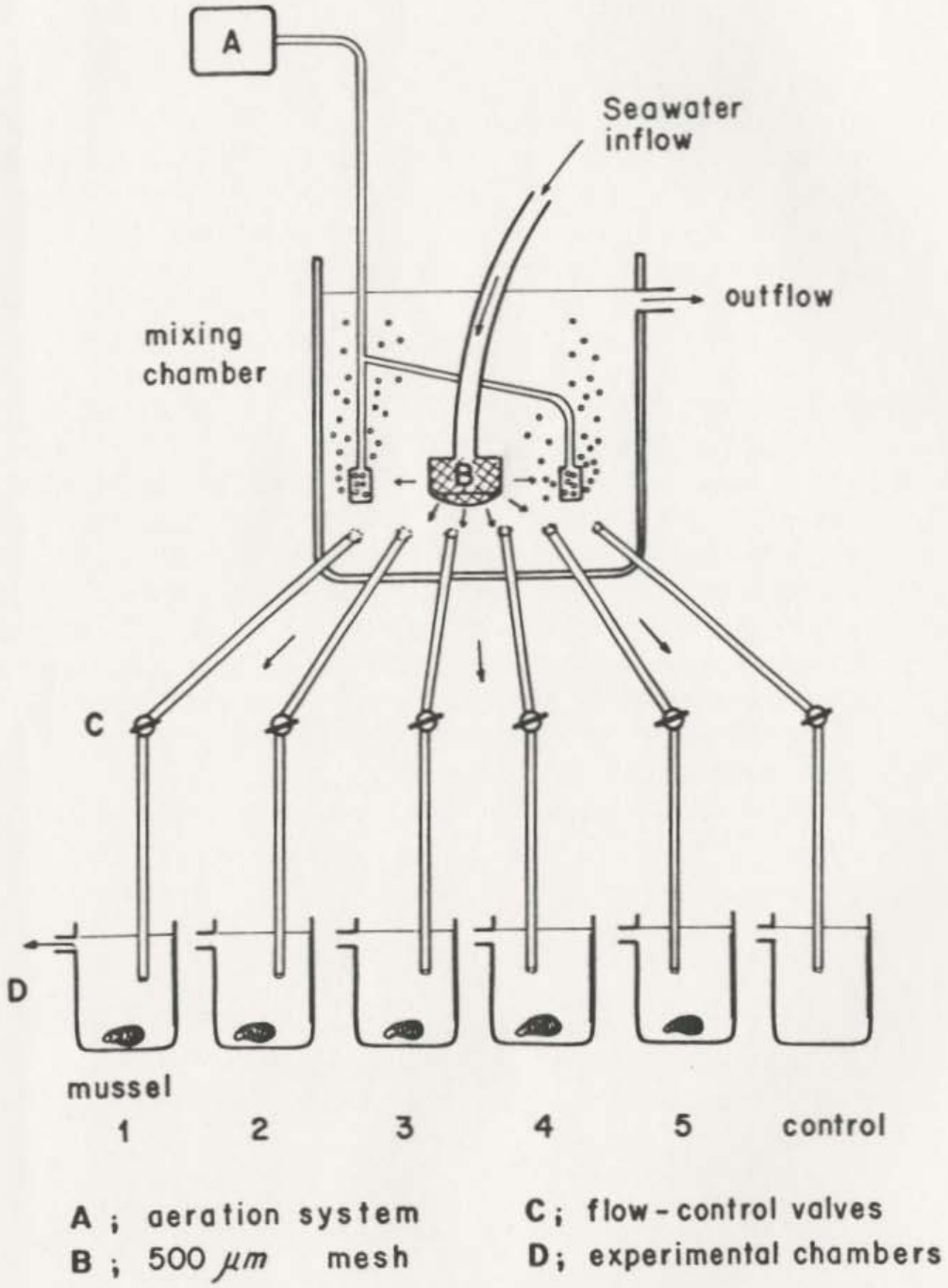


Fig. 1. Apparatus used to measure clearance rates in horse mussels.

II.2.3. Ingestion Rate

Ingestion rate is defined as the quantity of SPM consumed per unit time ($mg.l^{-1}$) and was calculated as the product of clearance rate ($l.h^{-1}$) and the concentration of SPM ($mg.l^{-1}$). The ingested ration ($mg.h^{-1}$) was converted to energy equivalents by multiplying it by the energy content of the SPM, using the conversion factors 1 mg protein = 24.0 J; 1 mg carbohydrate = 17.5 J; 1 mg lipid = 39.5 J (Gnaiger, 1983).

II.2.4. Absorption Efficiency

Absorption efficiency (AE) was estimated by the method proposed by Conover (1966), which requires the determination of weight loss on ignition for subsamples of both food and faeces. At the end of each series of clearance rate measurements, faeces produced by individual mussels were collected with Pasteur pipettes and filtered by vacuum onto precombusted (450°C), weighed Whatman GF/C filters (2.5 cm diameter). Care was taken to exclude any pseudofaeces present. The loaded filters were washed with 10 ml isotonic (3%) ammonium formate, dried at 80°C for 24 hours, weighed, combusted at 450°C for 3 hours and weighed again after cooling in a desiccator. Two or three water samples from the mixing chamber were taken during each CR series and filtered as described above (Section II.1.2.). Dry weight and ash-free dry weight of the seston were obtained as described for faeces. Absorption efficiency was calculated as follows:

$$AE = \frac{(F - E)}{(1-E) \times F} \times 100$$

where: AE = Absorption Efficiency (%)
F = Ash-free dry weight seston:total dry weight seston
E = Ash-free dry weight faeces:total dry weight faeces

II.2.5. Oxygen Uptake

Oxygen uptake (VO_2) was determined for individual mussels between August 1986 and May 1988. Each mussel was removed from the clearance rate system (running seawater) and placed individually in a sealed glass chamber. The volume of the chambers varied from 0.3 to 3.2 l, according to the size of the experimental animal. All measurements were made at field ambient temperature and natural concentration of SPM.

Oxygen uptake was measured with a polarographic electrode (Radiometer E 5046-0) coupled to a Radiometer PHM71 MK2 acid-base analyzer fitted with a PHA934 oxygen module. The output signal was monitored continuously on a chart recorder. The water in the respirometer was mixed by placing the latter on a submersible magnetic stirrer. The chamber and stirrer were immersed in a temperature-controlled water bath (Fig. 2).

It has been shown in other species of bivalves that VO_2 is often independent of oxygen tension (PO_2) only to ≈70% saturation (Bayne, 1971; Vahl, 1978; Shumway, 1980; Shumway et al., 1988). Therefore, oxygen consumption was never measured at ambient pO_2 lower than 70% saturation. Considering that the mussels were always maintained under conditions of running unfiltered seawater from Logy Bay, the measured rates of oxygen consumption are assumed to represent the routine metabolism of horse mussels.

Values of oxygen uptake were expressed as ml $O_2.h^{-1}$ and transformed to energy equivalents using the conversion factor 1 ml O_2 = 20.3 Joules (Elliot and Davison, 1975).

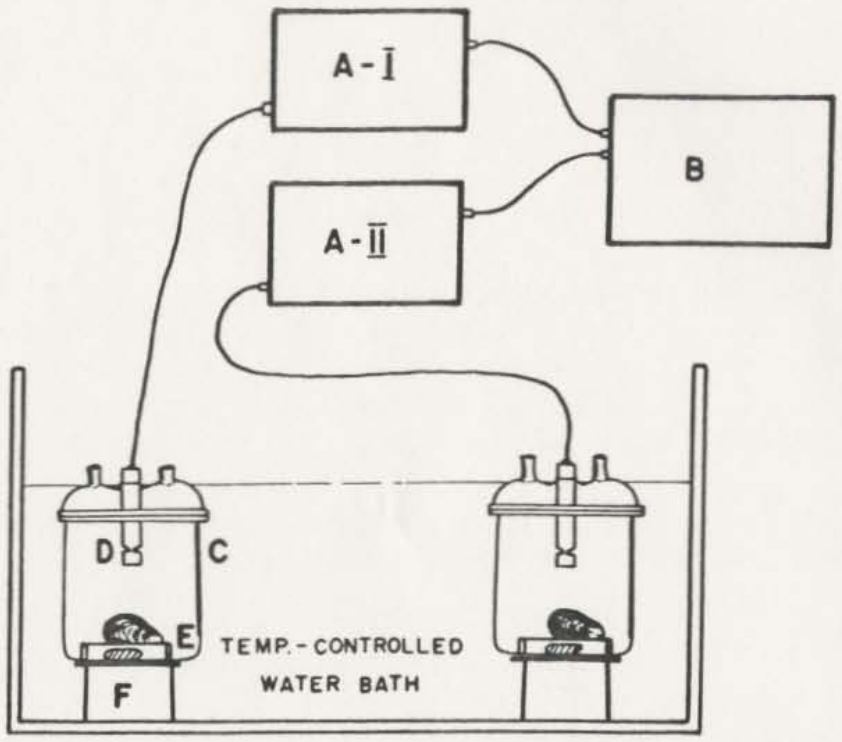
II.2.6. Ammonia Excretion

Ammonia excretion (VNH_4-N) was determined by the phenol-hypochlorite method of Solorzano (1969) as modified by Widdows (1985). Horse mussels were removed from the holding trays and placed individually in glass beakers containing 0.2 l to 1.0 l of filtered (0.45 μm) seawater, according to the size of the animal. One additional beaker containing filtered seawater, but with no animal, served as a control. Measurements were made at field temperatures using a temperature-controlled incubator.

Preliminary experiments indicated that the NH_4-N excretion rate in *Modiolus modiolus* is not affected by the increasing concentration of ammonia in the experimental chamber during the first 20 hours (see Appendix I). The incubation time and the volume of water were therefore adjusted according to temperature and body size. Values for ammonia excretion were expressed in μg NH_4-N.h^{-1} and transformed to Joules using the conversion factor 1 μg NH_4-N = 0.025 J (Elliot and Davison, 1975).

II.2.7. Scope for Growth

Warren and Davis (1967) developed the concept of scope for growth (SFG), which is a physiological index of energy balance to estimate production (growth +



A-Ⅰ and A-Ⅱ ; oxygen modules (Radiometer PHA 934)

B ; chart recorder

C ; experimental chambers

D ; polarographic electrode (Radiometer E 5046-0)

E ; perforated base plate

F ; submersible magnetic stirrer

Fig. 2. Apparatus used to measure oxygen uptake in horse mussels.

reproduction) by an individual animal. Scope for growth was calculated from the balanced energy equation given by Winberg (1960) after converting all the physiological rates to energy equivalents ($J.h^{-1}$):

$$C - F = A = R + U + P_s + P_g$$

or $$SFG = A - (R + U)$$

where:
- C = Ingestion rate ($mg.d^{-1}$) x energy content of the food ($J.mg^{-1}$)
- F = Energy lost as faeces ($J.d^{-1}$)
- A = Energy absorbed (C x absorption efficiency) ($J.d^{-1}$)
- R = Oxygen uptake (ml $O_2.d^{-1}$) x 20.3 J
- U = Ammonia nitrogen excretion rate (μg NH_4-$N.d^{-1}$) x 0.025 J
- P_s = Production of somatic tissue ($J.d^{-1}$)
- P_g = Production of gametes ($J.d^{-1}$)
- SFG = Scope for growth (calculated from physiological measurements)

II.2.8. Net Growth Efficiency

Net growth efficiency (K_2) is another physiological index which provides a measure of the efficiency with which food is converted into body tissues. Net growth efficiency represents the growth per unit absorbed energy and was calculated as follows:

$$K_2 = \frac{A - (R + U)}{A}$$

where:
- A = Energy absorbed from the food
- R = Energy lost in respiration
- U = Energy lost in excretion

II.3. COMPARISON OF METHODS FOR ABSORPTION EFFICIENCY

II.3.1. General

Absorption efficiency in *Modiolus modiolus* was compared by using different inert tracers (ash and silicate) and different absorbable substances (organic matter, chloropigments and organic carbon) present in the food. All the calculations were based on the ratio method proposed by Conover (1966), in which it is necessary to measure the concentrations of both the inert (nonabsorbable) and the absorbed

components in both the seston and the faeces. Comparisons of absorption efficiency using ash and silicate as nonabsorbable substances were made approximately every month between June 1987 and May 1988 for mussels feeding on natural seston, using organic matter (weight loss on ignition) as the absorbable component. During the phytoplankton bloom of 1988 (April-May) two other components of the seston (chloropigments and organic carbon) were used as absorbable substances, as well as organic matter, and included in the comparison.

Five or more mussels were held individually in running seawater (natural seston and ambient temperature) and faeces removed after 20 to 24 h. Each of the faecal samples was resuspended in filtered seawater and divided into two or four subsamples, depending on the number of comparisons being made. Several seston samples were taken during each experiment to determine the ratio of the relevant components in food and faeces.

II.3.2. Ash

This method was developed by Conover (1966) and assumes no absorption of the inorganic matter present in the food, using this fraction as the inert component. The procedure used here has been described above under Absorption Efficiency (Section II.2.4.).

II.3.3. Silicate

Absorption efficiency was measured using biogenic silica as the nonabsorbed component present in the food. The procedure followed was a modification of the method of Tande and Slagstad (1985). Seston and faeces were collected on pre-weighed 1.0 μm Nuclepore filters of 2.5 cm diameter. All the samples were rinsed with 3% ammonium formate and dried at 80°C for $\approx$24 h. Weights of the samples and filter blanks were determined to $\pm$0.01 mg with a Cahn microbalance.

Preliminary experiments showed that the extraction of silica is high during the first hour of hydrolysis, decreasing for the next 2 hours and becoming negligible after 3 hours of hydrolysis (see Appendix II). Accordingly, to determine the concentration of biogenic silica, food and faeces were hydrolyzed for 3 h in 0.5% sodium carbonate solution at 85°C. The content of dissolved silicon hydroxide was measured colorimetrically by the molybdate reaction according to Strickland and Parsons (1972).

Absorption efficiency was calculated from the formula given by Tande and Slagstad (1985):

$$A = 1 - \left[\frac{(I_I : N_I)}{(I_F : N_F)} \right] \times 100$$

where: I_I= concentration of biogenic silica (tracer) in the seston
I_F= concentration of silica in faeces
N_I= concentration of organic matter (absorbable) in the seston
N_F= concentration of organic matter in faeces

II.3.4. Chloropigments

Absorption efficiency measurements using chloropigments as the absorbed fraction were made during the phytoplankton bloom of 1988 (April-May). The concentration of chloropigments in food (seston) and faeces was determined with a Turner Designs Fluorometer Model 10 using the procedure described above for the determination of chlorophyll *a* (Section II.1.4.). Absorption efficiency for chloropigments was calculated by the ratio method according to the formula:

$$AE = \frac{(Chl_F - Chl_E)}{(1-Chl_E)(Chl_F)} \times 100$$

where: AE= Absorption Efficiency (%)
Chl_F= Chloropigments : chloropigments + ash in the food ingested
Chl_E= Chloropigments : chloropigments + ash in the faeces

II.3.5. Carbon

Particulate organic carbon (POC) was also used as an absorbable substance present in the food to measure absorption efficiency. Faeces and food (seston) were collected on GF/C filters and analysed with a CHN Elemental Analyzer as described above for POC and PON (Section II.1.5.). The inorganic fraction was used as the nonabsorbable component and absorption efficiency was based on the ratio method, in which the increase in the concentration of the inert fraction of the food is measured after passage through the gut.

II.4. FAECES AND PSEUDOFAECES PRODUCTION

II.4.1. Biodeposition

Faeces and pseudofaeces produced by individual mussels were sampled during April-May 1988. To determine the deposition rate of faeces and/or pseudofaeces, individual mussels were held undisturbed for a period of 24 h in running seawater (natural seston) and biodeposits collected quantitatively. A 500 μm mesh was used in the overflow to avoid loss of biodeposits. Faeces and pseudofaeces were clearly distinguishable on the bottom of the experimental chamber, facilitating their collection separately with pasteur pipettes.

II.4.2. Microscopic Analysis

Seston samples as well as subsamples of the biodeposits were preserved in Lugol's iodine and examined with a Zeiss inverted microscope to determine the composition of the particles rejected as pseudofaeces.

II.4.3. Chlorophyll *a*, Carbon, Nitrogen and Silicate Content

To estimate the nutritional value of the faeces and pseudofaeces produced during April-May, subsamples of the biodeposits were analyzed for chloropigments, carbon, nitrogen and biogenic silica using the appropriate procedures described in sections II.1.4, II.1.5. and II.3.3.

II.5. ENERGY STORAGE CYCLES

II.5.1. General

Biochemical analysis was carried out on tissues from horse mussels of shell length 8-10 cm, which were collected approximately every month between August 1986 and November 1988. Five individuals (males and females pooled) from each sample were shucked and the somatic tissue, gonad and digestive gland removed separately. These tissues were dried for 24 hours at 95°C, weighed and stored at -20°C. For analysis the dried tissues were ground to a fine powder in a ball-mill and appropriate weighed samples taken for lipid, carbohydrate and protein determinations. Ash content was determined by ignition of a subsample of tissue at 450°C for 16 h. Powdered samples were re-dried immediately before each analysis, and kept in a desiccator. Lipid, carbohydrate and protein were expressed

as percentages of dry weight as well as total weight of each constituent present in the tissue.

II.5.2. Lipid

Lipids were determined on approximately 50 mg dry weight of tissue by the gravimetric method of Bligh and Dyer (1959). Lipids were extracted with chloroform:methanol (2:1) from a weighed subsample of dry homogenized tissue and weighed after drying at 50°C.

II.5.3. Carbohydrate

Total carbohydrate was determined on a weighed sample (approximately 10 mg) of dry tissue, using the phenol-sulphuric acid method of Dubois et al. (1956) after extraction by boiling in 5% trichloroacetic acid (TCA) containing 0.1% silver sulphate (Barnes and Heath, 1966), centrifuging and washing. Carbohydrate in the supernatant was estimated in triplicate by reading absorbance at 490 nm, using glucose as a standard.

II.5.4. Protein

Nitrogen content was determined by combustion of a weighed sample (approximately 5 mg) of dry tissue in oxygen in a Perkin Elmer CHN Analyzer (Model 240A), using acetanilide as a standard. Protein was calculated by multiplying the nitrogen values by a conversion factor of 5.8 (Gnaiger and Bitterlich, 1984).

II.6. STATISTICAL ANALYSIS

Environmental and physiological data were analyzed by Pearson product-moment correlation and multiple linear regression following $\log_{10}$ or arcsine transformation of the variables to reduce the dependence of the sample variance on the mean and to normalize the distribution of the data.

The relationships between physiological rates and body weight and also between somatic, gonad or digestive gland weight and shell length were described by the simple allometric equation of the form $Y=aX^b$, where 'Y'= the dependent variable (e.g. physiological rate), 'X'= the independent variable (e.g. body weight) and 'a' and 'b' represent the intercept and slope of the log 'Y' vs. log 'X'

regression, respectively. Both variables were transformed to logarithms and the data fitted by least squares regression to a straight line. For most of the physiological rates, data were pooled to provide monthly groups and analyzed by least squares regressions.

SYSTAT version 4.0 for use on a microcomputer (SYSTAT INC. 1986) was used for these statistical analyses.

III. RESULTS

III.1. ENVIRONMENTAL FACTORS

III.1.1. Temperature and Suspended Particulate Matter

Seasonal changes in water temperature in Logy Bay over a two year period are shown in Fig. 3. Temperature increased from a minimum value of ≈ -1.0°C during February-March to a maximum of ≈ 14.0°C in August. This maximum value was not maintained for very long, decreasing throughout late summer and early winter.

Throughout the study, comparisons of the total particulate matter (TPM) and particulate organic matter (POM) were made between water pumped from 6 m depth into the laboratory and water collected by divers from 20 m depth, adjacent to the mussel bed. A t-test using the method of paired comparisons showed that neither TPM nor POM was significantly different between pumped and collected samples (Table 1).

The seasonal pattern of seston weight in the particle size range ca. 1-275 μm is shown in Figure 4 and Table 2. Data for TPM and POM are presented as individual values (Fig. 4a,b) and also grouped on a monthly basis (Fig. 4c). Maximum values for TPM were observed in April-May and lower values during the rest of the year. The fluctuations in TPM in Logy Bay were attributable largely to the POM and only in exceptional cases were they caused by changes in the PIM component.

III.1.2. Chlorophyll *a* and Phaeopigments

The concentration of chlorophyll *a* exhibited a marked spring peak (April-May), then declined abruptly during late spring to show a minimum in fall and winter (Fig. 5a; Table 2). In 1987 the peak was higher (9.9 $\mu g.l^{-1}$) than in 1988 (6.9 $\mu g.l^{-1}$), although the duration of both peaks was very similar (4-5 weeks).

Phaeopigments (expressed in chlorophyll *a* equivalents) fluctuated in a similar fashion to chlorophyll *a*, with lower values in 1988 than in 1987 (Fig. 5b). Higher values (≈2.0 $\mu g.l^{-1}$) were recorded during the spring bloom, but a second peak (≈1.0 $\mu g.l^{-1}$) appeared in June of each year.

The ratio chlorophyll *a*:phaeopigments is presented in Figure 5c. For most of the year the concentration of phaeopigments was higher than that of chlorophyll

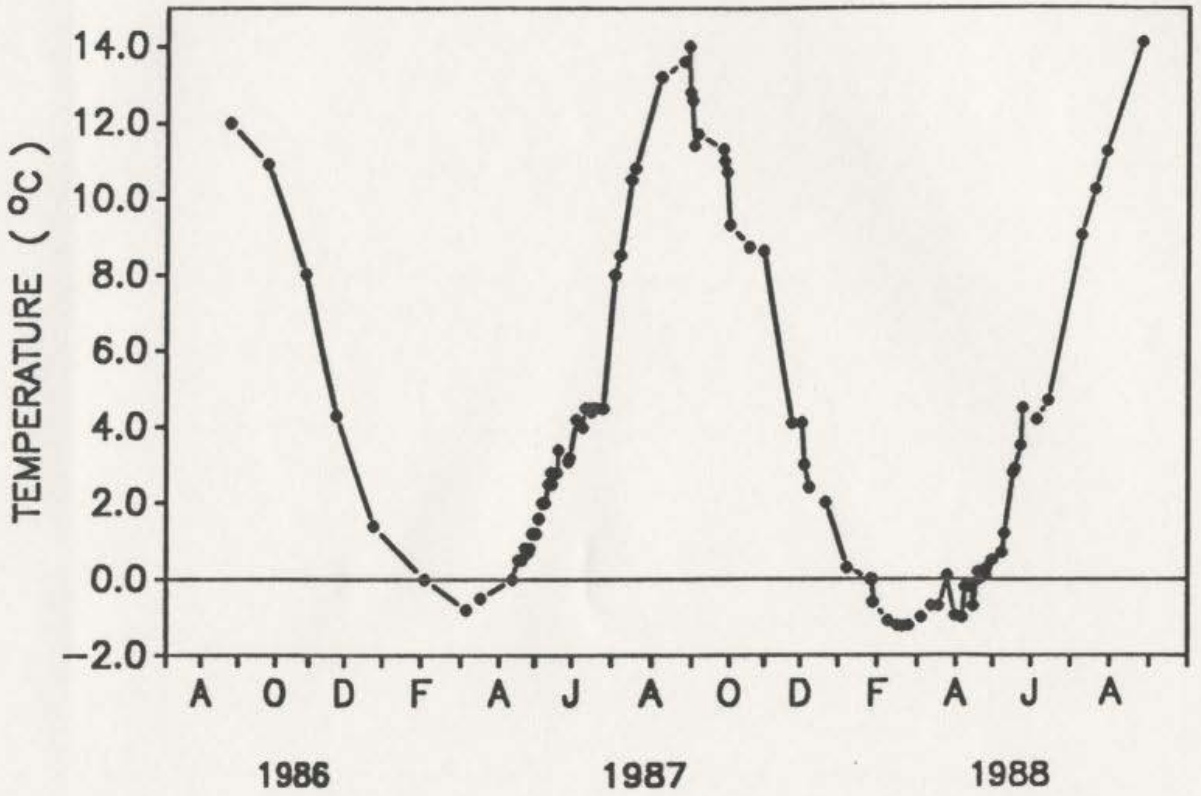


Fig. 3. Seasonal temperature cycle in Logy Bay.

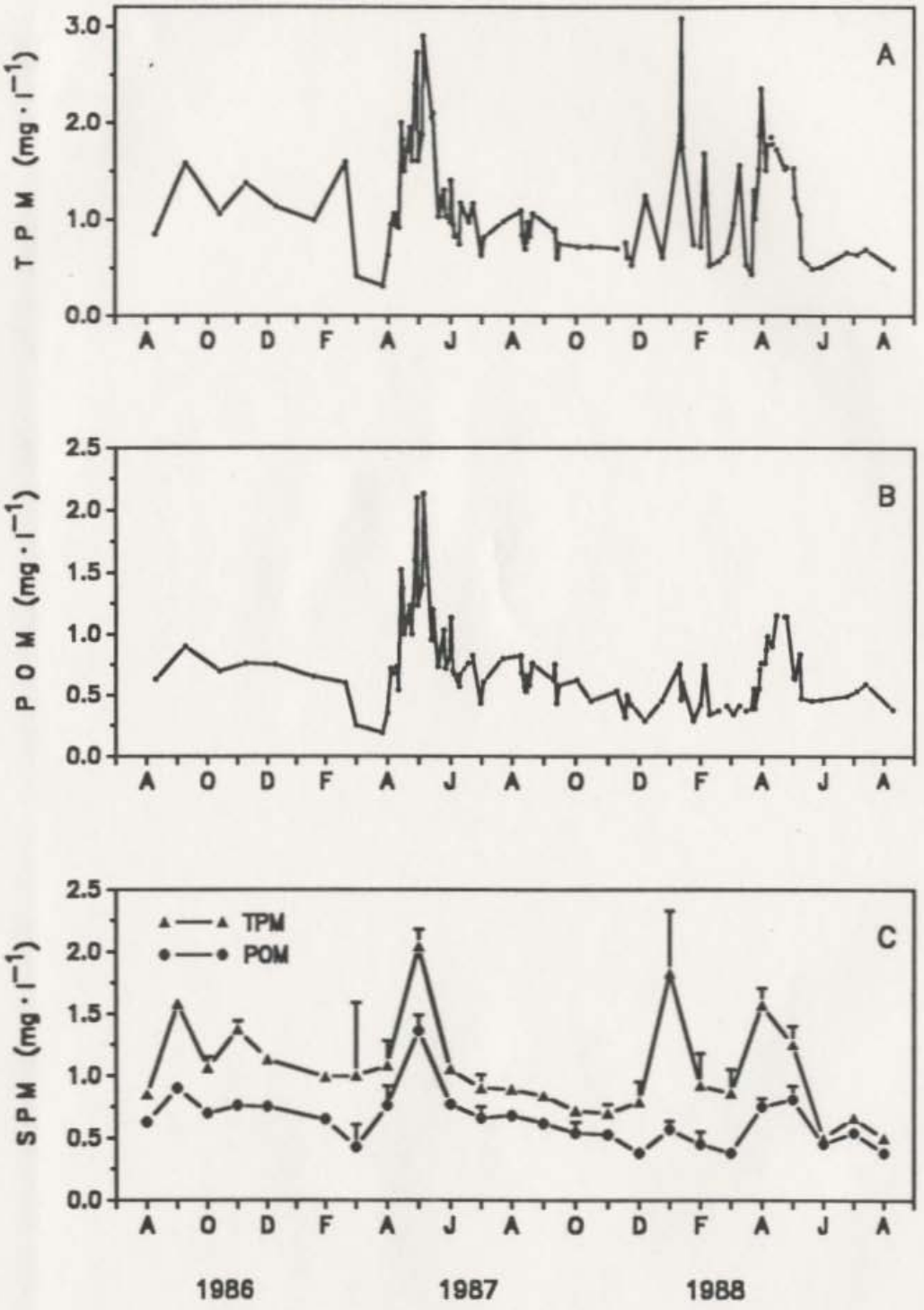


Fig. 4. Seasonal cycles of suspended particulate matter (SPM) in Logy Bay. (A) Total particulate matter (TPM); (B) particulate organic matter (POM); (C) monthly means (± S.E.) for TPM and POM. For clarity only plus S.E. bars are shown. When no S.E. bars are shown they were smaller than the symbols.

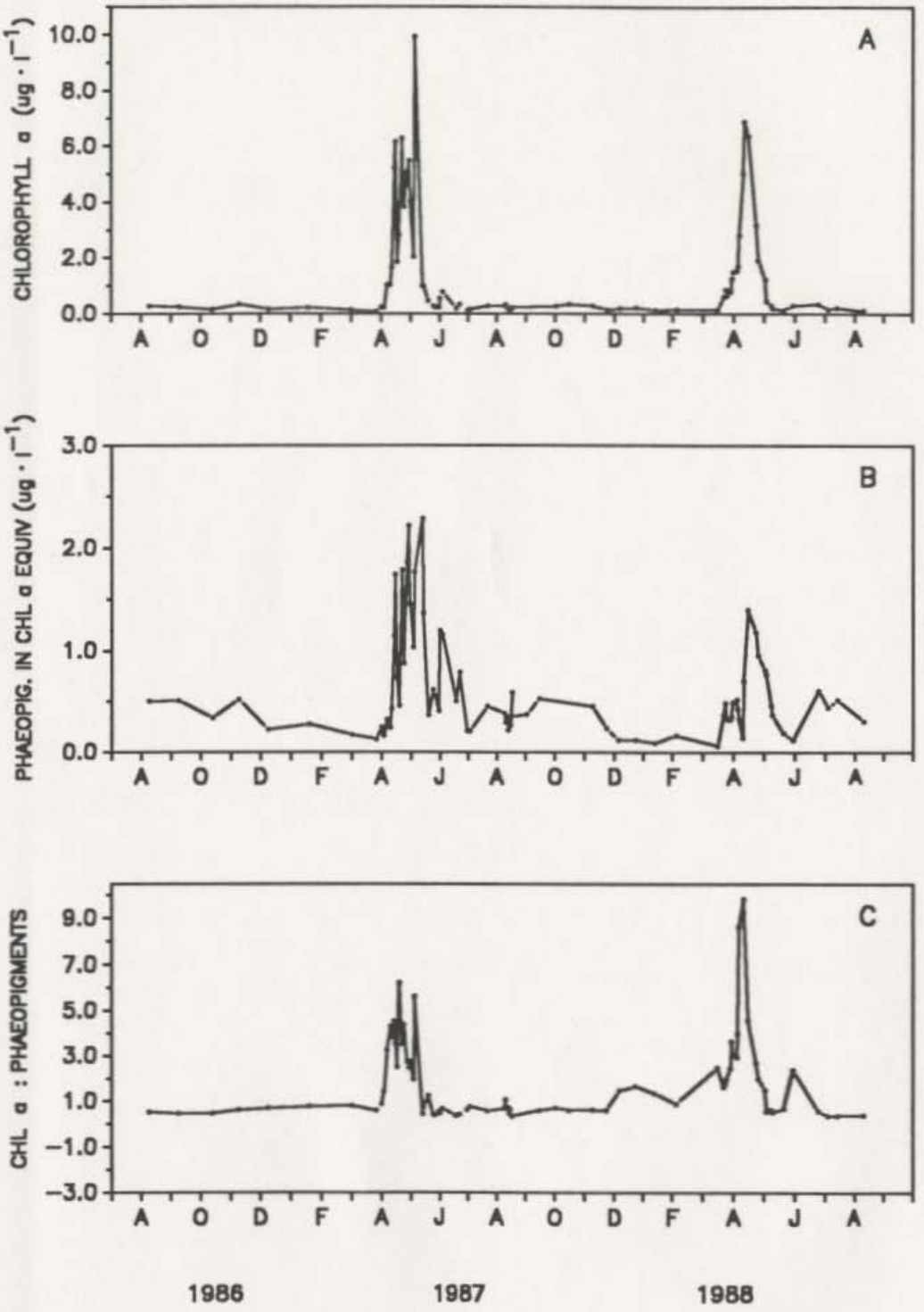


Fig. 5. Seasonal cycles of chlorophyll *a* (A), phaeopigments as chlorophyll *a* equivalents (B) and chlorophyll *a*: phaeopigments ratio (C) in Logy Bay.

Table 1. Comparison of TPM and POM between samples collected and pumped from Logy Bay. Significance was measured by a t-test of paired comparisons

Date		TPM		POM	
		Collected ($mg.l^{-1}$)	Pumped ($mg.l^{-1}$)	Collected ($mg.l^{-1}$)	Pumped ($mg.l^{-1}$)
April	15-87	0.59	0.63	0.32	0.35
May	18-87	1.13	0.93	0.73	0.70
July	14-87	0.70	0.63	0.42	0.43
Oct.	19-87	0.92	0.90	0.63	0.62
Jan.	24-88	0.79	0.77	0.50	0.53
March	20-88	0.61	0.59	0.40	0.32
April	5-88	0.52	0.49	0.39	0.28
April	22-88	1.51	1.42	1.07	1.02
	Mean	0.85	0.80	0.56	0.53
	± SD	0.33	0.30	0.25	0.25
		$t = 0.42$ (df=6)		$t = 0.40$ (df=6)	
		$P \geq 0.05$		$P \geq 0.05$	

Table. 2.- Gravimetric, electronic and chemical analyses of suspended particulate matter in Logy Bay (Monthly mean values).

DATE		TPM ($mg.l^{-1}$)	POM ($mg.l^{-1}$)	Particle number ($x10^3.l^{-1}$)	Particle volume ($mm^3.l^{-1}$)	Chl a ($ug.l^{-1}$)	PON ($ug.l^{-1}$)	POC ($ug.l^{-1}$)	Lipid ($ug.l^{-1}$)	Carbohydrate ($ug.l^{-1}$)	Temp. (ºC)
AUG.	86	0.85	0.63	--	--	0.262	28.0	123.3	19.5	11.9	12.0
SEPT.	86	1.58	0.90	--	--	0.235	22.2	85.3	20.1	11.3	10.9
OCT.	86	1.06	0.70	--	--	0.154	20.3	158.8	25.4	14.3	8.0
NOV.	86	1.37	0.76	--	--	0.320	23.7	111.7	25.7	13.8	4.3
DEC.	86	1.13	0.75	--	--	0.154	12.0	59.3	17.8	4.8	1.4
FEB.	87	0.99	0.65	--	--	0.212	16.4	60.9	17.0	10.6	0.0
MARCH.	87	1.00	0.43	5481	0.70	0.136	12.5	65.3	18.4	11.0	-0.7
APRIL	87	1.08	0.76	9434	1.78	1.938	56.3	283.3	48.9	53.1	0.8
MAY	87	2.04	1.36	18165	3.96	3.927	90.5	515.5	63.8	77.5	2.5
JUNE	87	1.05	0.77	7012	0.68	0.411	52.1	211.8	41.0	14.8	4.4
JULY	87	0.90	0.66	7889	0.50	0.200	55.4	238.7	22.5	25.0	9.5
AUG.	87	0.89	0.68	8412	0.58	0.220	38.3	295.3	21.3	15.3	13.4
SEPT.	87	0.84	0.62	7230	0.59	0.210	37.8	181.9	26.0	12.5	11.1
OCT.	87	0.72	0.54	7833	1.35	0.290	29.4	165.3	20.2	6.4	8.7
NOV.	87	0.70	0.53	6605	0.77	0.276	38.5	202.4	34.4	9.3	4.1
DEC.	87	0.79	0.38	9499	1.10	0.156	26.5	90.3	23.4	7.2	2.9
JAN.	88	1.83	0.57	11328	2.06	0.170	33.1	186.0	18.4	8.4	-0.1
FEB.	88	0.92	0.45	6428	0.77	0.294	22.8	119.7	15.3	16.3	-1.2
MARCH	88	0.86	0.38	5933	0.85	0.149	24.0	126.2	32.3	14.7	-0.9
APRIL	88	1.57	0.75	15876	2.25	2.494	48.2	282.6	42.6	61.9	-0.1
MAY	88	1.25	0.81	12561	2.21	1.198	52.1	312.8	59.8	70.7	2.6
JUNE	88	0.50	0.45	7053	0.43	0.201	30.8	150.3	40.5	23.9	4.5
JULY	88	0.66	0.54	6965	2.19	0.230	33.6	177.7	46.4	25.5	10.1
AUG.	88	0.50	0.38	--	--	0.118	22.2	122.6	--	--	14.1

a, with a chl *a*:phaeopigment ratio of 0.40-0.80. However, during the phytoplankton bloom the concentration of chlorophyll *a* was so high that the ratio chlorophyll *a*:phaeopigment reached values as great as 6.2 during 1987 and 9.8 during 1988.

III.1.3. Particulate Organic Carbon (POC) and Nitrogen (PON)

Seasonal changes in particulate organic carbon (POC) and nitrogen (PON) are shown in Figures 6a and 6b, respectively. Both cycles resembled those of chlorophyll *a* and POM, the highest concentrations usually occurring during the spring phytoplankton bloom. Thus POC was a maximum in April-May of 1987 and 1988, with values near 800 and 450 $\mu g.l^{-1}$ respectively. The seasonal pattern of PON (Fig. 6b) was very similar to that described above for POC, with major peaks during the phytoplankton blooms of 1987 (125 $\mu g.l^{-1}$) and 1988 (85 $\mu g.l^{-1}$).

The carbon:chlorophyll *a* ratio is presented in Figure 6c. This ratio estimates the relative detrital content of the seston (Zeitzschel, 1970), and values of 100 or less are considered to indicate that the carbon is primarily from living phytoplankton. Carbon:chlorophyll *a* ratios were low during the phytoplankton bloom in both years, with ratios lower than 100, but values greater than 100 were obtained during the rest of the year.

The C:N ratio has been used as an index to estimate the amount of living material in relation to detritus (inversely proportional; Poulet et al., 1986). In seston from Logy Bay, this ratio did not show a clear seasonal pattern and values fluctuated from as low as 2.5 (June 15, 1987) to as high as 12.2 (August 23, 1987), with an average of 5.5 for the entire period of study (Fig. 6d).

III.1.4. Biochemical Composition of the Seston

The biochemical composition of the seston is considered as a valuable indicator of the nutritional value of the diet for suspension feeding organisms (Miklestad and Hang, 1972).

Seasonal fluctuation of particulate carbohydrate in Logy Bay is shown in Fig. 7a. Carbohydrate concentration showed a very similar seasonal pattern in both years of the study. The mean for the entire sampling period was 30.6 $\mu g.l^{-1}$, and peak values were recorded during the phytoplankton bloom of each sampling year (April-May), with smaller peaks occurring during summer (June-July).

The seasonal variation in particulate lipid (Fig. 7b) was similar to the cycles shown by other components of the seston (e.g. chlorophyll *a*, carbohydrate, PON,

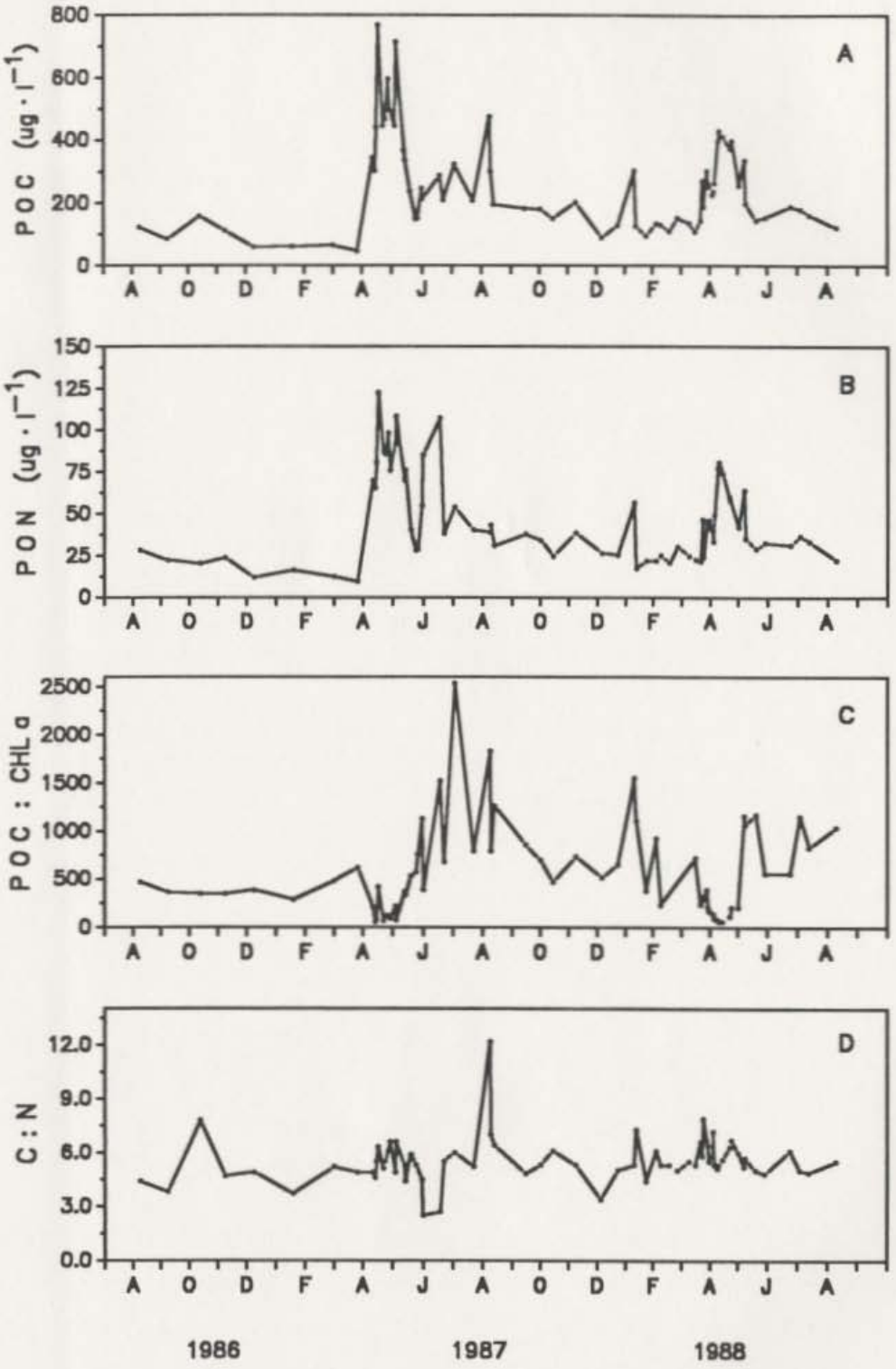


Fig. 6. Seasonal variation in (A) particulate organic carbon (POC); (B) particulate organic nitrogen (PON); (C) POC :chlorophyll *a* ratio; (D) C:N ratio in Logy Bay.

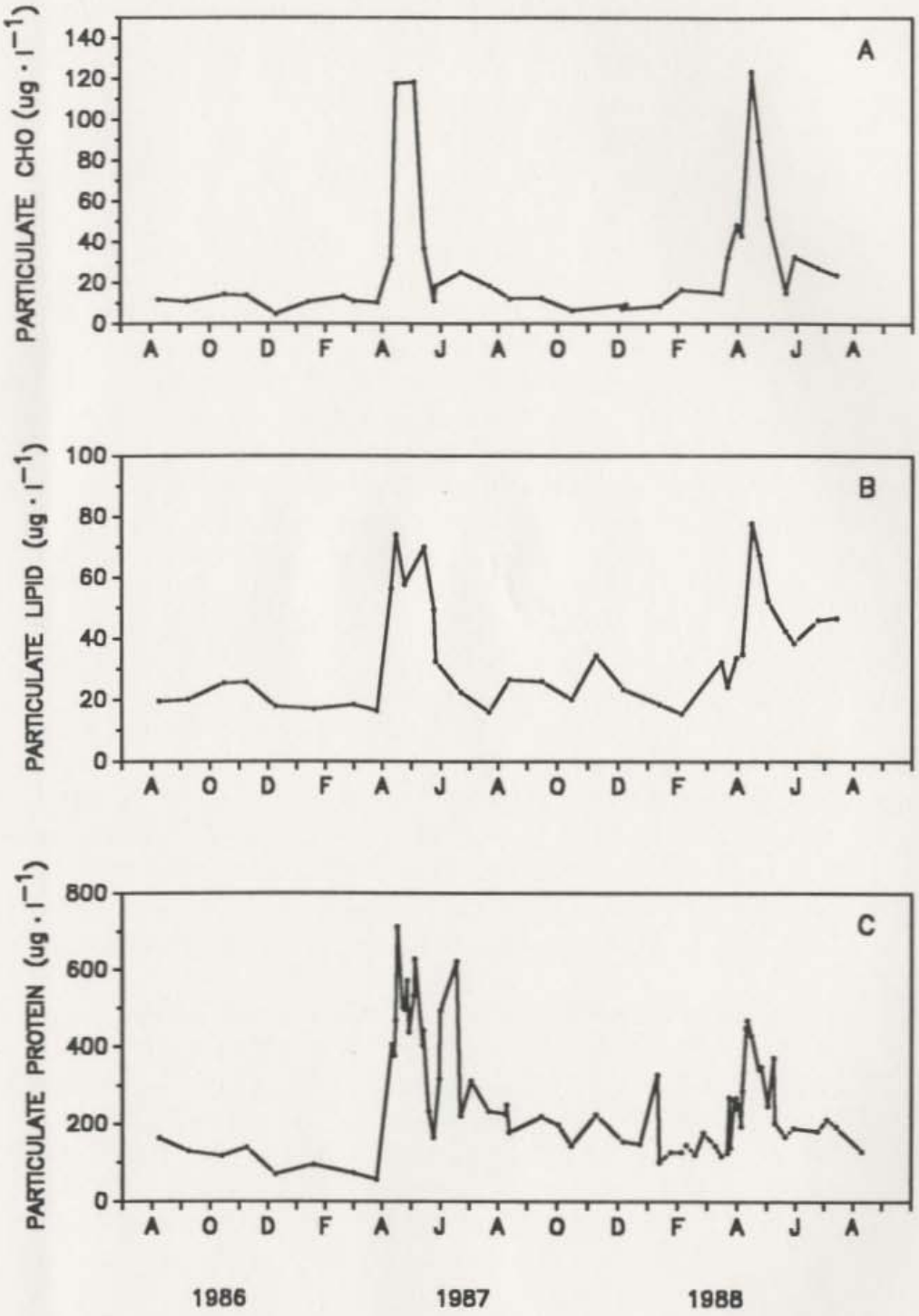


Fig. 7. Seasonal cycle in particulate carbohydrate (A), lipid (B) and protein (C) in Logy Bay.

POC). The lipid content of the seston was lower during fall and winter, increasing significantly during the 4-5 weeks of the phytoplankton bloom. The mean concentration over two years of sampling was 35.3 $\mu g.l^{-1}$.

Protein concentration showed the same seasonal pattern as PON because protein values were calculated from PON measurements using the conversion factor of 5.8 given by Gnaiger and Bitterlich (1984). Maximum protein levels were observed during April-May in both years of the study, representing the major component of the organic matter in the seston (Fig. 7c). At certain periods of the year, such as during the phytoplankton bloom, particulate protein accounted for more than 70% of the organic seston (e.g. May 1st, 1987). In contrast, very low values were found during the winter months (e.g. February, 1987; January, 1988), when protein comprised about 10% of the mass of organic seston.

III.1.5. Food Index

Of special interest in the present study are the relationships among the various organic components of the SPM that may be utilized by the mussels as a nutritional source. The food material (FM) present in the total seston (Fig. 8) is represented by the sum of carbohydrate, lipid and protein concentrations (Widdows et al., 1979; Soniat et al., 1984). The food material reached a maximum during the phytoplankton bloom of each year, with values of 671 $\mu g.l^{-1}$ in 1987 and 630 $\mu g.l^{-1}$ in 1988. The lowest values occurred during the winter season of 1987 and 1988, with concentrations of 100 and 120 $\mu g.l^{-1}$, respectively (Fig. 8a).

The food material (carbohydrate+lipid+protein) expressed as a percentage of the SPM (by weight) represents an index of the quality of the food available to a suspension feeder (Fig. 8b). Peak values for the food index coincided with the spring bloom (53.6% in April 1987 and 42.1% in April 1988). In winter, the food index dropped to a small percentage of the total seston (ca. 8% in 1987 and ca. 7% in 1988), because the seston was then composed mainly of inorganic matter (ca. 66%), representing a low quality diet for the mussels.

III.1.6. Particle Size Distribution

The total particle distribution was strongly influenced by the spring bloom and by resuspension during storms. This is shown in Fig. 9, where the main peaks in total particles (PARTN) as well as in total volume (PARTV) occurred during the spring bloom of each year of the study. The spring peaks of total particles and total volume (Fig. 9a,b) were composed mainly of single diatoms and chain-forming diatoms, such as *Fragilaria*, *Thalassiosira*, *Coscinodiscus*, and *Chaetoceros*.

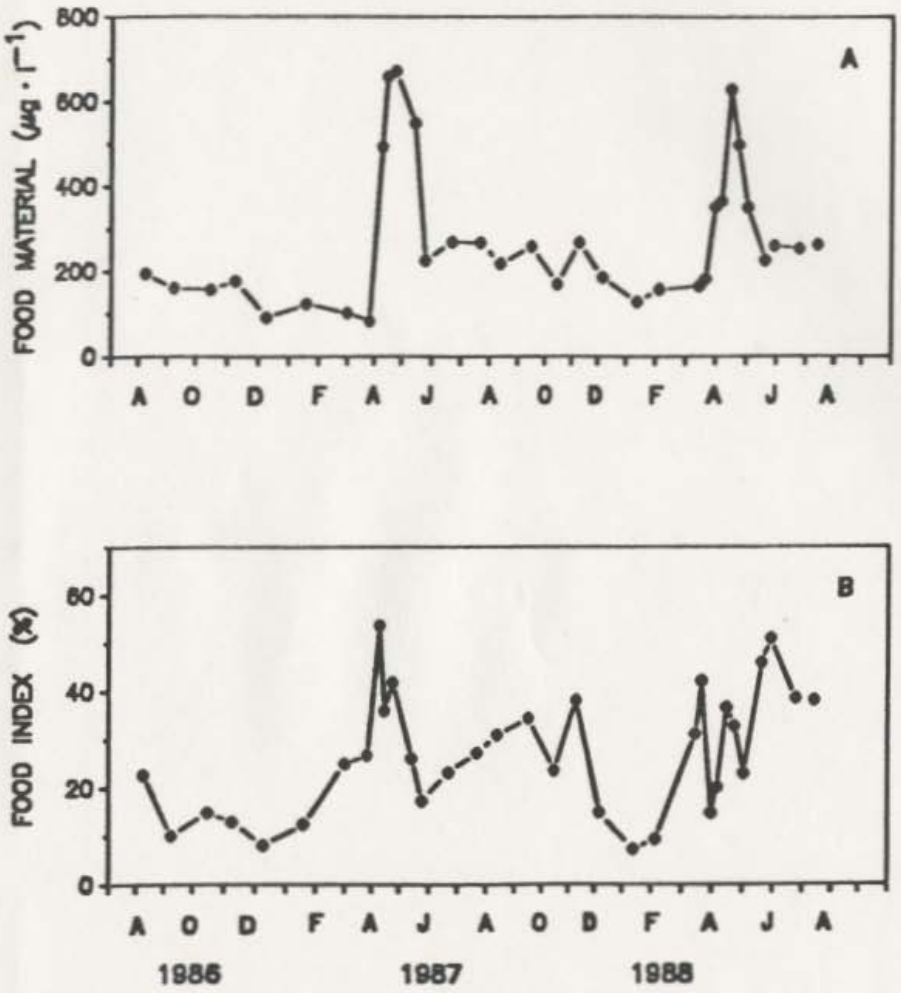


Fig. 8. Seasonal fluctuation in the concentration of food material (FM) and the food index (FIDX).

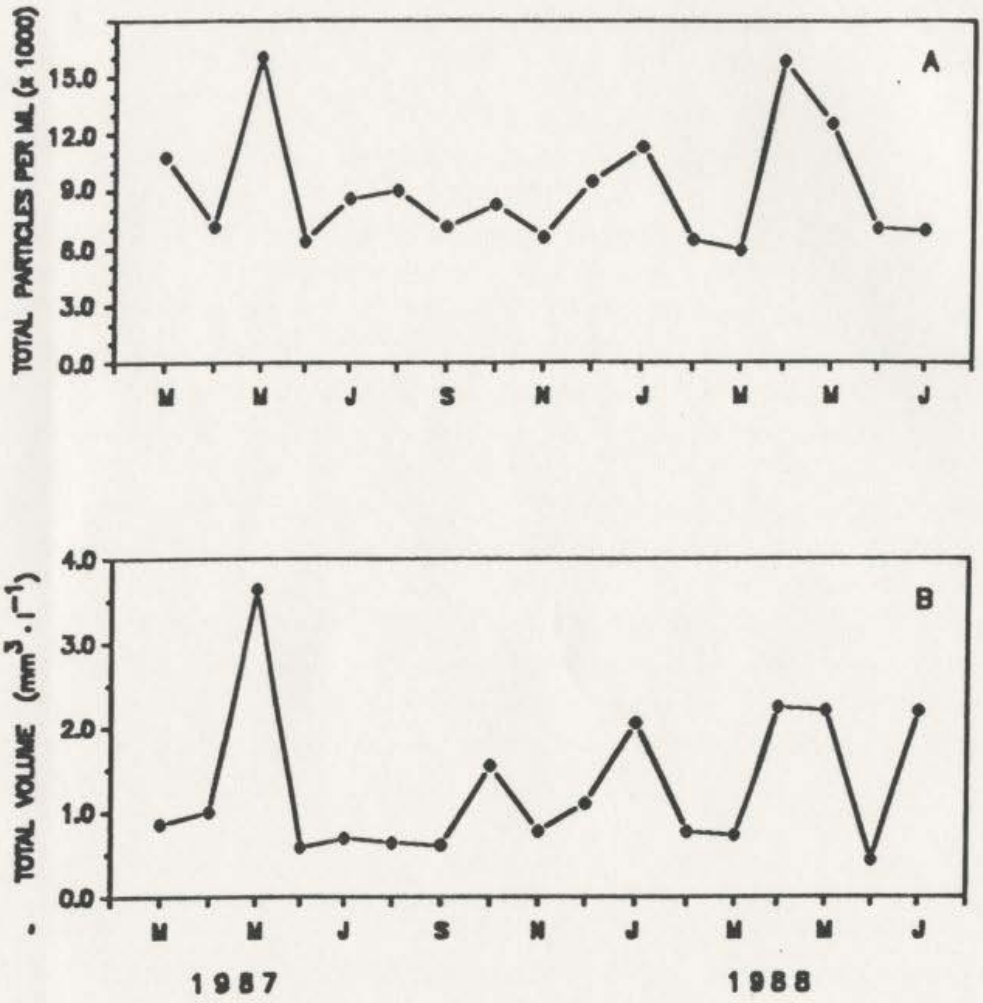


Fig. 9. Seasonal variation in the size frequency distribution of the SPM in Logy Bay, expressed as total particles per ml (A) and total volume (B).

Autotrophic flagellates were more abundant during the last part of the phytoplankton bloom (May-June), with diameters from 6-12 μm.

Figure 10 shows how the size frequency distribution of the particles varied during the spring and summer of 1987. Before the phytoplankton bloom occurred (March-1987) there was a flat spectrum, followed in April by a small peak in the particle concentration in the range 10-30 μm diameter, increasing considerably during May with a peak in the range 20-60 μm diameter. June of 1987 was characterized by a marked decrease in the peak, representing the spring bloom crash and suggesting a reduced number of diatoms. The peak in volume observed in October (Fig. 11) corresponded to large detrital particles (50-100 μm), a situation that was also observed during the following winter months (December-February).

The size spectrum for May 1988 was similar to that of the year before, although the magnitude was lower in 1988 than in 1987. June of 1988 showed two peaks, the first in the range of 30-40 μm, representing the bloom diatoms, and the second in the range of 4-5 μm, probably reflecting the presence of a population of flagellates (Fig. 12).

III.1.7. Correlation Analysis

With the exception of temperature, most of the environmental variables were significantly correlated with each other (Table 3). POM was highly correlated with most of the seston variables, such as TPM, CHLA, PON, POC, PARTN, PARTV and FM. PIM was only positively correlated with PARTN and a negative correlation was found with food index (FIDX). All the nutritive components of the seston, i.e. CHLA, PON, POC, LIPID and CHO, were highly correlated with each other (Table 3). POM, PARTN and PARTV were correlated with FM, although their coefficients were considerably lower (Table 3). FIDX was also positively correlated with the main nutritive components of the seston (although the coefficients were never higher than 0.57), but was negatively correlated with TPM and PIM. Temperature was not correlated with any of the other environmental variables measured in the present study.

III.2. PHYSIOLOGICAL PROCESSES

III.2.1. Clearance Rate

Clearance rate (CR) was determined for animals of various sizes and was expressed as a function of dry tissue weight (DTW) on various time scales (diurnal, seasonal), and subsequently related to environmental conditions. Horse mussels

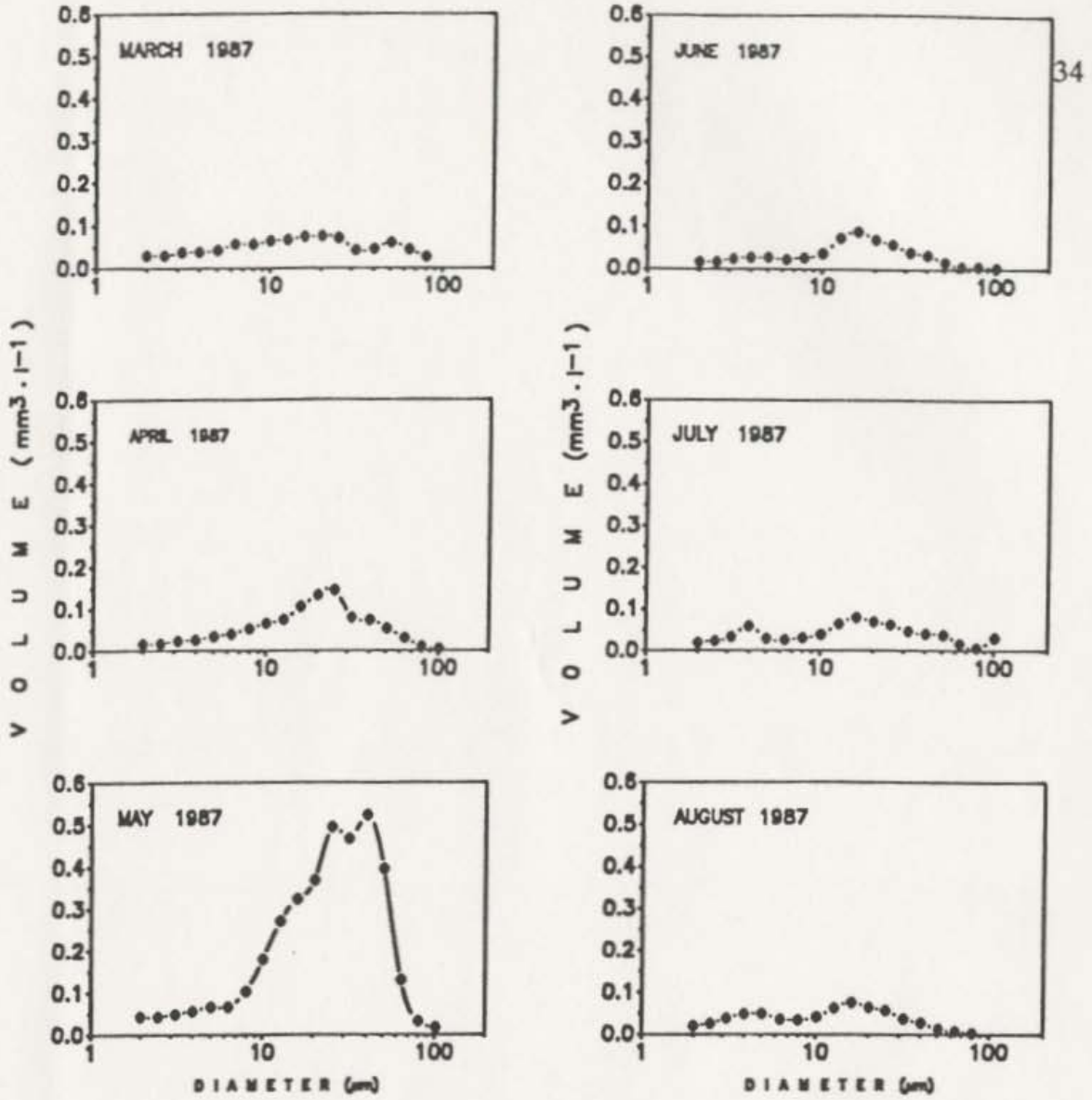


Fig. 10. Size frequency distribution of the SPM in Logy Bay (March-Aug. 1987).

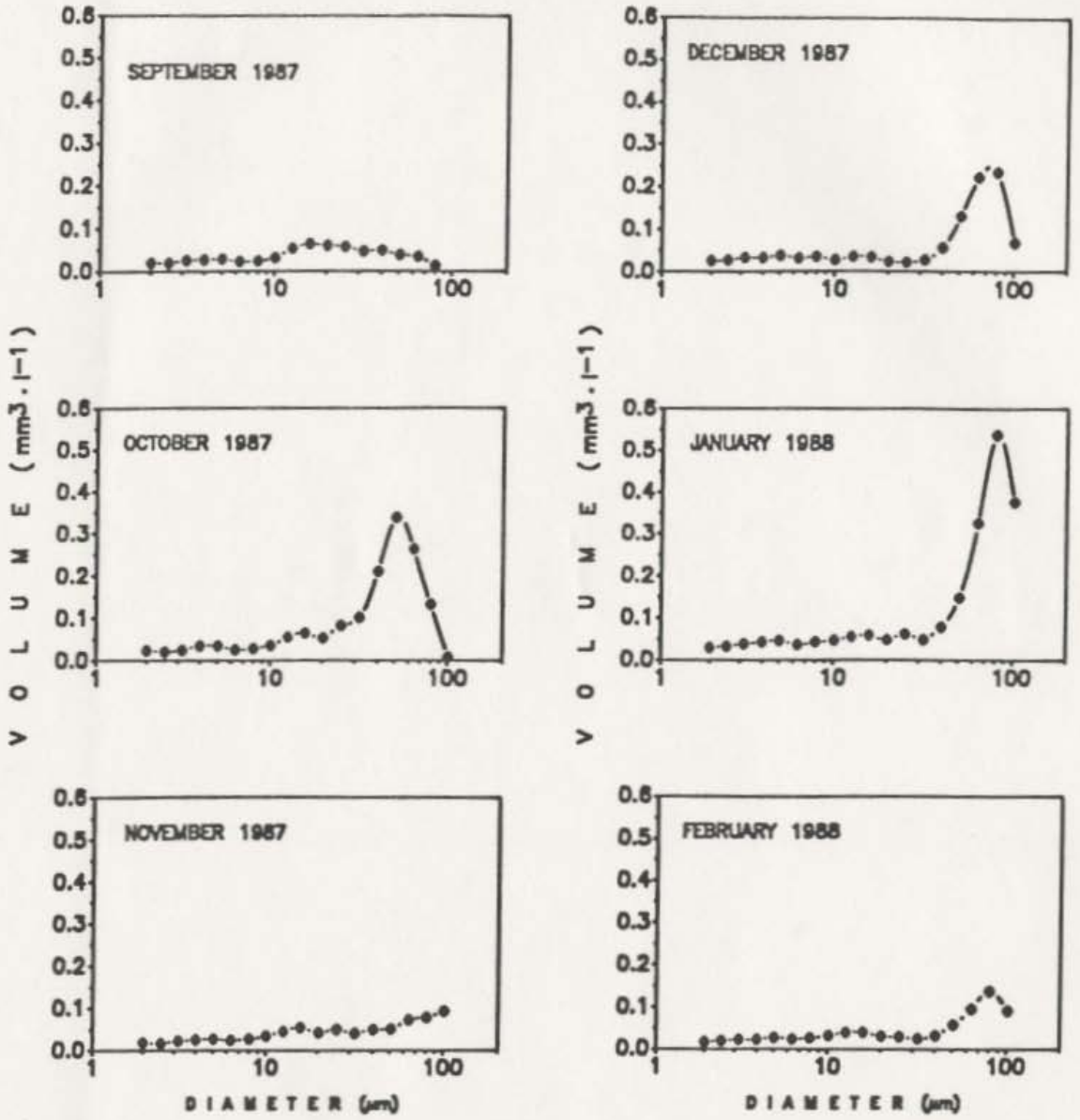


Fig. 11. Size frequency distribution of the SPM in Logy Bay (Sept. 1987-Feb. 1988).

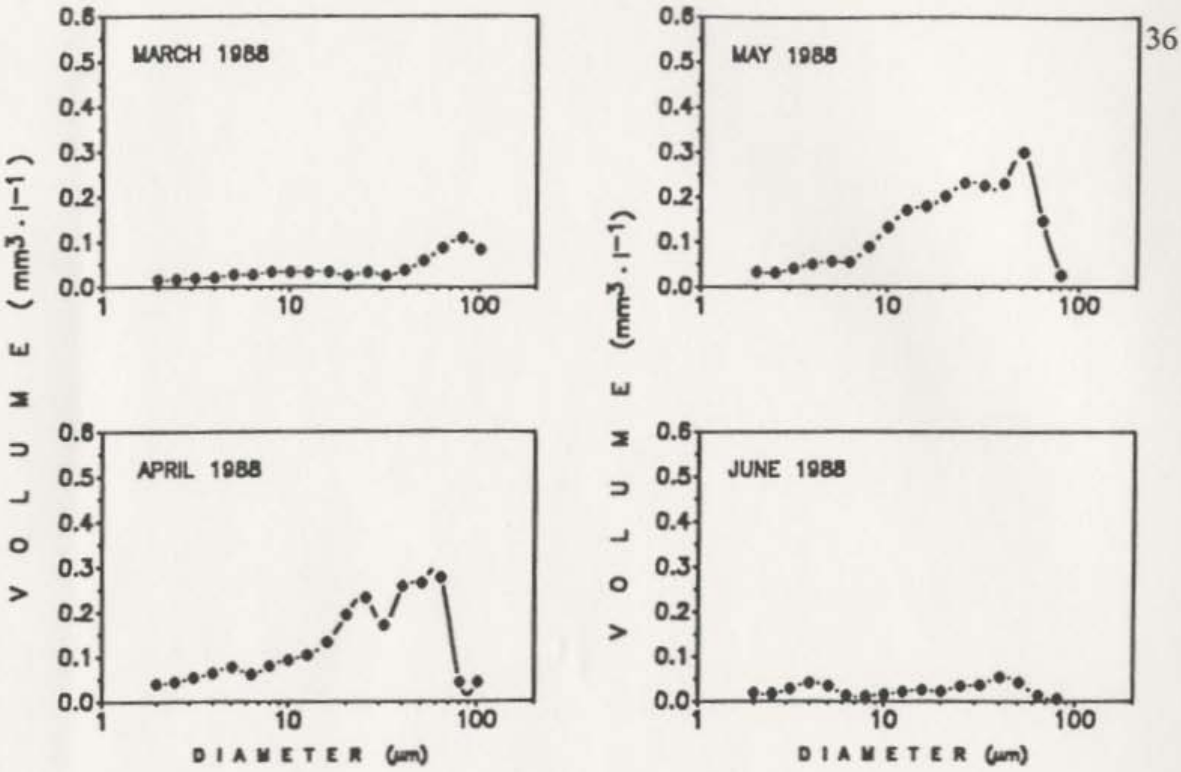


Fig. 12. Size frequency distribution of the SPM in Logy Bay (March-June 1988).

Table 3.- Pearson product-moment correlation coefficients between environmental variables $P<0.05$ (*); $P<0.01$ (**). Number of cases in parenthesis.

	TPM	POM	PIM	CHLA	PON	POC	LIP	CHO	PARTN	PARTV	FM	FIDX	TEMP
TPM	1.00 (96)	0.77** (96)	0.86** (96)	0.72** (81)	0.63** (70)	0.63** (70)	0.27 (34)	0.40* (34)	0.78** (65)	0.65** (65)	0.50** (33)	-0.38* (33)	-0.14 (94)
POM		1.00 (96)	0.37** (96)	0.72** (81)	0.75** (70)	0.74** (70)	0.46** (34)	0.53** (34)	0.58** (65)	0.59** (65)	--	-0.12 (33)	0.21 (94)
PIM			1.00 (96)	0.53** (81)	0.34** (70)	0.36** (70)	0.04 (34)	0.18 (34)	0.67** (65)	0.49** (65)	0.24 (33)	-0.51** (33)	-0.37* (94)
CHLA				1.00 (81)	0.73** (67)	0.75** (67)	0.71** (34)	0.88* (34)	0.69** (59)	0.78** (59)	--	0.32 (33)	-0.25 (79)
PON					1.00 (70)	0.93** (70)	0.78** (33)	0.79** (33)	0.54** (51)	0.52** (51)	--	0.50** (33)	0.18 (68)
POC						1.00 (70)	0.76** (33)	0.82** (33)	0.62** (51)	0.56** (51)	--	0.54** (33)	0.15 (68)
LIP							1.00 (34)	0.74** (34)	0.42* (24)	0.51** (24)	--	0.57** (33)	0.06 (34)
CHO								1.00 (34)	0.63** (24)	0.70** (24)	--	0.46** (33)	-0.18 (34)
PARTN									1.00 (65)	0.74** (65)	0.71** (23)	-0.06 (23)	0.01 (65)
PARTV										1.00 (65)	0.68** (23)	0.18 (23)	-0.15 (65)
FM											1.00 (33)	0.53** (33)	0.10 (33)
FIDX												1.00 (33)	0.22 (33)
TEMP													1.00 (94)

showed periods of high and low clearance rate. Higher values of CR were the rule rather the exception during the spring and early summer, when most of the experimental animals were open and actively feeding for most of the time (Fig. 13). In the experiment of June 1987, for example, CR was maintained in the range of 0.84 to 1.95 $l.h^{-1}$ for 10 hours in a mussel of 1.5 g dry tissue weight (Fig. 13a). In the same experiment, a mussel of 6.68 g dry tissue weight showed CR values between 1.03 and 3.61 $l.h^{-1}$, although most of the values were in the range of 2-3 $l.h^{-1}$ (Fig. 13b). Figures 13c,d show the relatively continuous feeding of this species during an experiment in April 1988. For 9 hours a mussel of 3.16 g dry weight cleared between 2.08 and 3.20 $l.h^{-1}$. Similar results were obtained in the same experiment for a mussel of 5.01 g dry tissue weight. During fall and especially in winter, the CR of *Modiolus modiolus* fluctuated widely, with some periods of low and others of high activity (Fig. 14). In the experiment of November 1986, for example, CR varied from 0 to 4.38 $l.h^{-1}$ over a 12 h period in a mussel of 3.43 g DTW (Fig. 14a), and from 0 to 2.59 $l.h^{-1}$ in an individual of 3.80 g dry weight (Fig. 14b). Figures 14c,d illustrate the highly fluctuating CR of *Modiolus modiolus* during January 1988.

Modiolus modiolus also showed considerable variation in CR throughout the year as well as during the experimental time. The seasonal pattern of CR in three size classes of *Modiolus modiolus* is shown in Fig. 15. High values were observed during spring-summer of 1987, followed by a decrease in the fall to reach minimum values in winter. On the other hand, high values were also observed during fall 1986. During March and April of 1987 it was not possible to measure CR, because the behaviour of the horse mussels was adversely affected by gas bubbles resulting from supersaturation of the inflowing seawater.

Highly significant regressions were found between clearance rate and dry tissue weight at almost all times of the year. Only in September-October 1986 and July-August 1988 (Table 4) were no significant regressions obtained, possibly because a small number of experimental animals was used during these months. When all the data for CR were pooled in one regression equation (Table 4), this was highly significant ($F_{1, 178} = 197.4$).

III.2.2. Ingestion Rate

Ingestion rate (IR) was calculated as the product of CR and the concentration of the suspended particulate matter present in Logy Bay. The seasonal fluctuation of IR in *Modiolus modiolus* is presented in Fig. 16. High values during the spring reflected higher clearance rates as well as higher TPM and POM during the phytoplankton bloom in both years of the study, but the high

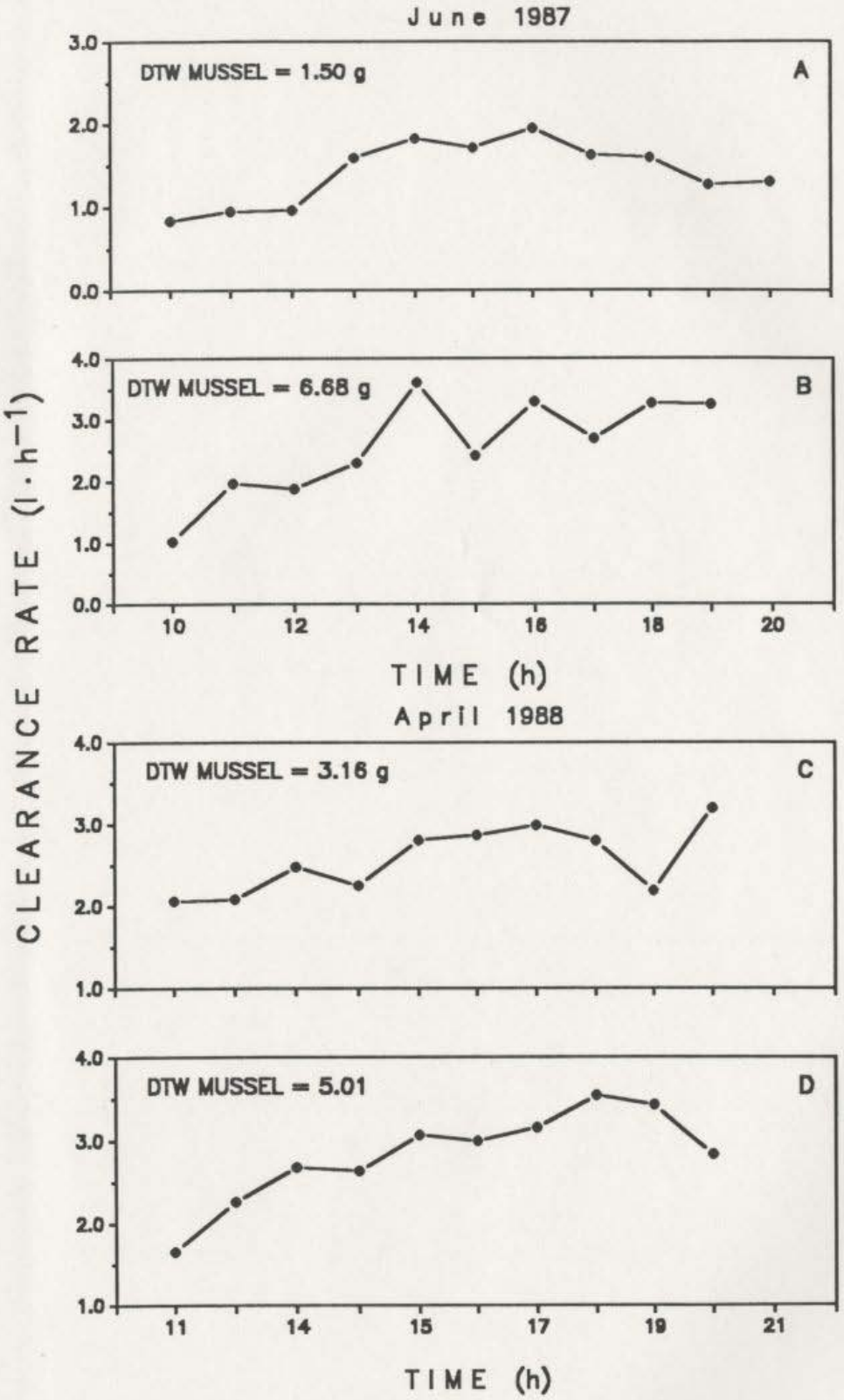


Fig. 13. Representative short-term patterns of clearance rates for individual horse mussels during early summer 1987 (A,B) and spring 1988 (C,D). DTW=Dry tissue weight.

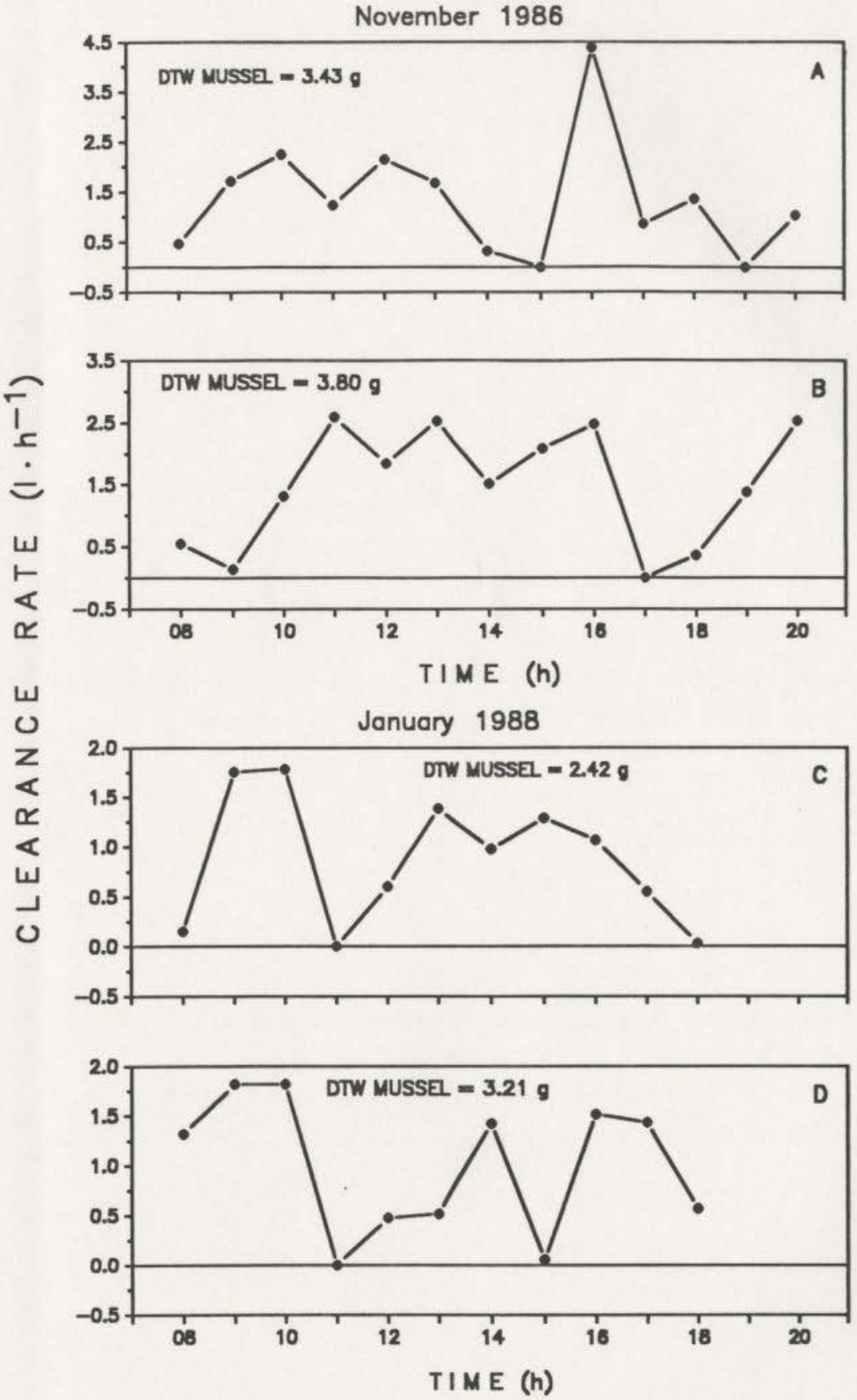


Fig. 14. Representative short-term patterns of clearance rates for individual horse mussels during fall 1986 (A,B) and winter 1988 (C,D). DTW=Dry tissue weight.

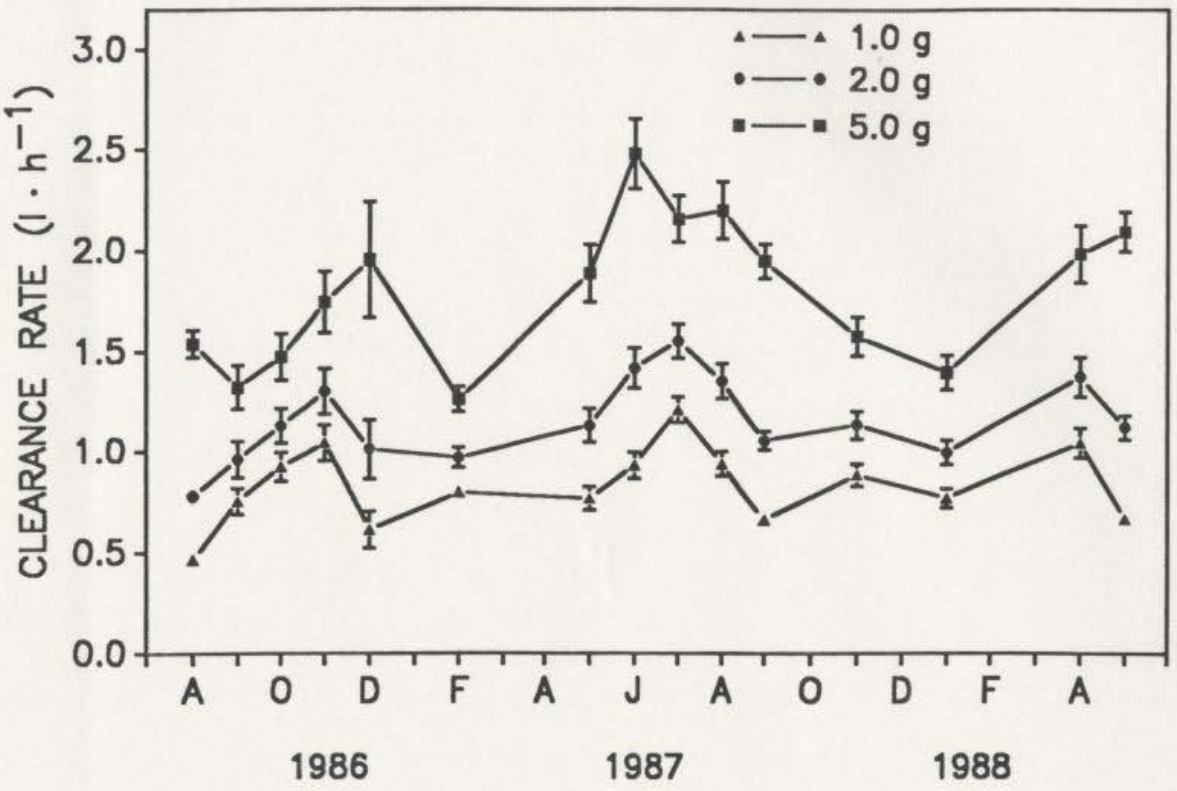


Fig. 15. Clearance rates in three size classes of *Modiolus modiolus*. Values are monthly means ± S.E. When no S.E. bars are shown they were smaller than the symbols.

Table 4.- Modiolus modiolus. Regressions of clearance rate ($l.h^{-1}$) against dry weight (g) for different dates. Regression equations are of the form ($Y=aW^b$), where Y=clearance rate and W=dry weight. The statistic F tests the significance of the difference between b and zero

Date	n	a	b	r	F
AUG.- 86	10	0.48	0.73	0.90	32.0**
SEPT.-86	10	0.73	0.36	0.51	2.8 +
OCT.- 86	8	0.90	0.28	0.59	3.2 +
NOV.- 86	9	1.01	0.32	0.74	8.3*
DEC.- 86	10	0.56	0.72	0.71	7.9*
FEB.- 87	14	0.78	0.29	0.77	17.2**
MAY.- 87	8	0.75	0.56	0.91	28.0**
JUNE- 87	14	0.89	0.61	0.88	42.3**
JULY- 87	14	1.17	0.36	0.80	21.8**
AUG.- 87	15	0.91	0.53	0.87	41.9**
SEPT.-87	14	0.66	0.67	0.92	66.1**
NOV.- 87	14	0.86	0.35	0.71	12.2**
JAN.- 88	12	0.75	0.37	0.72	10.9**
APRIL-88	14	1.02	0.39	0.57	5.6*
MAY - 88	14	0.66	0.71	0.90	51.8**
Pooled Data	170	0.84	0.46	0.72	179.1**

* Significant at $P<0.05$; ** significant at $P<0.01$; + Not Significant

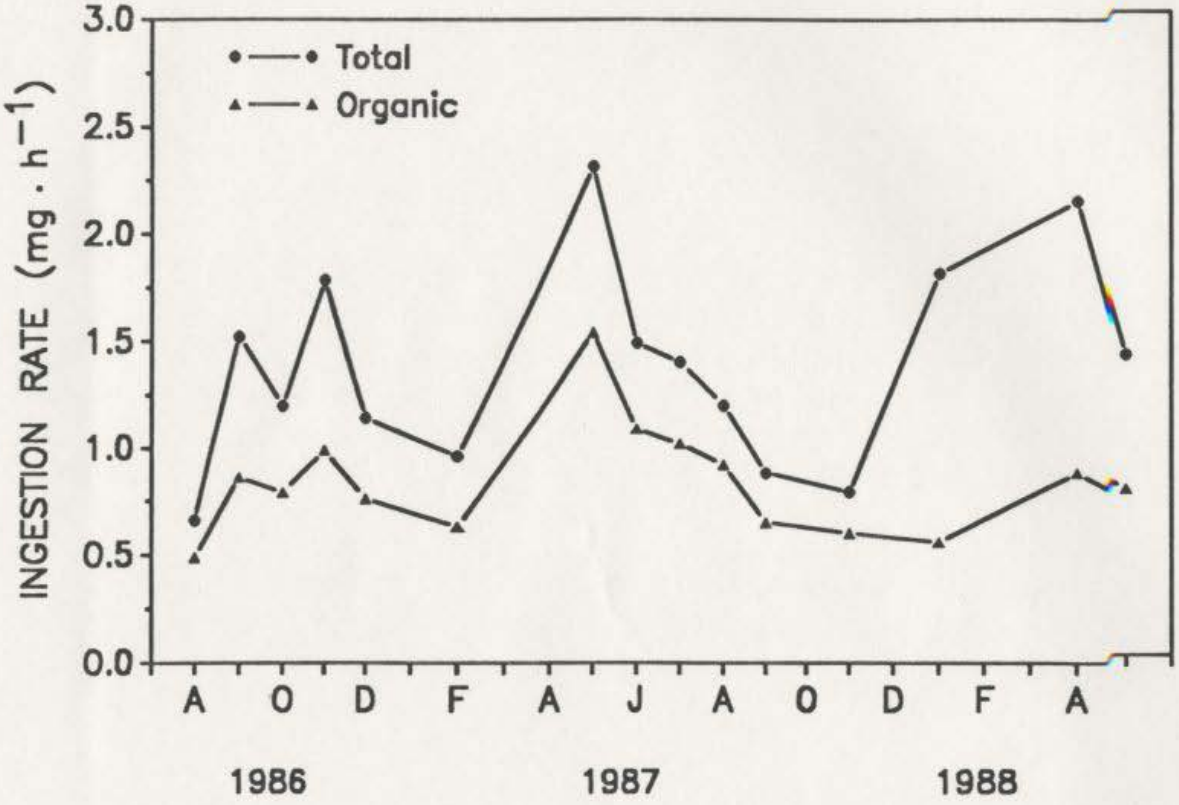


Fig. 16. Ingestion rate (TPM and POM) for a mussel of 2g dry tissue weight.

values recorded during fall 1986 resulted from high clearance rates and not from high seston levels.

III.2.3. Absorption Efficiency

Modiolus modiolus from Logy Bay absorbed the available food very efficiently, with a mean of 76.5 % for a mussel of 2 g when all the data were pooled. Absorption efficiency (AE) showed an erratic seasonal fluctuation and ranged from 50.3% in November 1986 to 93.3% in September 1987 for a mussel of 2 g dry tissue weight (Fig. 17). Only two low values were recorded during the entire period of the study (53.2% and 50.3% for October and November 1986, respectively).

Absorption efficiency was usually independent of body size, as evidenced by lack of significant regressions (Table 5) for all but 2 months (July and September of 1987). When all the data for AE were pooled in one regression equation, it was not significant at $P \geq 0.05$ ($F_{1, 186} = 0.048$).

III.2.4. Oxygen Uptake

Oxygen uptake (VO_2) presented a clear seasonal pattern, characterized by a marked summer peak followed by a rapid decline during the beginning of the fall to reach a minimum in winter (Fig. 18). Oxygen uptake showed no seasonal acclimation to temperature, with which it was strongly correlated (Fig. 19). There was also a significant relationship between VO_2 and the weight of the gonad (an index of gametogenic state) throughout the year.

Highly significant linear regressions of log VO_2 against log dry tissue weight were found in every month ($P \leq 0.01$), and also when the data were pooled in one regression equation (Table 6).

III.2.5. Ammonia Excretion

Ammonia excretion followed a similar seasonal pattern to VO_2 in all three size classes selected (Fig. 20), rising abruptly during the spring to reach maximum values in summer during the period of elevated rates of oxygen consumption and higher temperatures. Like VO_2, VNH_4-N decreased after August, attaining minimum values during winter and the beginning of spring. The rate of ammonia excretion was also correlated with temperature (Fig. 19).

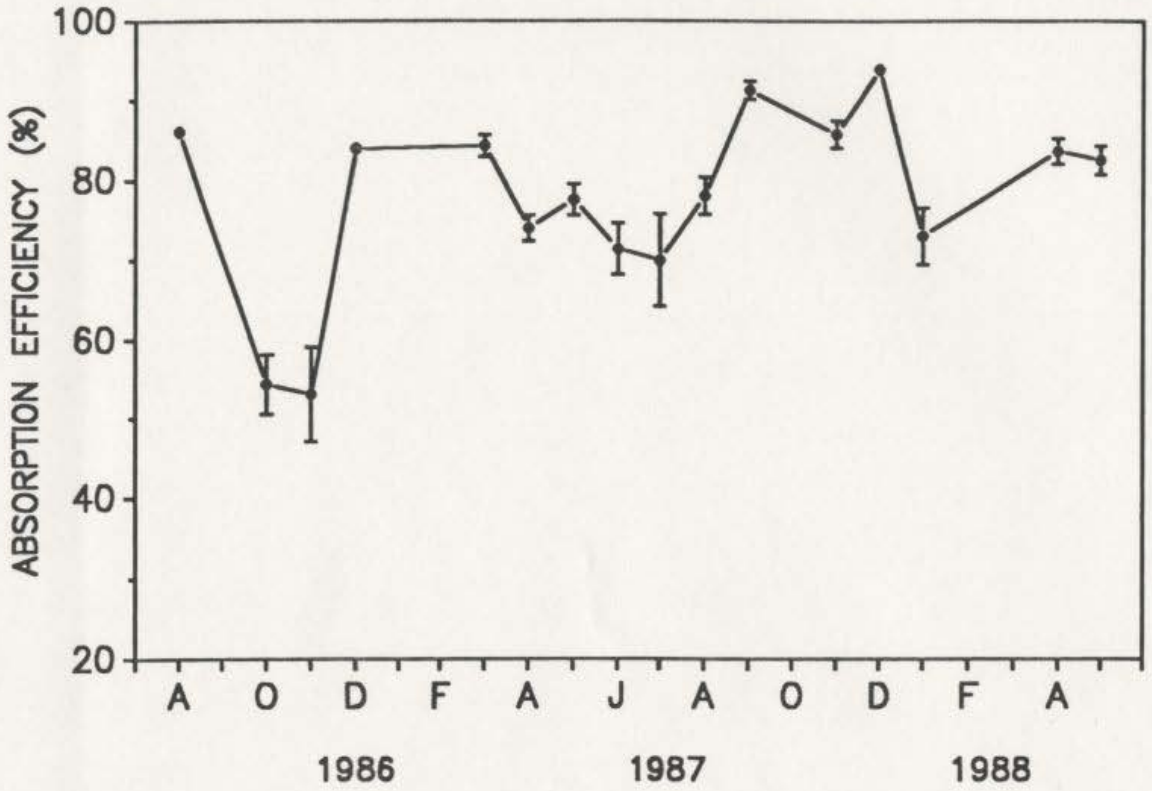


Fig. 17. Absorption efficiency in *Modiolus modiolus*. Values are monthly means ± S.E. When no S.E. bars are shown they were smaller than the symbols.

Table 5. *Modiolus modiolus*. Regressions of absorption efficiency (%) against dry weight (g) for different dates. Regression equations are of the form $Y=aW^b$, where Y=absorption efficiency and W=dry weight. The statistic F tests the significance of the difference between b and zero.

Date	n	a	b	r	F
AUG.- 86	9	86.5	-0.003	-0.124	0.109$^+$
OCT.- 86	10	53.1	0.002	0.005	0.000$^+$
NOV.- 86	8	47.1	0.095	0.287	0.538$^+$
DEC.- 86	8	81.1	0.037	0.412	1.224$^+$
MARCH-87	8	84.3	-0.016	-0.302	0.601$^+$
APRIL-MAY-87	15	71.1	0.057	0.320	1.478$^+$
JUNE- 87	14	73.5	-0.045	-0.188	0.437$^+$
JULY- 87	15	81.3	-0.167	-0.568	6.188*
AUG.- 87	15	82.8	-0.067	-0.458	3.450$^+$
SEPT.-87	13	97.5	-0.063	-0.626	7.079*
NOV.- 87	13	84.3	0.011	0.108	0.129$^+$
DEC.- 87	6	95.7	-0.036	-0.615	2.428$^+$
JAN.- 88	13	74.3	-0.042	-0.116	0.150$^+$
APRIL-88	77	81.3	0.017	0.076	0.144$^+$
MAY - 88	14	82.6	-0.004	-0.025	0.007$^+$
Pooled Data	188	76.2	0.005	0.015	0.048$^+$

* Significant at $P \leq 0.05$; ** significant at $P \leq 0.01$;

+ Not significant

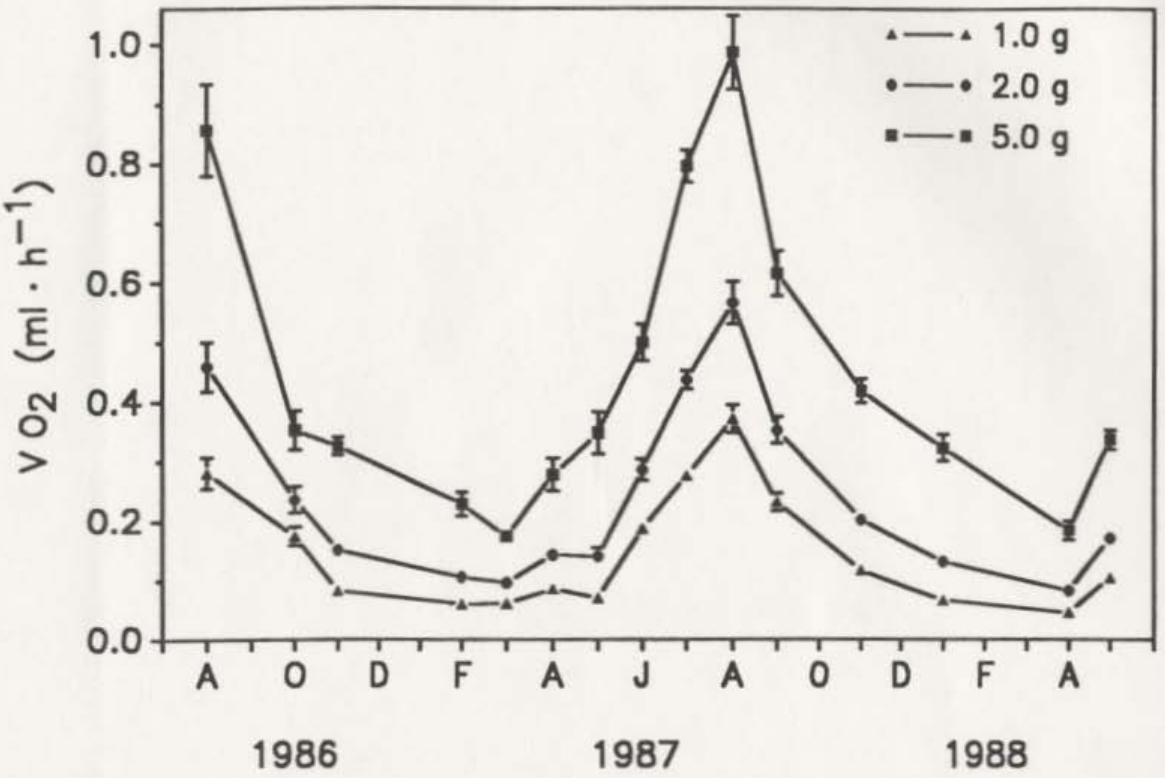


Fig. 18. Oxygen uptake (VO_2) in three size classes of *Modiolus modiolus*. Values are monthly means ± S.E. When no S.E. bars are shown they were smaller than the symbols.

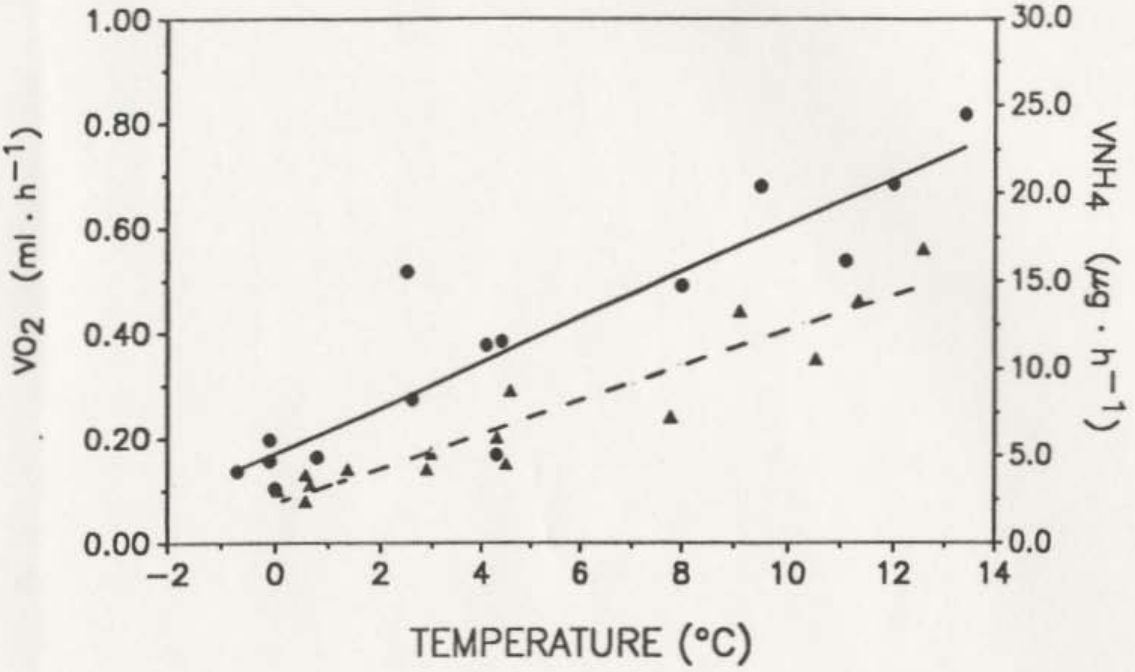


Fig. 19. Regressions of oxygen uptake (ml.h^{-1}; circles) and ammonia excretion (μg NH_4-N.h^{-1}; triangles) against temperature for a 5 g dry tissue weight *Modiolus modiolus*.

Table 6. *Modiolus modiolus*. Regressions of oxygen uptake (ml $0_2.h^{-1}$) against dry weight (g) for different dates. Regression equations are of the form $Y=aW^b$, where Y = oxygen uptake and W = dry weight. The statistic F tests the significance of the difference between b and zero.

Date	n	a	b	r	F*
AUG.- 86	9	0.279	0.72	0.96	89.9
OCT.- 86	12	0.167	0.45	0.92	52.1
NOV.- 86	16	0.082	0.85	0.98	276.5
FEB.- 87	15	0.053	0.87	0.88	45.7
MARCH-87	15	0.059	0.66	0.91	61.5
APRIL-87	15	0.100	0.67	0.79	21.5
MAY - 87	10	0.070	0.96	0.95	66.1
JUNE- 87	14	0.180	0.62	0.92	65.8
JULY- 87	15	0.273	0.66	0.97	213.4
AUG.- 87	15	0.354	0.61	0.81	25.3
SEPT.-87	13	0.203	0.71	0.76	14.9
NOV.- 87	14	0.119	0.76	0.95	102.3
JAN.- 88	14	0.063	1.01	0.91	59.1
APRIL-88	14	0.043	0.87	0.78	18.5
MAY - 88	14	0.103	0.72	0.88	42.8
Pooled data	205	0.123	0.68	0.68	170.1

* All the F values are significant at $P \leq 0.01$

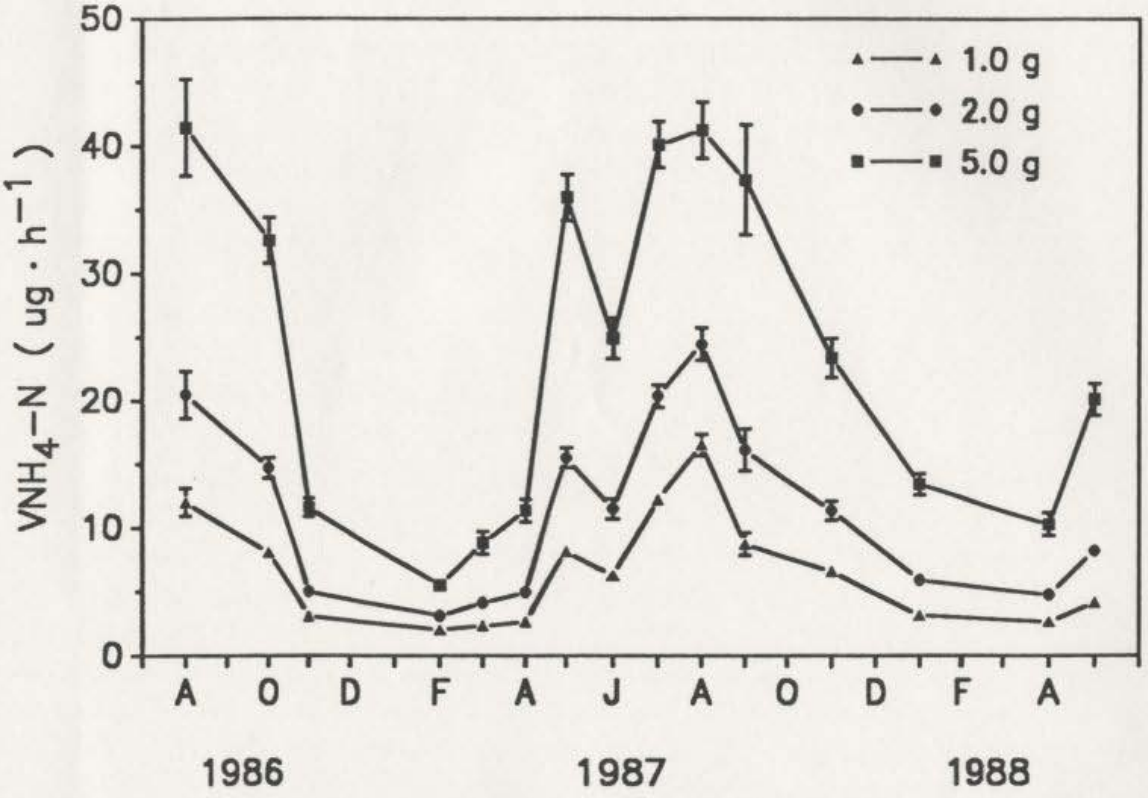


Fig. 20. Ammonia excretion (VNH_4-N) in three size classes of *Modiolus modiolus*. Values are monthly means ± S.E. When no S.E. bars are shown they were smaller than the symbols.

The results of linear regression of log VNH_4-N against log dry weight indicated that in all months there was a significant relationship at $P \leq 0.01$ (Table 7). Similar results were obtained when the data were pooled in one regression equation.

The atomic ratio between oxygen uptake and nitrogen excretion (O:N) indicates the proportion of protein relative to lipid and carbohydrate that is catabolized for energy metabolism. A high rate of protein relative to lipid and carbohydrate catabolism results in a low O:N ratio. The O:N ratio for *Modiolus modiolus* fluctuated around 25, although a higher value (≈52.8) was obtained in February 1987 and a lower value (≈11.4) was observed in May of the same year (Fig. 21).

III.2.6. Scope for Growth

The conversion of the physiological rates into calorific equivalents for each month and the subsequent calculation of scope for growth (SFG) for a mussel of 2 g dry tissue weight is presented in Table 8. Scope for growth in three size classes of *Modiolus modiolus* at intervals over two years is plotted in Figure 22. During the spring, SFG was higher in both years of the study and in all three size classes investigated. There was a considerable decrease in SFG from May to August, and negative values were reported in August and September for small mussels (Fig. 22a,b). This trend was even more apparent in larger animals (5g dry tissue weight), in which SFG was negative during summer, fall and early winter (Fig. 22c), with values as low as -300 $J.d^{-1}$. During winter, SFG was very close to zero, the available energy being just adequate for the maintenance of the basic physiological processes.

III.2.7. Net Growth Efficiency

Net growth efficiency (K_2) for *Modiolus modiolus* (Table 8) fluctuated widely according to season, with values as low as -2.0 during summer (August, 1986) and as high as 0.81 during spring (April,1988). As with SFG, the lower values for K_2 were associated with low CR, high VO_2, high temperature and low quality of the food supply. Conversely, higher values of K_2 were associated with low VO_2, low temperature and an energy-rich food supply provided by the phytoplankton bloom. Although clearance rate was not measured very often during the spring, the results suggest that this physiological process is also playing an important role in the gain of energy from the environment. Net growth efficiency was clearly dependent on body size (Fig. 23), ranging between 0.55 and 0.02 for mussels of 0.3 and 10 g dry tissue weight, respectively.

Table 7. *Modiolus modiolus*. Regressions of ammonia excretion (ug NH_4-N.h^{-1}) against dry weight (g) for different dates. Regression equations are of the form $Y=aW^b$, where Y = ammonia excretion and W = dry weight. The statistic F tests the significance of the difference between b and zero.

Date	n	a	b	r	F*
AUG.- 86	8	11.43	0.81	0.96	71.1
OCT.- 86	10	7.89	0.87	0.99	281.4
NOV.- 86	13	2.57	0.92	0.96	137.5
FEB.- 87	13	1.88	0.62	0.76	15.0
MARCH-87	14	2.16	0.83	0.89	47.7
APRIL-87	15	2.51	0.91	0.93	86.9
MAY - 87	10	8.09	0.92	0.98	218.1
JUNE- 87	14	5.98	0.89	0.94	83.0
JULY- 87	15	11.97	0.74	0.96	151.8
AUG.- 87	15	16.11	0.57	0.92	67.9
SEPT.-87	13	7.53	0.96	0.73	12.7
NOV.- 87	14	6.38	0.79	0.92	65.8
JAN.- 88	14	3.05	0.90	0.88	42.7
APRIL-88	14	2.43	0.87	0.79	19.2
MAY - 88	14	4.02	0.99	0.91	56.9
Pooled data	196	5.00	0.81	0.69	178.4

* All the F values are significant at $P \leq 0.01$

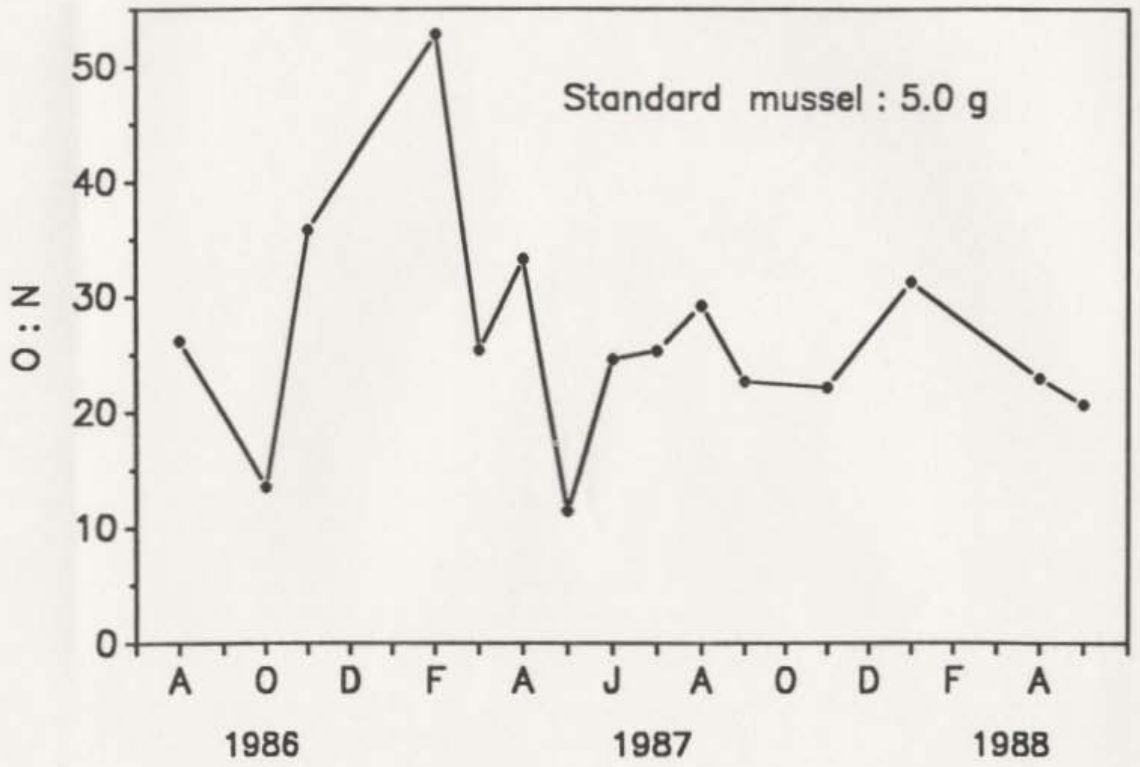


Fig. 21. Seasonal variation in the atomic ratio of oxygen consumed to the ammonia-nitrogen excreted in a horse mussel of 5g dry tissue weight.

Table 8.- Modiolus modiolus. Scope for growth for a standard mussel of 2.0 g dry weight. See "Material and Methods" for details of calculations.

Date	TPM	POM		Clearance Rate	Ingestion Rate (org.)		Absorption Effic.	Absorption Rate		Oxygen Uptake	Ammonia Excretion	SFG	K_2
	($mg.l^{-1}$)	($mg.l^{-1}$)	($J.l^{-1}$)	($l.d^{-1}$)	($mg.d^{-1}$)	($J.d^{-1}$)	(%)	($mg.d^{-1}$)	($J.d^{-1}$)	($J.d^{-1}$)	($J.d^{-1}$)	($J.d^{-1}$)	
AUG.- 86	0.85	0.63	4.89	18.7	11.8	91.5	86.0	10.1	78.7	224.0	12.2	-157.5	-2.00
SEPT.-86	1.58	0.90	4.10	23.0	20.7	94.5	-	-	-	-	-	-	-
OCT.- 86	1.06	0.70	4.08	27.1	19.0	110.6	54.4	10.3	60.2	115.2	8.8	- 63.8	-1.06
NOV.- 86	1.37	0.76	4.67	31.2	23.7	145.7	53.1	12.6	77.4	73.2	3.0	1.2	0.02
DEC.- 86	1.13	0.75	2.47	24.2	18.2	59.9	83.9	15.3	50.3	-	-	-	-
FEB.- 87	0.99	0.65	3.14	23.3	15.1	73.1	86.8	13.1	63.5	51.2	1.9	10.4	0.16
MAY - 87	2.04	1.36	16.48	27.1	31.4*	379.9*	77.6	24.4	294.8	68.3	9.3	217.2	0.74
JUNE- 87	1.05	0.77	9.13	34.1	26.2	311.2	71.4	18.7	222.2	139.1	6.9	76.2	0.34
JULY- 87	0.90	0.66	9.05	37.2	24.6	336.7	70.0	17.2	235.7	212.0	12.2	11.5	0.05
AUG.- 87	0.89	0.68	6.43	32.4	22.0	208.3	78.0	17.2	162.5	275.0	14.6	-127.1	-0.78
SEPT.-87	0.84	0.62	6.51	25.2	15.6	164.0	91.2	14.2	149.6	171.3	9.6	- 31.3	-0.21
NOV.- 87	0.70	0.53	6.87	27.1	14.4	186.3	85.7	12.3	159.7	98.1	6.8	54.8	0.34
JAN.- 88	1.83	0.57	5.49	23.8	13.5	130.4	72.9	9.8	95.1	63.9	3.5	27.7	0.29
APRIL-88	1.57	0.75	9.47	32.9	21.0*	264.7*	83.5	20.6	221.0	40.0	2.8	178.2	0.81
MAY - 88	1.25	0.81	10.85	26.9	18.5*	248.0*	82.4	18.0	204.4	83.4	4.9	116.1	0.57

* An average of 15% of the total food filtered was rejected as pseudofaeces during these experiments. This value was calculated from the results of biodeposition experiments in 1988 (see Table 13).

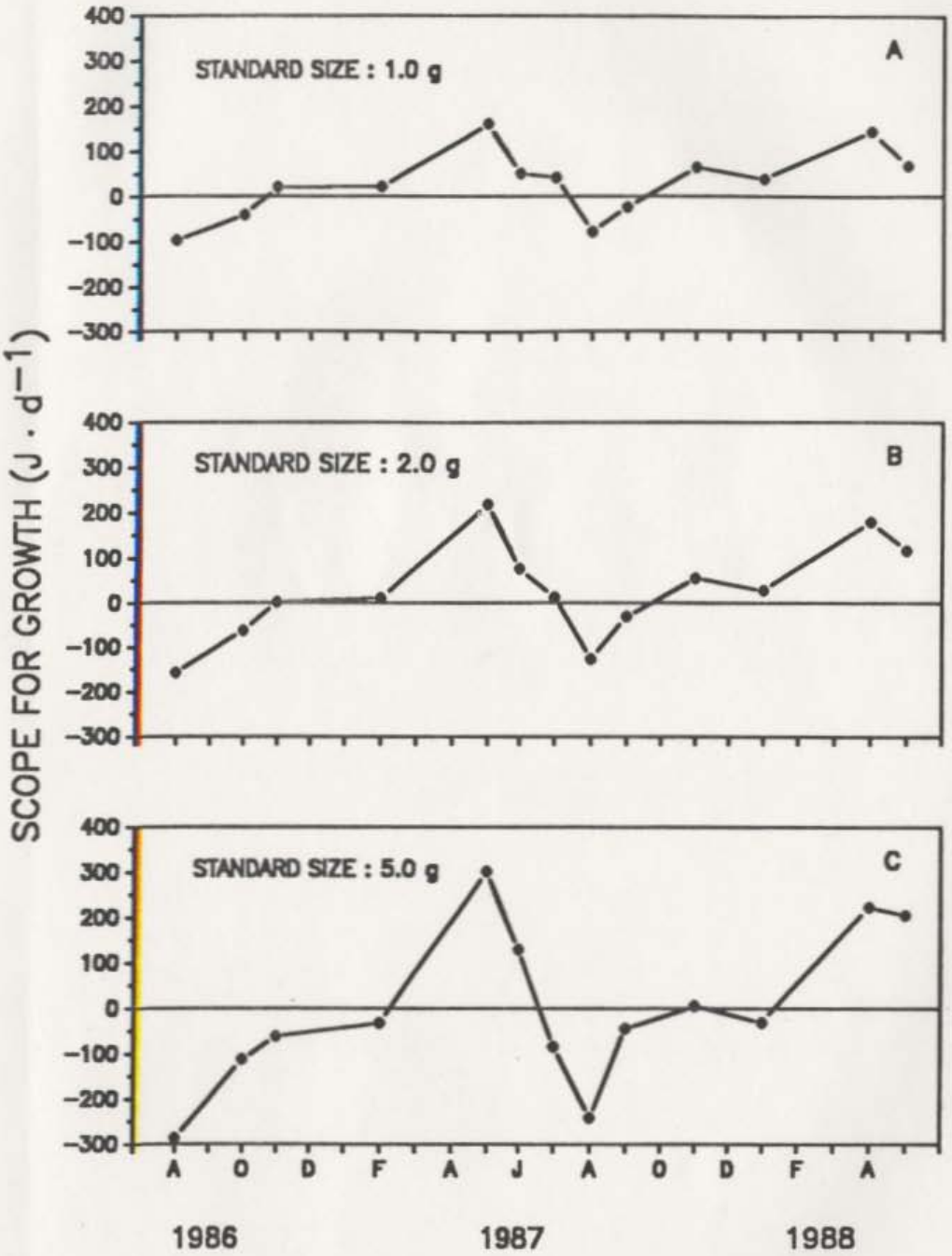


Fig. 22. Seasonal cycle in the scope for growth (SFG) for three size classes of *Modiolus modiolus*.

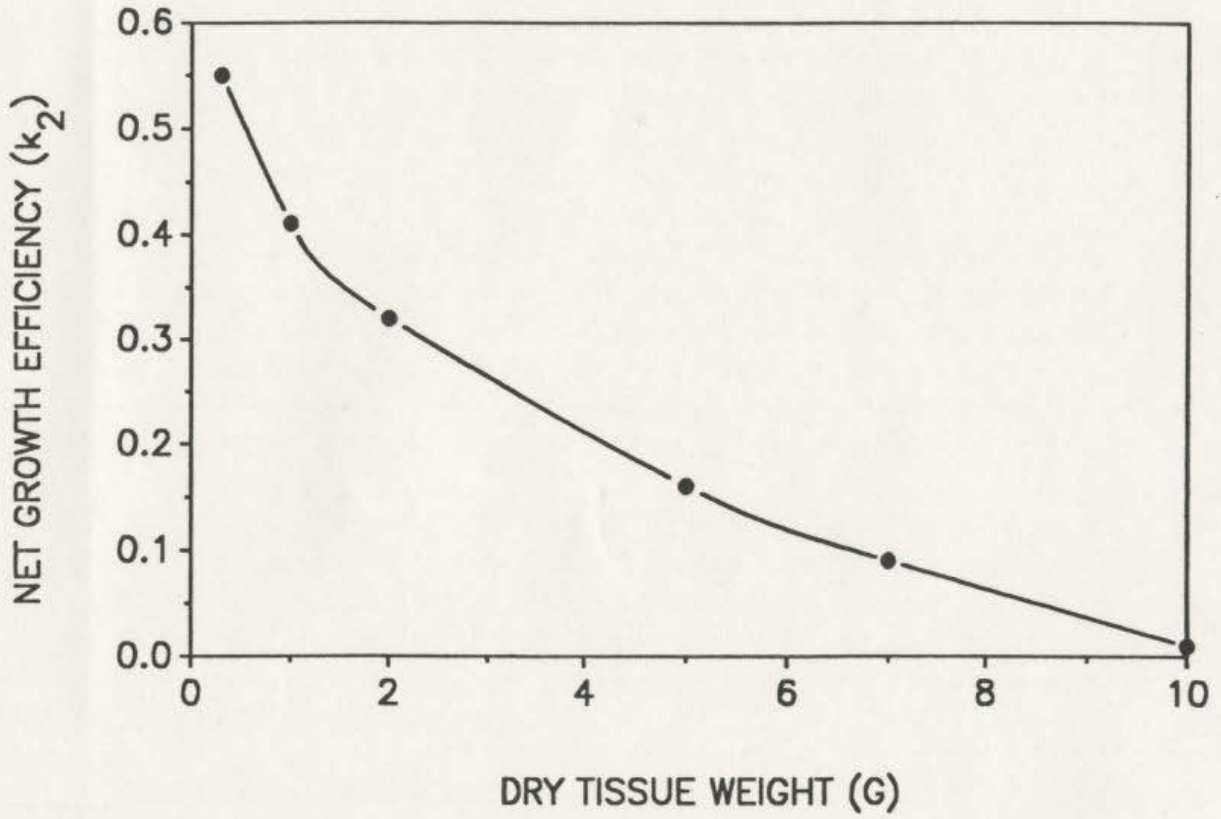


Fig. 23. Net growth efficiency (K_2) (based on regressions of pooled data of each physiological variable) vs. dry tissue weight for *Modiolus modiolus*.

III.2.8. Correlation Analysis and Multiple Regression

Clearance rate was not correlated with any of the environmental variables, and was correlated only with absorption rate ($P \leq 0.05$) among the physiological variables (Table 9). Multiple regression analysis between CR and the environmental variables showed that no variables were entered at $P \leq 0.05$. Similar results were obtained for absorption efficiency, where no physiological or environmental variable was entered at $P \leq 0.05$. In contrast, absorption rate (AR) was correlated with many of the environmental variables (i.e. POM, CHLA, PON, POC, LIPID, CHO and FM), showing that there was a good relationship between AR and the nutritive components of the seston (Table 9). The variation in AR was best explained by the model which included POM, PARTV and CHLA as independent variables, accounting for 97% of the variation (Table 10).

Oxygen uptake (VO_2) was positively correlated with temperature ($r=0.93$) and ammonia excretion (VNH_4-N; $r=0.88$), and negatively correlated with PARTV ($r=-0.85$) and PIM ($r=-0.63$). Temperature alone explained 86% of the total variance in VO_2, and when PARTV was included in the model, the proportion increased to 92% (Table 10). All the other independent variables accounted for a very small additional percentage.

The rate of ammonia excretion was highly correlated with temperature and VO2, and the former was the main environmental factor determining VNH_4-N in *Modiolus modiolus*. Multiple regression between VNH_4-N and the environmental variables showed that 79% of the total variance in excretion rate was explained by TEMP and 90% by including PARTV with TEMP (Table 10).

Scope for growth was correlated ($P \leq 0.05$) only with two environmental variables, PON and PARTV, and only with absorption efficiency among the physiological variables ($P \leq 0.05$). Multiple regression analysis showed that the best model (PARTV+CHLA) explained 63% of the variation in SFG, whereas PARTV alone accounted for 52% (Table 10). The introduction of other variables into the model made very little difference.

III.2.9. Nitrogen Balance

Measurements of PON in Logy Bay and of clearance rate, absorption efficiency and excretion rate for *Modiolus modiolus* were made approximately every month to calculate the nitrogen balance (absorbed nitrogen minus excreted nitrogen) as a percentage of the total nitrogen in the tissues of a mussel of 2.0 g dry weight. The protein content of the dry tissue of *Modiolus modiolus* was

Table 9.- Pearson product-moment correlation coefficients between physiological and environmental variables. $P < 0.05$(*); $P < 0.01$(**). Number of cases in parenthesis.

	CR	TIR	AE	AR	VO_2	VNH_4	SFG	K_2	TPM	POM	PIM	CHLA	PON	POC	LIP	CHO	PART N	PART V	TEMP	FM	FIDX
CR	1.00 (17)	0.39 (17)	-0.39 (14)	0.56* (14)	0.06 (13)	0.07 (13)	0.03 (13)	0.53 (13)	-0.03 (17)	0.06 (17)	-0.06 (17)	0.25 (16)	0.37 (17)	0.47 (17)	0.34 (16)	0.38 (16)	0.23 (10)	-0.47 (10)	0.04 (17)	0.39 (16)	0.28 (16)
TIR		1.00 (17)	-0.40 (14)	0.55** (14)	-0.52 (13)	-0.31 (13)	0.13 (13)	0.63* (13)	0.91** (17)	0.75** (17)	0.86** (17)	0.57* (16)	0.32 (17)	0.40 (17)	0.28 (16)	0.45 (16)	0.53 (10)	0.47 (10)	-0.52* (17)	0.28 (16)	-0.26 (16)
AE			1.00 (17)	0.06 (14)	-0.04 (15)	-0.01 (15)	0.56* (13)	0.04 (13)	-0.34 (17)	-0.32 (17)	-0.25 (17)	0.03 (17)	0.09 (17)	-0.14 (17)	-0.05 (17)	-0.10 (17)	-0.39 (11)	-0.02 (11)	-0.26 (17)	0.05 (17)	0.26 (17)
AR				1.00 (14)	0.12 (13)	0.40 (13)	0.32 (13)	0.40 (13)	0.33 (14)	0.72** (14)	0.07 (14)	0.65* (14)	0.72** (14)	0.69** (14)	0.67** (14)	0.60* (14)	0.42 (9)	0.24 (9)	0.14 (14)	0.71** (14)	0.48 (14)
VO_2					1.00 (15)	0.88** (15)	0.21 (13)	-0.61* (13)	-0.36 (15)	0.06 (15)	-0.63* (15)	-0.37 (15)	0.23 (15)	0.19 (15)	-0.22 (15)	-0.26 (15)	-0.17 (10)	-0.85** (10)	0.93** (15)	0.05 (15)	0.18 (15)
VNH_4						1.00 (15)	0.05 (13)	-0.49 (13)	-0.14 (15)	0.27 (15)	-0.46 (15)	-0.13 (15)	0.48 (15)	0.45 (15)	0.03 (15)	-0.02 (15)	-0.15 (10)	-0.61 (10)	0.89** (15)	0.30 (15)	0.32 (15)
SFG							1.00 (13)	0.40 (13)	0.13 (13)	0.17 (13)	0.06 (13)	0.41 (13)	0.60* (13)	0.48 (13)	0.44 (13)	0.41 (13)	0.43 (9)	0.72* (9)	-0.35 (13)	0.43 (13)	-0.21 (13)
K_2								1.00 (13)	0.44 (13)	0.29 (13)	0.42 (13)	0.46 (13)	0.29 (13)	0.34 (13)	0.51 (13)	0.39 (13)	0.40 (9)	0.70* (9)	-0.61 (13)	0.36 (13)	0.03 (13)

Table 10. *Modiolus modiolus*. Multiple regression statistics for several physiological variables vs subsets of independent variables. * $P \leq 0.05$; ** $P \leq 0.01$ and *** $P \leq 0.001$.

DEP. VAR.	INDEP. VAR.	R^2	n	F
A R	P O M	0.520	14	12.89**
	P A R T V	0.938	9	45.78**
	C H L A	0.966	9	47.48**
V O_2	T E M P	0.857	15	77.78***
	P A R T V	0.924	10	42.47***
V NH_4	T E M P	0.787	15	48.14***
	P A R T V	0.898	10	30.36***
S F G	P A R T V	0.515	9	7.44*
	C H L A	0.631	9	5.14*

AR ; Absorption rate
VO_2 ; Oxygen consumption
VNH_4 ; Ammonia excretion
SFG ; Scope for growth
POM ; Partic. Organic matter
PARTV; Particulate volume
CHLA ; Chlorophyll a
TEMP ; Temperature

measured every month for this purpose. It was assumed that the nitrogen content of the protein was 17.2% by weight (Gnaiger and Bitterlich, 1984).

Figure 24 shows the seasonal fluctuation of the nitrogen balance in *Modiolus modiolus*. There was only one negative value (October, 1986) during the entire period of the study, during which the mussel lost 0.03% of its body nitrogen per day. During spring the mussels gained up to 0.6% of their body nitrogen per day, largely as a result of low excretion rates and the high concentration of nitrogen in the seston.

III.3. ABSORPTION EFFICIENCY: COMPARISON AND EVALUATION OF DIFFERENT TECHNIQUES

Absorption efficiency (AE) can be estimated indirectly by balancing the energy budget equation after all the other components have been measured. However, AE has been commonly quantified by the ash-ratio technique developed by Conover (1966), which assumes that the organic component of the food is digested and absorbed while the indicator (inorganic matter) is not. To circumvent the uncertainty and controversy regarding this assumption, Tande and Slagstad (1985) measured AE in zooplankton using biogenic silica as the nonabsorbed component of the food. The use of biogenic silica as the inert substance generally restricts this method to situations in which diatoms are present as food, which is the case in many marine environments. Other authors, such as Conover et al. (1986) and Hawkins et al. (1986), have used chloropigment degradation to measure absorption efficiency.

One of the objectives of the present study was to apply these various techniques to *Modiolus modiolus* and to compare the results over a long period, using different qualities and quantities of food. Absorption efficiency determinations were made over a period of one year, using the ash-ratio and silicate ratio techniques, for *Modiolus modiolus* feeding on natural seston (Fig. 25a). Both techniques gave values of AE around 80%, although a few slightly higher values were obtained with the ash-ratio procedure. More variable data were obtained in the lower region of the silicate concentration range.

To establish the relationship between these two techniques, the results were expressed in terms of the AE (ash):AE (silicate) ratio measured under natural conditions throughout the year (Fig. 25b). The two methods gave very similar results over a wide range of silicate concentrations (40-240 $\mu g.mg^{-1}$ food), the AE (ash):AE (silicate) ratio being very close to 1.0. However, in the low range of silicate concentration (20-40 $\mu g.mg^{-1}$ food) ratios from 0.7 to 1.2 were observed.

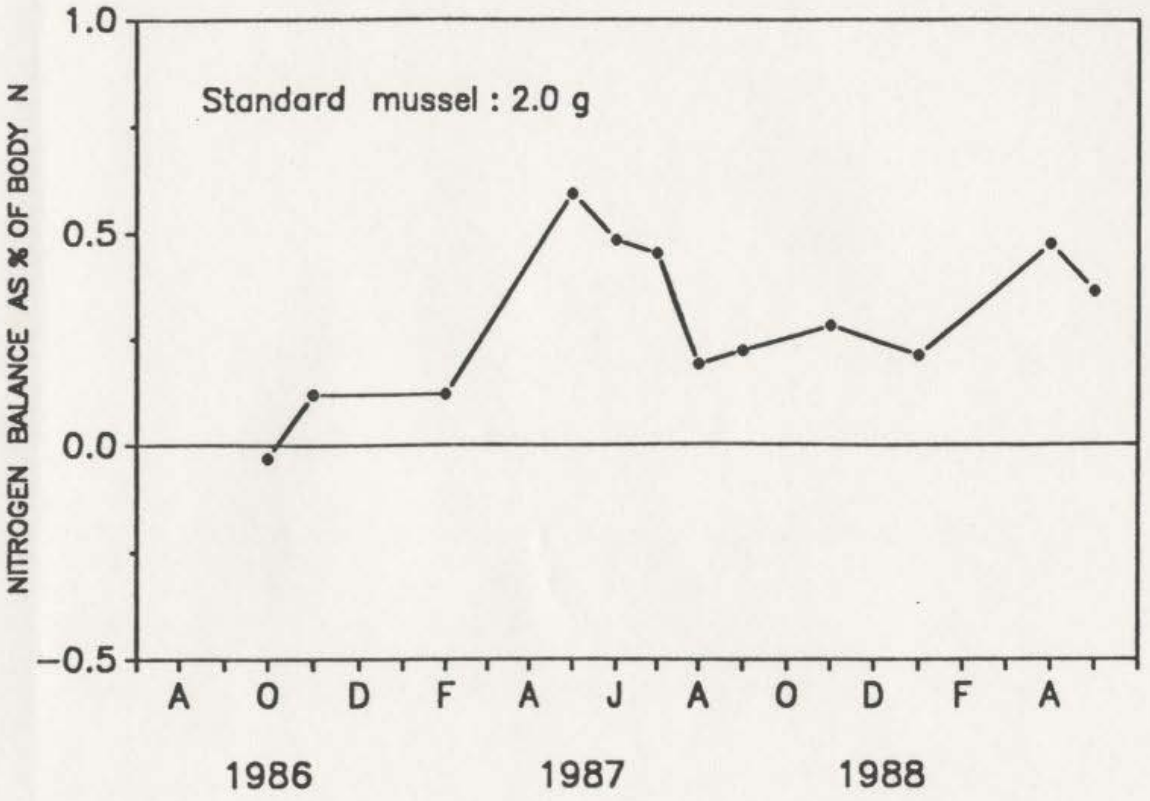


Fig. 24. Seasonal variation in the nitrogen balance (as % of body nitrogen) of a horse mussel of 2g dry tissue weight.

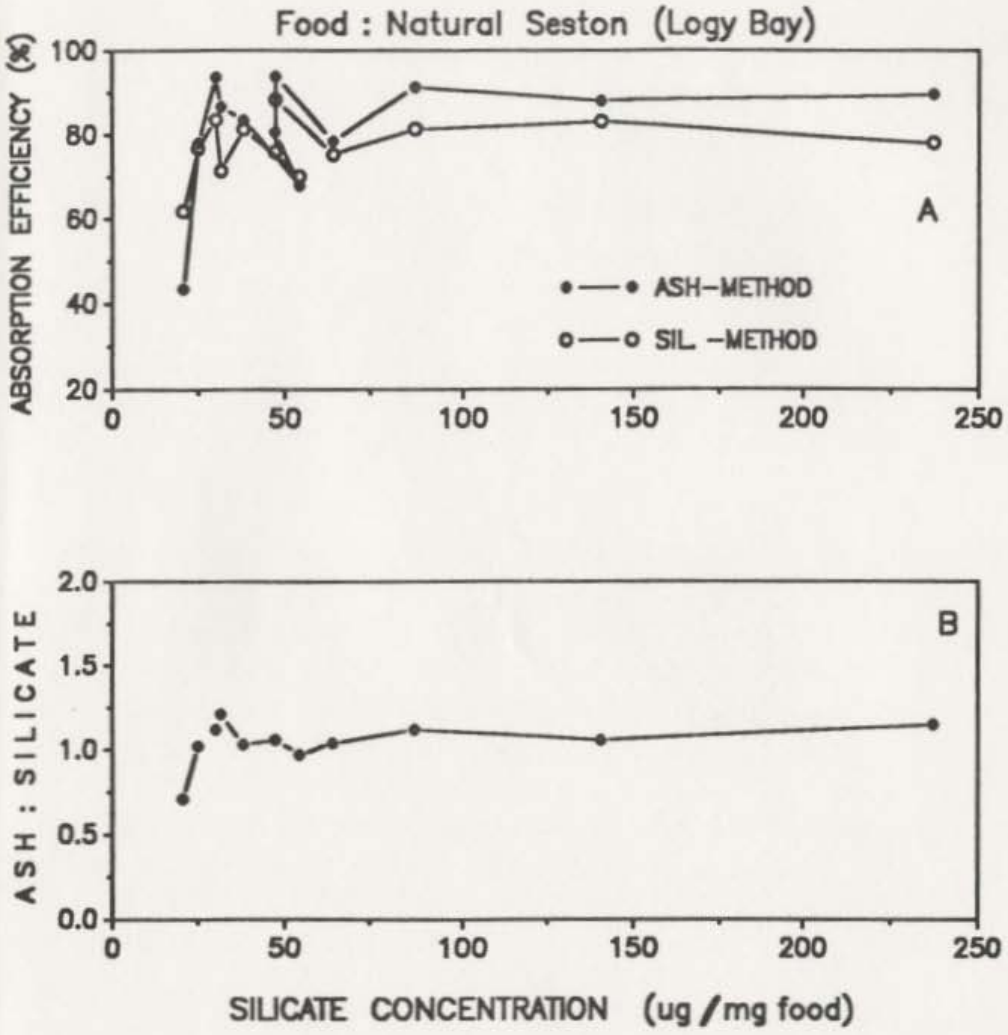


Fig. 25. Comparison of absorption efficiency values for *Modiolus modiolus* using the ash ratio and the silicate ratio methods. Horse mussels were feeding on natural seston from Logy Bay. (A) Absorption efficiency at different silica concentrations; (B) ratio of values from the ash method to those from the silicate method.

Nevertheless, the two methods were in good agreement for most silicate concentrations observed in the natural seston of Logy Bay.

A comparison of these two techniques was also made using pure cultures of microalgae. Two species of microalgae containing different concentrations of biogenic silica were used separately in these experiments (*Tetraselmis suecica* and *Chaetoceros affinis*) and the results are presented in Figure 26. Absorption efficiency varied between 50 and 80%, the lesser values occurring at lower silicate concentrations. Higher and more consistent values of AE (89.8% ± 0.51 S.E. for the ash method and 80.9% ± 1.01 S.E. for the silicate method) were obtained when natural seston was used as food (Table 11).

In addition to these techniques AE was estimated by using organic carbon and chloropigments as absorbable substances and inorganic matter as the indicator. The results of three experiments on absorption efficiency which were carried out with natural seston from Logy Bay during the phytoplankton bloom of 1988 (April-May) are presented in Figure 27. Estimates of AE from the ash-ratio and pigment techniques were consistently greater than those based on silicate or carbon (Table 11, Fig. 27). The data were analyzed by ANOVA after arcsine transformation of the AE values, followed by a multiple comparison test (Tukey-Kramer). There was a significant effect due to method ($F=195$, $df=3,47$, $P\leq0.001$). No significant differences ($P\geq0.05$) were found between the ash-ratio and chloropigment methods or between the silicate-ratio and organic carbon methods, but significant differences were found for all the other pairwise comparisons (Table 12).

III.4. FAECES AND PSEUDOFAECES PRODUCTION

III.4.1. Biodeposition

Modiolus modiolus from Logy Bay produced pseudofaeces only during the phytoplankton bloom. Daily observations of the feeding behaviour of horse mussels were carried out during and immediately after the phytoplankton bloom of 1988. Pseudofaeces production started on April 7, corresponding with the start of the spring bloom as measured by chlorophyll *a*, and continued for the next 5-6 weeks, during which time *Modiolus modiolus* was actively feeding and showed high clearance rates (Fig. 13). No pseudofaeces production was observed after May 22, 1988 (Tables 13, 14).

True faeces were clearly different in appearance from pseudofaeces, the latter being yellow-brown in colour and deposited via the inhalent siphon of the mussel, whereas the former were dark-brown and accumulated around the exhalent

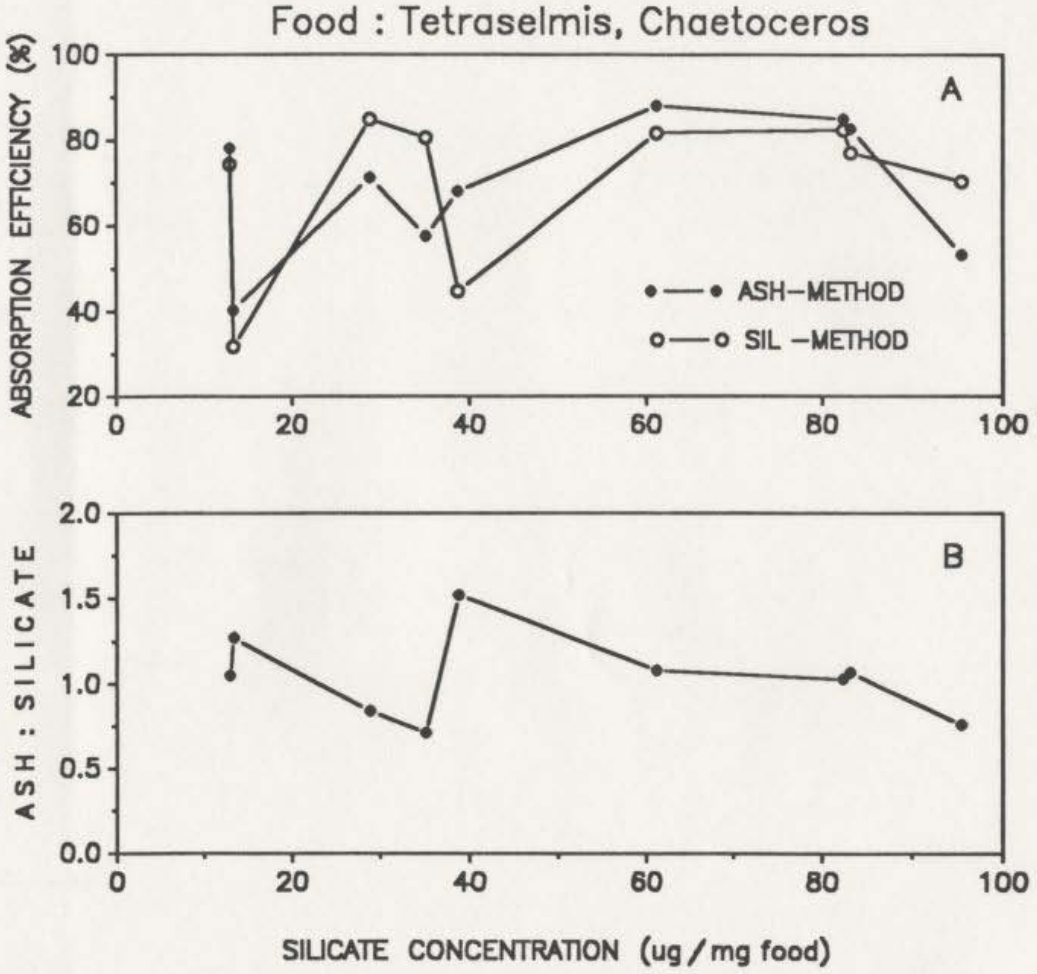


Fig. 26. Comparison of absorption efficiency values for *Modiolus modiolus* using the ash ratio and the silicate ratio methods. Horse mussels were feeding on cultured microalgae. (A) Absorption efficiency at different silicate concentrations; (B) ratio of values from the ash method to those from the silicate method.

Table 11. *Modiolus modiolus*. Absorption efficiency (%) of mussels feeding on natural seston, measured in terms of dry weight of organic matter (ash-ratio and silicate-ratio), organic carbon and chloropigments.

Indiv. N°	Ash-ratio (%)	Silicate Ratio (%)	Organic Carbon (%)	Chloropigments (%)
1	92.3	80.2	78.7	88.9
2	92.5	79.1	79.6	91.0
3	92.1	86.8	78.0	89.5
4	89.2	82.5	75.5	82.6
5	89.7	77.2	72.3	75.7
6	88.2	83.4	85.5	89.1
7	86.7	81.1	83.5	85.2
8	88.5	87.4	86.2	90.5
9	89.2	80.2	83.1	91.2
10	90.4	79.0	69.4	83.3
11	89.5	77.0	70.3	79.8
12	89.0	77.4	71.8	87.0
Mean	89.8	80.9	77.8	86.2
± S.E.	(±0.51)	(±1.01)	(±1.73)	(±1.42)

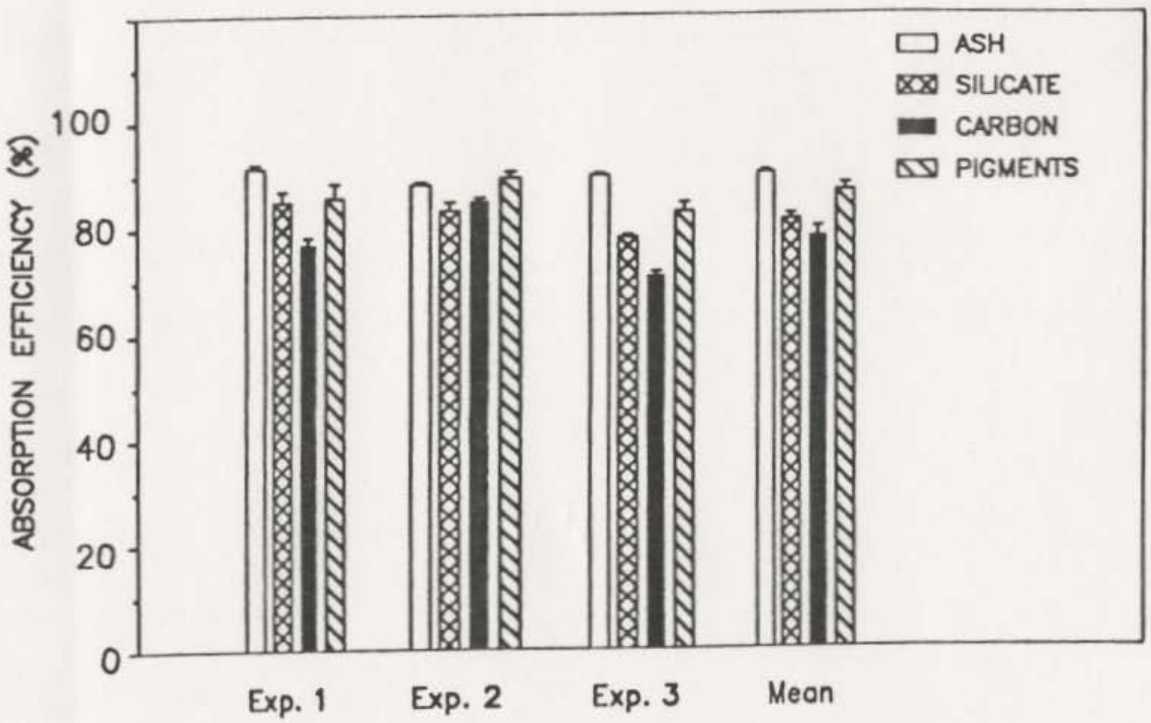


Fig. 27. Comparison of absorption efficiency values from four different methods for *Modiolus modiolus* feeding on natural seston during the phytoplankton bloom.

Table 12. *Modiolus modiolus*. Comparison of absorption efficiency measured by different methods. Significance was measured by the Tukey-Kramer test.

Group	Significance
Ash-Silicate	+++
Ash-Carbon	+++
Ash-Pigments	NS
Silicate-Carbon	NS
Silicate-Pigments	+++
Carbon-Pigments	+++

+++ = Significant differences

NS = Not significant

Table 13.- Modiolus modiolus. Biodeposition rate (faeces and pseudofaeces) during and after the phytoplankton bloom. SE is expressed in parentheses.

Exp.Nº	Date	Chl.a ($ug.l^{-1}$)	Nº of mussels	Mean dry tissue wt (g)	Biodeposition Rate			Total Chlorophyll a		
					Faeces ($mg.d^{-1}$)	Pseudo-faeces ($mg.d^{-1}$)	Total mussel ($mg.d^{-1}$)	Faeces ($ug.d^{-1}$)	Pseudo-faeces ($ug.d^{-1}$)	Ratio
1	April-12-88	0.78	4	4.879(±0.7)	27.3(±1.9)	4.8(±1.0)	32.1	7.6(±0.9)	5.8(±1.3)	0.76)
2	April-18-88	1.52	5	4.946(±1.0)	29.9(±4.9)	4.3(±1.0)	34.2	4.8(±1.0)	7.4(±1.9)	1.54
3	April-24-88	5.03	5	4.870(±1.0)	33.1(±4.5)	7.8(±4.6)	40.9	14.4(±4.6)	41.9(±12.1)	2.91
4	May - 7-88	3.16	4	6.110(±0.8)	25.8(±1.6)	1.9(±0.2)	27.7	13.9(±1.7)	10.6(±1.5)	0.76
5	MaY -22-88	0.29	7	5.465(±0.9)	4.3(±0.7)	---	---	---	---	---
6	May -24-88	0.19	4	5.474(±0.9)	8.1(±1.6)	---	---	---	---	---

Table 14. Modiolus modiolus. Chemical composition of the food supply and of biodeposits (faeces and pseudo-faeces) produced during the phytoplankton bloom of 1988. SE is expressed in parentheses

Exp. N° (Date)	Material	Organic (%)	Inorganic (%)	Chl.a ($ug.mg^{-1}$)	POC ($ug.mg^{-1}$)	PON ($ug.mg^{-1}$)	Silicate ($ug.mg^{-1}$)
1 (April-12-88)	Food	31.1(±2.1)	62.9(±2.8)	0.59(±0.08)	171.0(±0.3)	26.0(±3.9)	----
	Faeces	15.7(±0.1)	84.4(±0.95)	0.27(±0.02)	52.6(±1.4)	5.5(±0.2)	----
	Pseudofaeces	----	----	1.16(±0.08)	90.5(±5.0)	12.6(±1.2)	----
2 (April-18-88)	Food	52.8(±3.7)	47.5(±4.1)	1.20)±0.20)	147.0(±7.0)	24.3(±1.8)	87.0(±5.6)
	Faeces	8.9(±0.7)	91.1(±0.6)	0.18(±0.05)	38.4(±2.1)	3.6(±0.2)	101.1(±0.3)
	Pseudofaeces	34.8(±4.0)	65.2(±4.0)	1.73(±0.28)	58.3(±3.2)	8.3(±0.7)	93.0(±5.2)
3 (April-24-88)	Food	50.5(±0.2)	49.5(±0.2)	3.30(±0.6)	228.4(±13.4)	43.7(±1.7)	140.9(±11.8)
	Faeces	10.9(±0.4)	89.1(±0.4)	0.40(±0.1)	43.7(±1.6)	4.8(±0.2)	181.3(±17.0)
	Pseudofaeces	28.0(±2.4)	72.0(±2.4)	5.22(±0.5)	117.0(±20.2)	20.4(±3.7)	202.0(±4.2)
4 (May - 7-88)	Food	74.5(±0.5)	25.5(±0.5)	1.69(±0.4)	252.0(±7.0)	38.9(±0.1)	237.0(±21.6)
	Faeces	23.6(±0.6)	76.4(±0.6)	0.53(±0.1)	90.4(±2.0)	11.2(±0.3)	335.0(±8.2)
	Pseudofaeces	59.5(±1.6)	40.5(±1.6)	5.43(±0.3)	266.0(±42.0)	37.6(±8.4)	276.8(±29.7)

siphon. These differences facilitated the collection of the two components separately for examination and analysis.

The biodeposition rate per mussel (faeces plus pseudofaeces) increased as the phytoplankton bloom progressed (Table 13). The highest value (40.9 mg dry weight.d^{-1}) was recorded during the main peak of chlorophyll *a* (April 24). The same pattern was observed when faeces and pseudofaeces were analyzed independently. Biodeposition rate decreased considerably after the bloom, due to a large reduction in the rate of faecal output and the cessation of pseudofaeces production.

Although faeces production was five or more times greater than pseudofaeces production when expressed as mg dry matter.d^{-1}, the pseudofaeces were more important in recycling chlorophyll *a* to the ecosystem by a factor of 1.5 to 3, depending on the stage of the phytoplankton bloom. Thus during the peak of chlorophyll *a* (April 24), when faeces production was 33.1 mg.d^{-1}, compared with 7.8 mg.d^{-1} for pseudofaeces, the deposition rates of chlorophyll *a* through the same faeces and pseudofaeces were 14.4 and 41.9 μg.d^{-1}, respectively (Table 13). Such comparisons were possible only in four experiments, because pseudofaeces were not produced in the post-bloom period.

III.4.2. Microscopic Analysis of the Biodeposits; Microalgae Composition

The pseudofaeces produced by *Modiolus modiolus* were characterized by the presence of abundant large diatoms, including many chain forms, although smaller diatoms were also present.

The experiments were carried out during the phytoplankton bloom of 1988. Microscopic analysis of the biodeposits produced by five mussels ranging from 5-12 cm in length showed that during the beginning of the bloom single cells as well as chains of the diatom *Thalassiosira* sp. were very abundant in the pseudofaeces. *Coscinodiscus* and two species of *Fragilaria* were less abundant, but were larger than *Thalassiosira*. Flagellates were very scarce and few single small diatoms were observed in these samples. In contrast, the faeces contained only small, empty diatom chains, indicating that *Modiolus modiolus* concentrates the large chains in the seston and rejects them in the pseudofaeces.

Modiolus modiolus showed the highest production of biodeposits (Table 13) during the middle of the bloom, when the pseudofaeces were mainly composed of large diatoms such as *Coscinodiscus* sp. and other chain-forming diatoms such as *Fragilaria*, *Chaetoceros* and *Thalassiosira*. The composition of the faeces was different from that of the pseudofaeces, there being no chain diatom frustules in

the former, although many diatom spines and single frustules were present. Phytoplankton samples contained the same species of diatoms found in the pseudofaeces, *Coscinodiscus* sp. being the most common. *Modiolus modiolus* showed a decrease in the production of biodeposits at the end of the bloom, when the pseudofaeces and faeces contained few diatoms, and the phytoplankton was characterized by a reduction in the number of long diatom chains and large microalgae.

III.4.3. POC, PON, Chlorophyll *a* and Silicate Content of Food, Faeces and Pseudofaeces

The analysis of these components of the biodeposits was carried out during the period April-May 1988, corresponding to the phytoplankton bloom in Logy Bay.

Particulate organic carbon (POC) was more concentrated in the seston than in the biodeposits, except in experiment 4 (Table 14, Fig. 28a). Values of 40-80 μg POC per mg dry faeces of *Modiolus modiolus* were recorded in the present study, compared with 50-250 μg POC per mg of pseudofaeces and 120-250 μg POC per mg of seston.

Particulate organic nitrogen (PON) in the faeces and pseudofaeces followed a similar pattern to POC (Table 14, Fig. 28b). Faecal PON ranged from 12 to 29% of the PON values for the seston, whereas pseudofaeces contained greater amounts of PON, with values between 36 and 98% of those found in the seston.

Chlorophyll *a* was always higher in the pseudofaeces than in the food (Table 14; Fig. 29a), while faeces showed the lowest chlorophyll *a* concentrations in all the experiments. Chlorophyll *a* accounted for 21 to 30% by weight of total pigments in the faeces at the four experimental food conditions tested in *Modiolus modiolus* from Logy Bay (Table 15), whereas in the pseudofaeces chlorophyll *a* represented 80 to 93% of the total pigments, values very similar to those found in the natural food at this time of the year, suggesting the importance of these biodeposits as a supplementary food source for benthic organisms. The highest percentages of chlorophyll *a* recovered in faeces and pseudofaeces occurred during experiment 3, which corresponded to the peak of the phytoplankton bloom, when large diatoms (e.g. *Coscinodiscus*) and long chains of diatoms (e.g. *Fragilaria*, *Chaetoceros*) were very abundant in Logy Bay.

A pigment budget carried out during the phytoplankton bloom of 1988 is shown in Table 16. Most of the chloropigments filtered by horse mussels were absorbed and lesser amounts were present in the faeces and pseudofaeces. The latter represented only 10-20% by weight of the faeces (Table 13), but the total

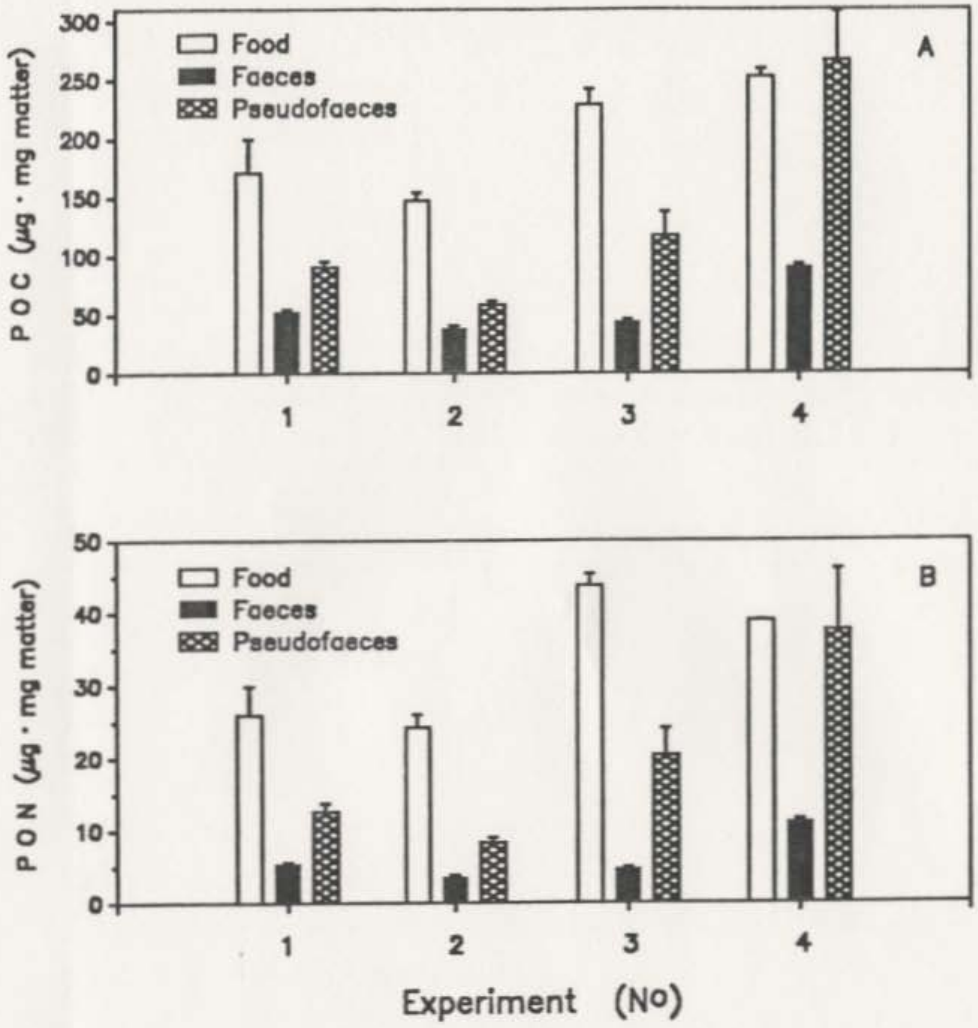


Fig. 28. Organic carbon (A) and nitrogen (B) content of the food, faeces and pseudofaeces during the phytoplankton bloom.

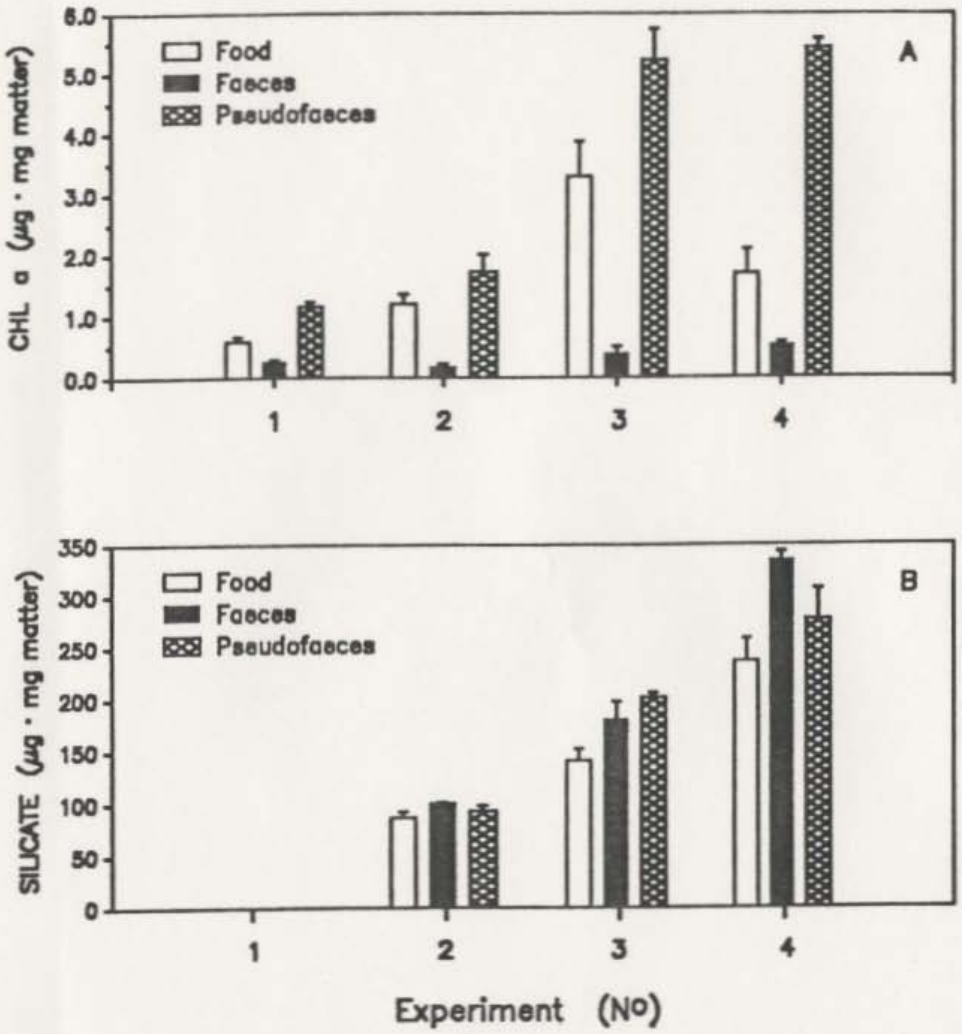


Fig. 29. Chlorophyll *a* (A) and biogenic silica content (B) of the food, faeces and pseudofaeces during the phytoplankton bloom.

Table 15.- Modiolus modiolus. Relative content of chlorophyll a (by weight) in food faeces and pseudofaeces. SE is expressed in parentheses.

Exp. Nº (Date)	FOOD $\frac{\text{Chl.a}}{\text{Total Pigments}} \times 100$	Nº of mussels	FAECES $\frac{\text{Chl.a}}{\text{Total Pigments}} \times 100$	PSEUDOFAECES $\frac{\text{Chl.a}}{\text{Total Pigments}} \times 100$
1 (April.12.88)	71.1	4	26.2(±1.61)	80.9(±4.01)
2 (April.18.88)	74.7	5	21.7(±2.31)	82.4(±1.88)
3 (April.24.88)	97.2	5	30.7(±7.63)	93.0(±3.71)
4 (May . 7 .88)	72.8	4	21.9(±1.77)	86.4(±2.13)

Table 16.- Modiolus modiolus. Pigment budget for a standard mussel of 2.0 g dry weight during the phytoplankton bloom of 1988.

Exp. Nº (Date)	TOTAL PIGMENTS In Food (ug.l-1)	Filtered (ug.d-1)	Ingested (ug.d-1)	Rejected as Pseudofaeces (ug.d-1)	Absorbed (ug.d-1)	In Faeces (ug.d-1)
2 (April-18-88)	4.9	161.2	145.1	16.1	124.1	21.0
3 (April-24-88)	12.8	421.0	357.8	63.2	319.2	38.6
4 (May - 7 -88)	7.2	193.7	184.0	9.7	151.8	32.2

pigment content of the pseudofaeces in experiments 2 and 4 was very similar to or higher than that of the faeces.

The biogenic silica content in the seston and biodeposits was compared (Tables 14 and 17, Fig. 29b). One ANOVA followed by a multiple range test for experiment 2 (April 18, 1989) showed no significant differences ($P \geq 0.05$) in the silica content of food, faeces and pseudofaeces. Significant differences between food and pseudofaeces were observed only in experiment 3 (April 24, 1989), where the latter contained a larger amount of silica, and in experiment 4 (May 7, 1989), between food and faeces, where the silica content was considerably higher in the faeces (Table 17).

III.5. WEIGHT AND ENERGY STORAGE CYCLES

III.5.1. Seasonal Changes in Tissue Weight

Seasonal fluctuations in dry tissue weight (total, somatic, gonad and digestive gland) for a horse mussel of 10 cm shell length were calculated from regression equations (Table 18) and they are shown in Figure 30. The dry weight of the somatic tissue, gonad and digestive gland increased considerably during the phytoplankton bloom of 1986, with maximum values in July for digestive gland and somatic tissue and in August for the gonad, which accounted for 37% of the total dry weight of the mussel at that time. These peaks were followed by a marked decline, especially in the gonad (from 2.34 g in August to 0.41 g in October), which during October represented only 10% of the total dry tissue weight. This decrease in gonad tissue weight was associated with spawning, which occurred at this time of the year in Logy Bay, as observed in all the holding tanks as well as in the horse mussel bed. Indirect evidence for spawning was provided by a tenfold increase in the particle concentration measured in the seawater above the mussel bed on August 23, 1986 as a result of the high concentration of sperm.

The dry weight of the somatic tissue was relatively constant during fall and early winter and then decreased to a minimum during late winter (March, 1987). This decrease in somatic weight was reversed rapidly during the spring bloom of April-May 1987. A very similar seasonal pattern was observed during the second year of the study. The digestive gland showed similar trends in dry weight, with peaks occurring during May-June of each year (Fig. 30). The gonadal peak weight represented only 22% of the total tissue weight in 1987, compared with 37% in 1986. A slight decrease was observed in gonad weight during August 1987, which may be related to a possible minor spawning. This was followed by a gradual rise throughout the fall of 1987, then a cessation of growth during winter before a marked increase during spring to a maximum in July of 1988, when gonad weight

Table 17. *Modiolus modiolus*. Comparison by ANOVA of the biogenic silica content in food, faeces and pseudofaeces followed by a multiple range test (NS, not significant at $P \geq 0.05$).

EXP. N° (Date)	F	Significance
EXP. 2 (April-18-89)		
Food v/s Faeces	1.97	NS
Food v/s Pseudofaeces	2.44	NS
Faeces v/s Pseudofaeces	0.00	NS
EXP. 3 (April-25-89)		
Food v/s Faeces	3.59	NS
Food v/s Pseudofaeces	8.67	$P \leq 0.05$
Faeces v/s Pseudofaeces	1.50	NS
EXP. 4 (May-7-89)		
Food v/s Faeces	10.93	$P \leq 0.05$
Food v/s Pseudofaeces	1.63	NS
Faeces v/s Pseudofaeces	4.95	NS

Table 18.- Modiolus modiolus. Regressions of shell length (cm) against dry tissue weight (g) for different dates. Regression equations are of the form $Y = aW^b$, where Y=dry tissue weight and W shell length. The statistic F tests the significance of the difference between the slope b and zero.

Date	n	a	b	r	F
AUG.- 86	23	0.005	3.07	0.99	1422.5**
OCT.- 86	19	0.007	2.77	0.99	1443.8**
NOV.- 86	18	0.006	2.91	0.98	443.5**
FEB.- 87	15	0.017	2.39	0.96	168.4**
MARCH-87	15	0.011	2.57	0.98	320.2**
APRIL-87	15	0.010	2.61	0.99	472.2**
MAY - 87	10	0.011	2.65	0.99	343.4**
JUNE- 87	14	0.016	2.52	0.99	509.9**
JULY- 87	15	0.011	2.66	0.97	211.4**
AUG.- 87	15	0.011	2.63	0.99	484.8**
SEPT.-87	13	0.041	2.04	0.98	315.1**
OCT.- 87	8	0.003	3.27	0.64	6.5*
NOV.- 87	14	0.010	2.71	0.98	259.7**
JAN.- 88	14	0.013	2.55	0.98	275.8**
FEB.- 88	7	0.098	1.62	0.64	7.3*
APRIL-88	14	0.013	2.67	0.97	188.5**
MAY - 88	14	0.044	2.12	0.98	336.6**
JUNE- 88	7	0.116	1.67	0.68	7.8*
JULY- 88	8	0.023	2.41	0.84	14.3**
AUG.- 88	7	0.030	2.28	0.75	6.3*
SEPT.-88	8	0.049	2.11	0.68	8.7*
NOV.- 88	7	0.008	3.02	0.75	6.6*
Pooled Date	280	0.008	2.82	0.98	5517.6

* Significant at $P<0.05$; ** significant at $P<0.01$

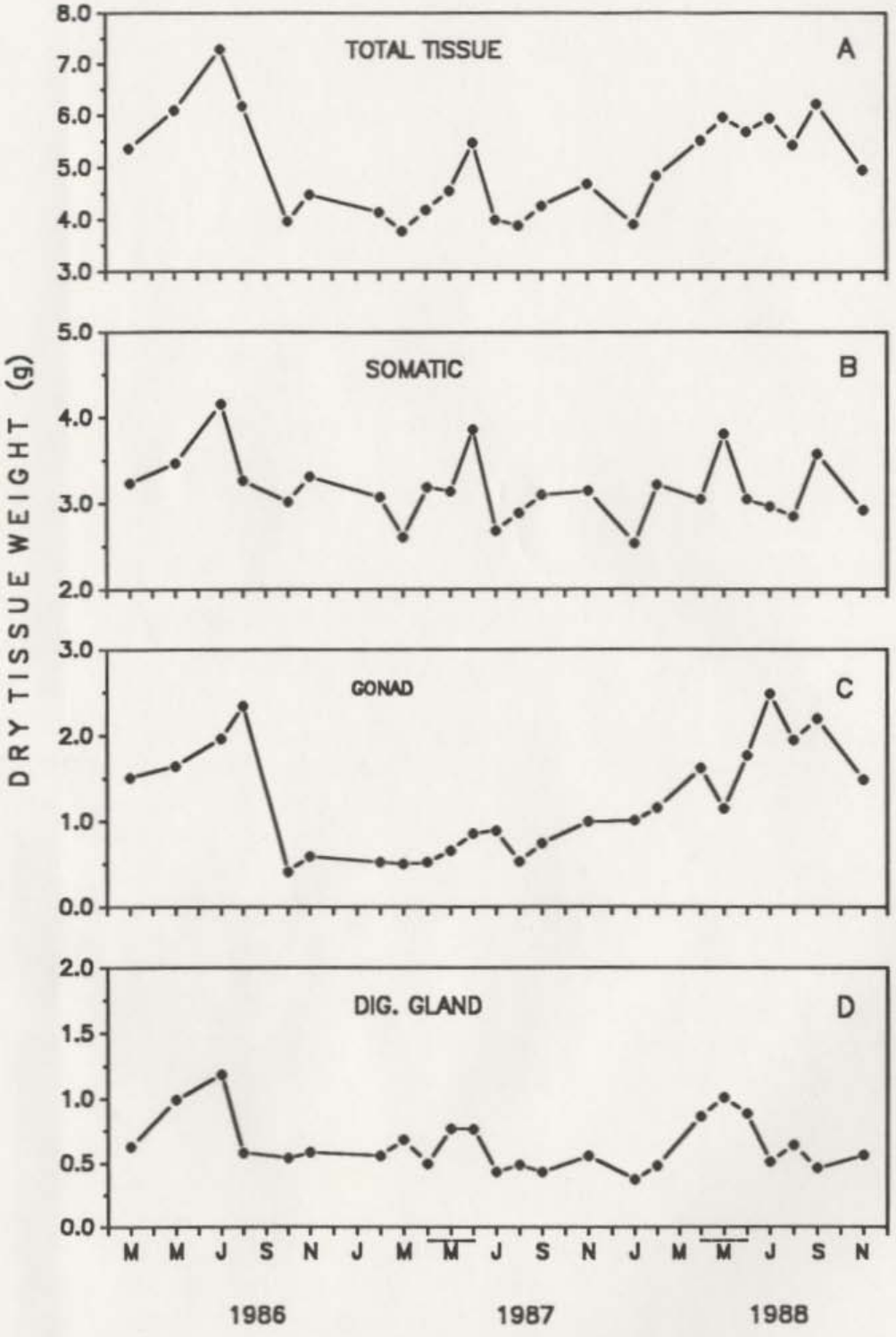


Fig. 30. Seasonal fluctuation in the dry tissue weight for total (A), somatic (B), gonad (C) and digestive gland (D) of a horse mussel of shell length 10 cm. Periods of spring blooms in 1987 and 1988 are shown on the horizontal axis.

represented 41% of total tissue weight. After July a decline in gonad weight was observed, which may have been associated with spawning, although this decrease was not as pronounced as that observed during the summer of 1986.

III.5.2. Seasonal Synthesis and Utilization of Biochemical Energy Reserves

III.5.2.1. Introduction

Protein, lipid, carbohydrate and ash are often expressed as percentages of tissue weight, but this may produce problems in interpretation, since changes in the concentration of any given component result in reciprocal changes in percent by weight values for all the others. Alternatively, data can also be presented as the total weight of a constituent present in a given tissue, although this approach can be complicated by different seasonal patterns of growth. Both means of data presentation were employed in the present work to complement one another.

III.5.2.2. Somatic tissue

The percentage composition by weight of protein, lipid, carbohydrate and ash in the somatic tissue are shown in Figure 31. The seasonal pattern of carbohydrate was characterized by two peaks, one during the late spring-early summer of 1987, the other during the early spring of 1988 (Fig. 31a). The synthesis of carbohydrate was associated with the phytoplankton bloom, which occurred during April-May in Logy Bay. Carbohydrate ranged from 3-10% of the somatic weight, depending on the time of the year.

Lipid comprised 2-5% by weight of the somatic tissue of *Modiolus modiolus* (Fig. 31b). From October 1986 to March 1987, percent lipid showed little change, but a gradual decrease was observed during the early spring, followed by a gradual rise from May to October 1987. This peak was followed by a decline during fall and winter with a more pronounced decrease during the early spring of 1988, followed by a recovery of the lipid level during late spring and summer.

Protein accounted for ≈75% of somatic dry weight during fall 1986 and winter 1987, decreasing to 65% in March 1987 (Fig. 31c), which corresponded to a period of poor food conditions in Logy Bay. Protein level partly recovered by April, but decreased again to a minimum of 65% in June before increasing to 80% in August 1987, after which there was no pronounced seasonal cycle.

Ash represented a high percentage of somatic weight, reaching values as high as 22% during some months. The lowest values were observed in spring and early

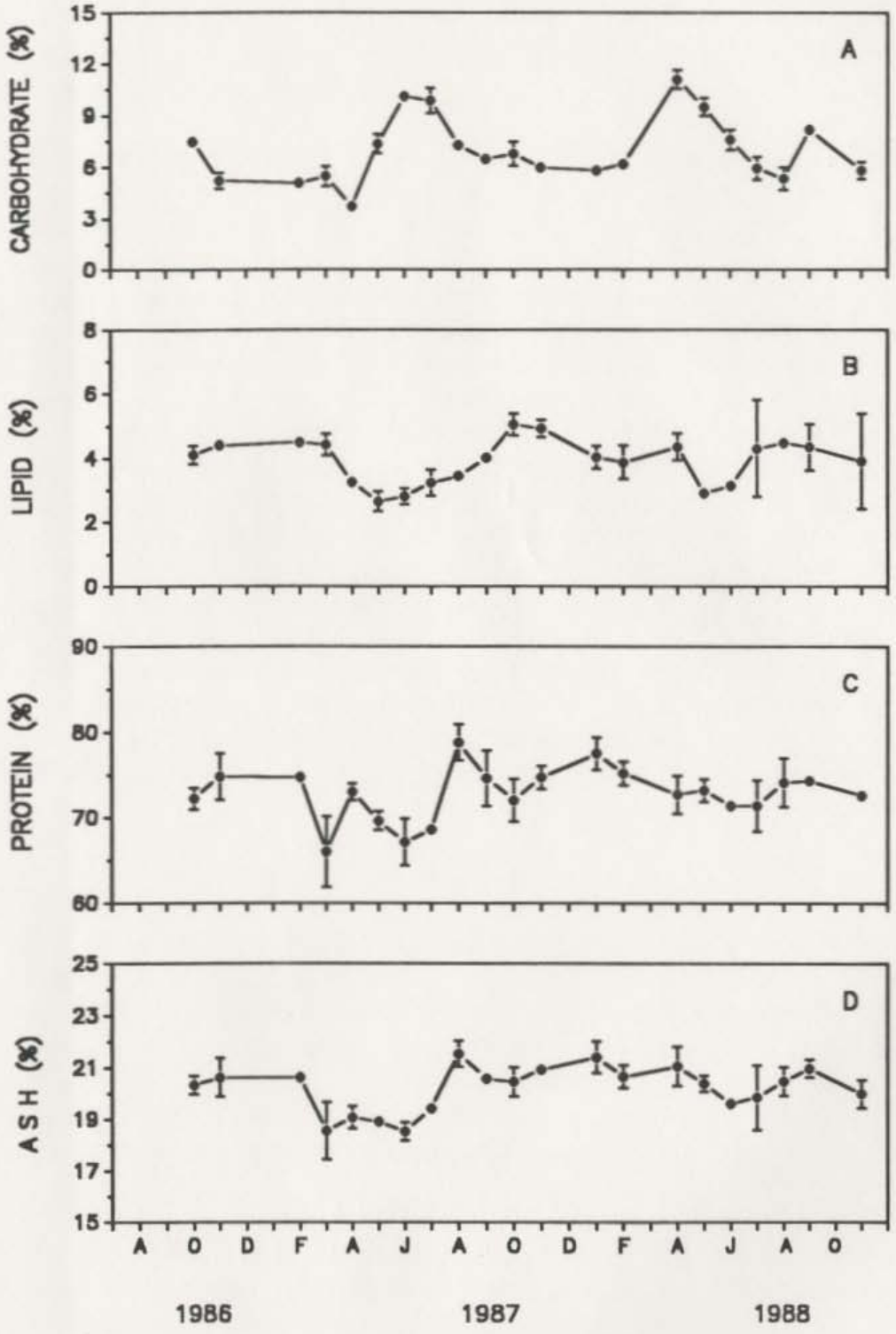


Fig. 31. Seasonal fluctuation in the proximate biochemical composition of the somatic tissue of *Modiolus modiolus*. Biochemical constituents are expressed as percentages of dry weight (monthly means ± S.E., n=5).

summer, corresponding with the maximum organic content expressed as a proportion of dry weight (Fig. 31d).

Figure 32 shows the changes in absolute amounts of the biochemical components in the soft parts of a standard mussel (10 cm shell length). Carbohydrate content (Fig. 32a) showed a clearer seasonal pattern than protein or lipid, with a major peak in each year of the study, the first occurring in June 1987 and the second in May 1988. These peaks were preceded by a gradual increase in carbohydrate from April (1987) and January (1988) respectively. The magnitude of these peaks in carbohydrate content was very similar in both years. Lipid content showed a seasonal cycle characterized by a decrease during winter-spring (February-June 1987) followed by a gradual increase from late summer (August) throughout the fall, reaching a peak in November 1987. Lipid content fell sharply during December-January 1988, increased slightly during the following spring and increased again during late spring-summer, reaching a peak in September 1988 (Fig. 32b). Protein content fluctuated throughout the year, with lower values during late winter followed by a recovery during spring, when food conditions were favourable (phytoplankton bloom). Ash content showed a high value during the spring of 1987, as a result of the increase in the somatic tissue growth associated with the favourable food conditions found during the phytoplankton bloom. This increase may be attributable to the fact that the experimental animals were not depurated prior to dissection. A smaller peak was observed in the spring of 1988.

III.5.2.3. Gonad tissue

Figure 33 shows the percentages of protein, lipid, carbohydrate and ash in the gonad of *Modiolus modiolus*. Carbohydrate represented 10-12% of the gonad dry weight from October 1986 to May 1987, then increased during the late spring to summer with a peak of 13% in June and a second one of ≈14% in August 1987 (Fig. 33a). This was followed by a decrease to a constant level of ≈10% from October 1987 to January 1988. Carbohydrate rose sharply from February to May 1988 (peak 14%), followed by a gradual decrease.

Lipid accounted for 7-15% of the gonad dry weight during the two years of the study (Fig. 33b). After the beginning of the increase in gonad weight in late April 1987, presumably related to gametogenesis, lipid increased to reach maximum values (12% of gonad weight) during June-July, then fell to 8% in September 1987, perhaps as a result of a minor spawning. A second larger peak in lipid (16%) was observed during the summer of 1988, which seems to be associated with gametogenic activity, as in the year before. This peak was also followed by a decrease in lipid level, presumably as a result of spawning.

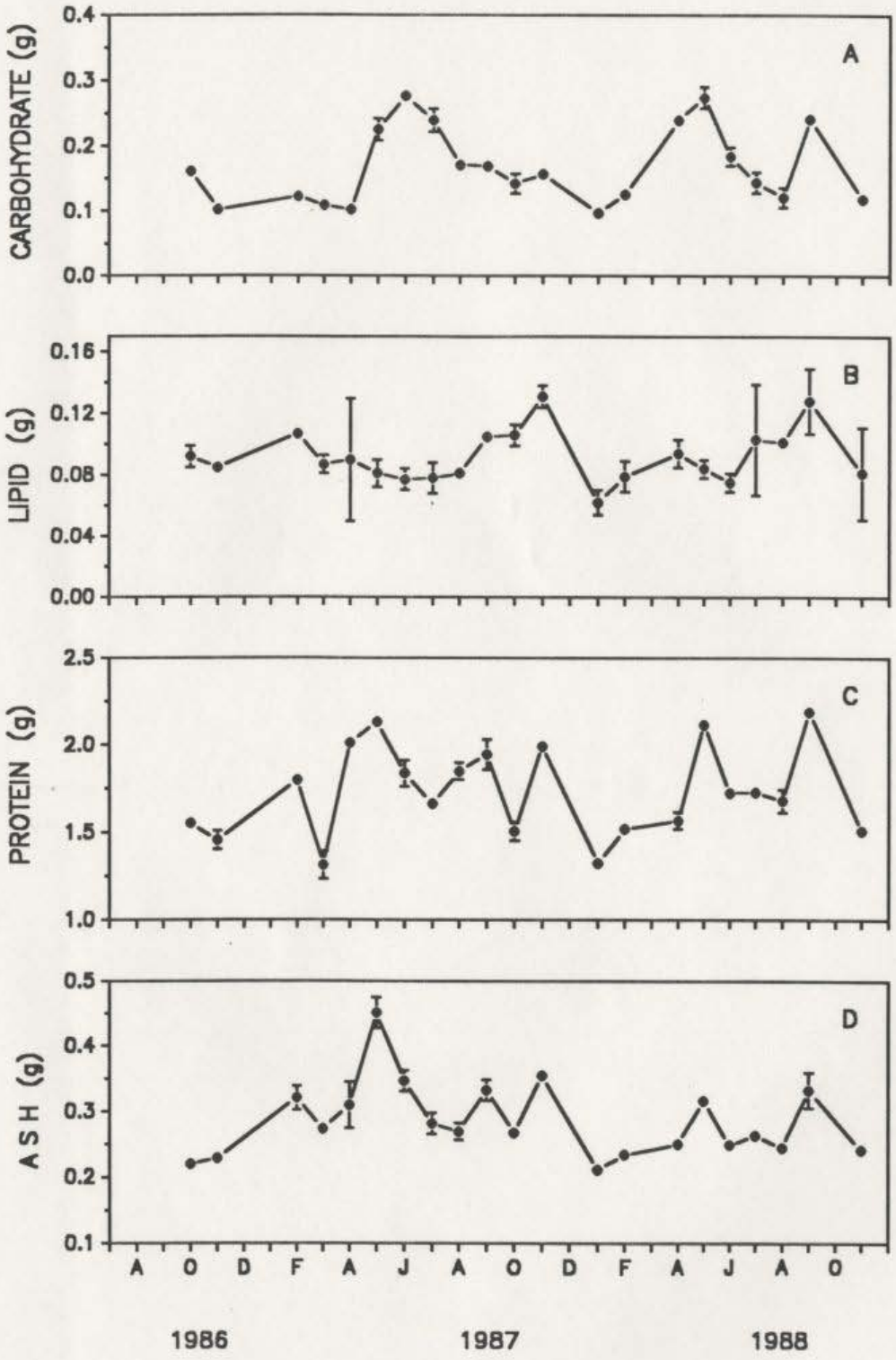


Fig. 32. Seasonal variation in the weights of the biochemical constituents of the somatic tissue in *Modiolus modiolus* ("standard" animal of length 10 cm). Values are monthly means ± S.E., n=5.

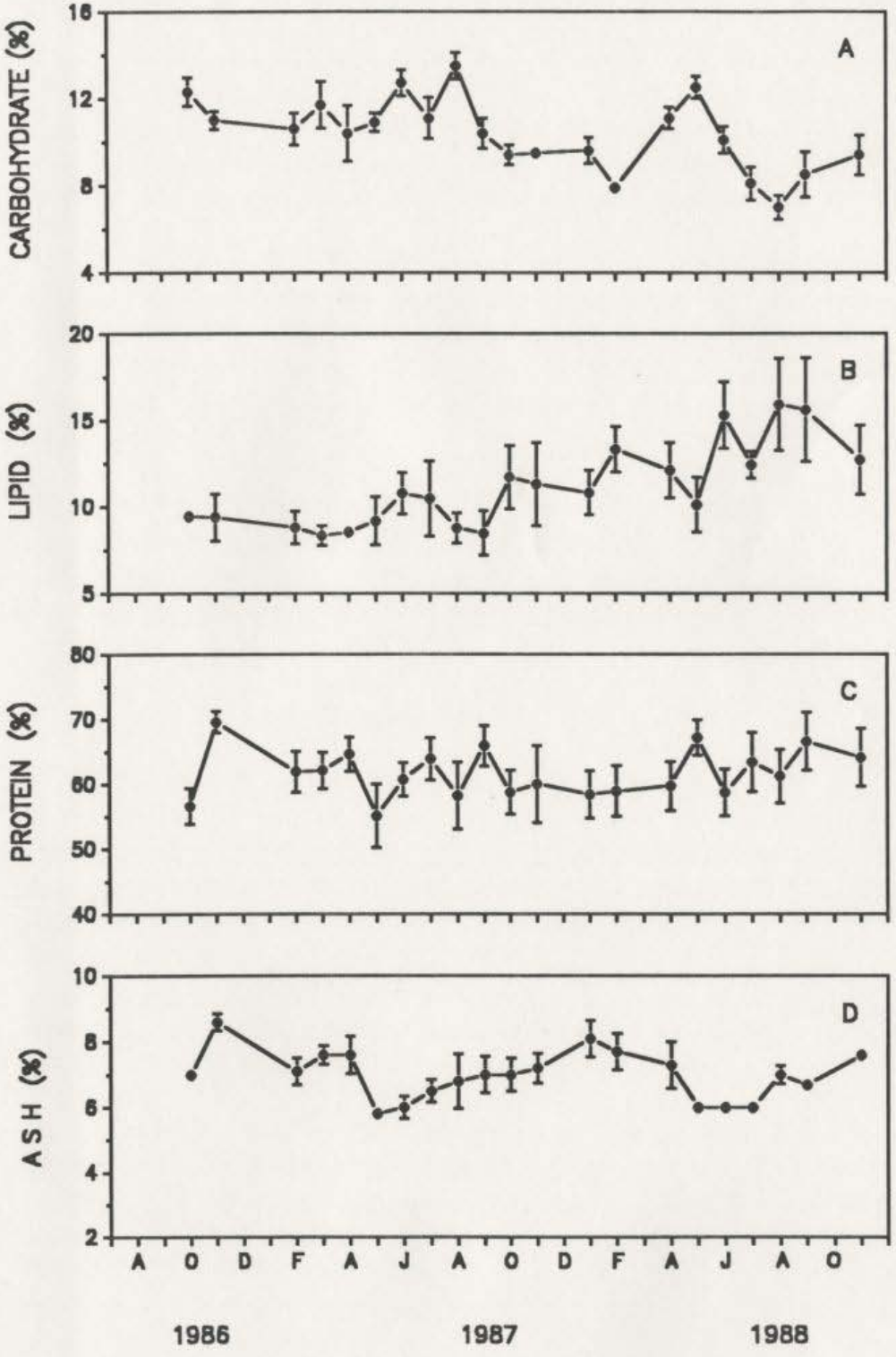


Fig. 33. Seasonal fluctuation in the proximate biochemical composition of the gonad in *Modiolus modiolus*. Biochemical constituents are expressed as percentages of dry tissue weight (monthly means ± S.E., n=5).

Protein accounted for the largest proportion of the dry gonad weight, fluctuating in the range 55-70% (Fig. 33c). There was a decline from November 1986 to May 1987 followed by an increase through the summer. Protein remained constant through fall and winter (October 1987-March 1988), followed by a small peak in May and a gradual increase during the summer.

The proportion of ash in the gonad was lower than in the somatic tissue, representing less than 9% of the dry gonad weight. Ash level was greatest immediately after spawning in August 1986, decreasing through the winter and spring of 1987. Minimum values were obtained in May 1987 and during May-July 1988, corresponding with the maximum organic content expressed as a proportion of dry weight.

Seasonal fluctuations in the biochemical content of the gonad (Fig. 34) were largely correlated with the fluctuations of the gonad weight (Fig. 30). There was an increase in each biochemical component from October 1986 to November 1988, corresponding to the trend shown by the gonad dry weight during the same period.

III.5.2.4. Digestive gland

The results of the biochemical determinations for the digestive gland are shown in Figs 35 and 36. The carbohydrate level ranged between 7 and 11% of the digestive gland dry weight (Fig. 35a). Considerable fluctuation was observed throughout the study period, with larger values during the fall of 1986 (October) and 1988 (September-October). The corresponding peak for 1987 occurred in September, but it was considerably smaller than in 1986 or 1988. There were also peaks for carbohydrate in June 1987 and April-May 1988, which were coincident with the phytoplankton bloom. The lowest values occurred in the early spring and late fall of 1987, and also during the winter of 1988.

The lipid level in the digestive gland was considerably higher than in the somatic and gonad tissue, and there was a discrete seasonal cycle (Fig. 35b). A decrease was observed from 25% in November, 1986 to a minimum of 19% during March, 1987. A gradual increase was recorded from March to August, 1987 (≈28%), followed by a decrease with a minimum value in November. A second peak was observed during the spring of 1988, similar in magnitude to that observed in 1987.

Protein accounted for a lower percentage of dry weight than in the somatic and gonad tissue, with the largest value (58%) during May 1987 and the lowest value (42%) during August of the same year (Fig. 35c). There was no clear seasonal cycle after August, and the protein level remained essentially stable.

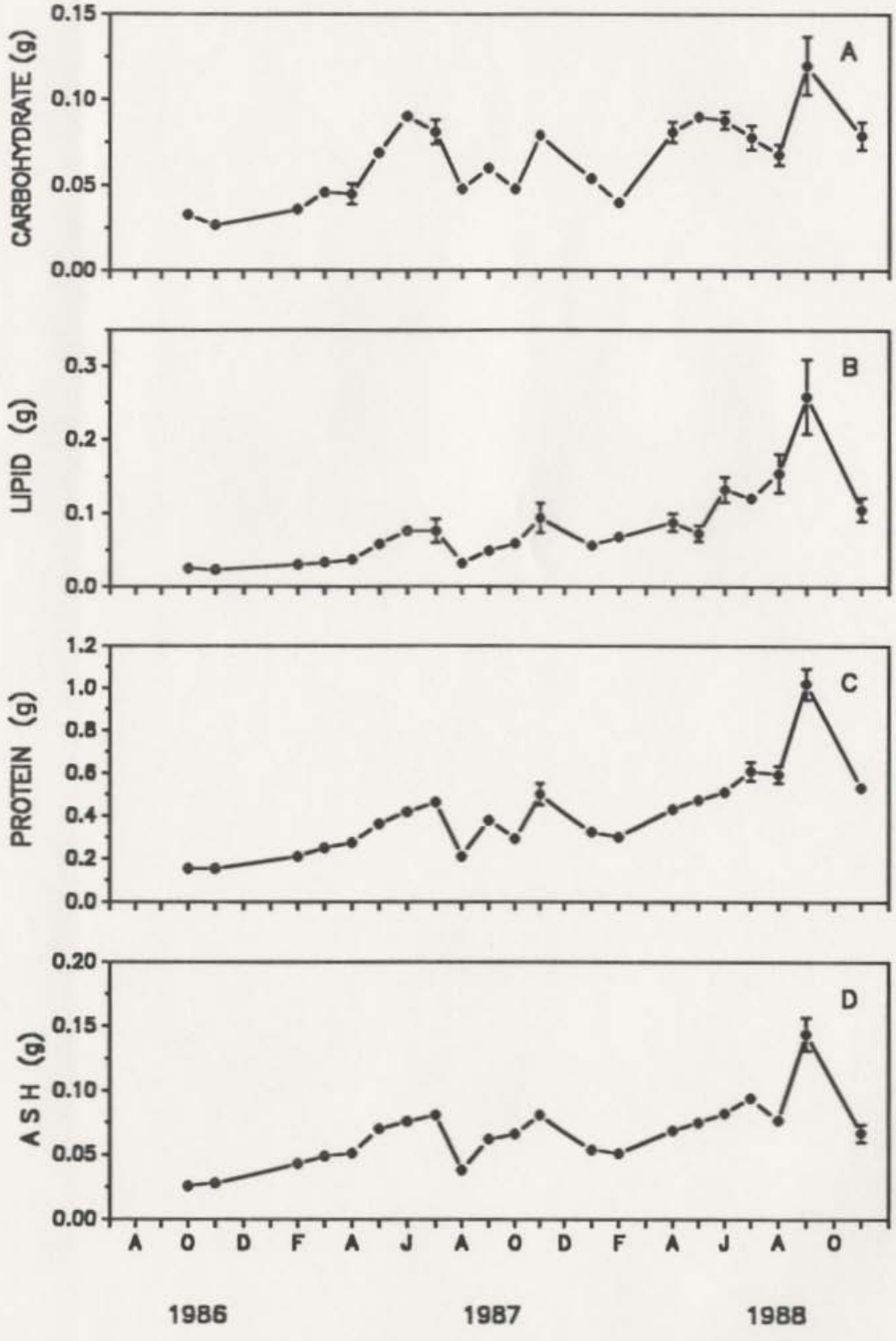


Fig. 34. Seasonal changes in the weights of the biochemical constituents of the gonad in *Modiolus modiolus* ("standard" animal of length 10 cm). Values are monthly means ± S.E., n=5.

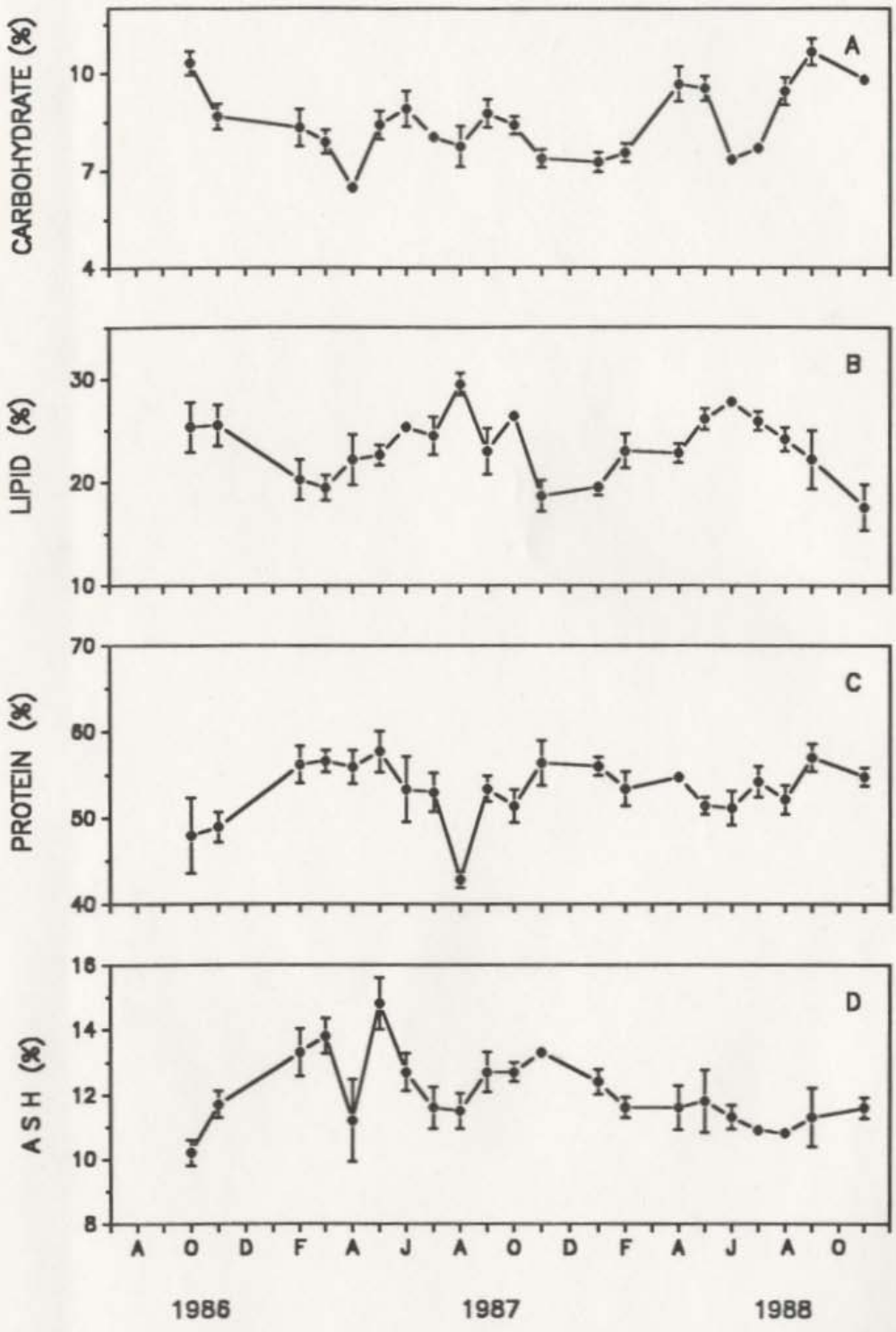


Fig. 35. Seasonal variation in the proximate biochemical composition of the digestive gland in *Modiolus modiolus*. Biochemical constituents are expressed as percentages of dry weight (monthly means ± S.E., n=5).

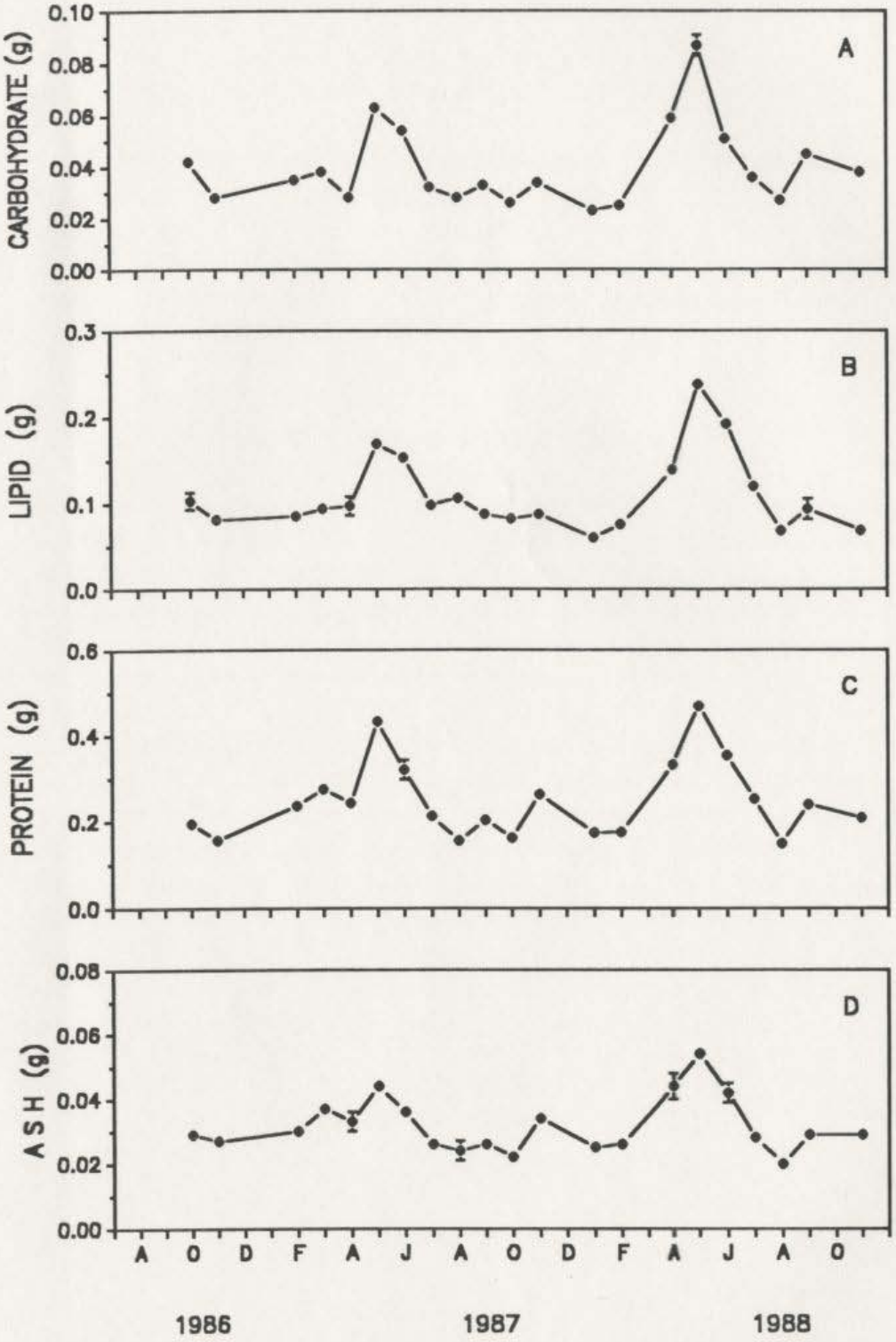


Fig. 36. Seasonal fluctuation in the weight of the biochemical constituents of the digestive gland of *Modiolus modiolus* ("standard" animal of length 10 cm). Values are monthly means ± S.E., n=5.

The proportion of ash represented between 10-15% of the dry tissue weight and, as in the other tissues, showed no clear seasonal cycle (Fig. 35d).

Seasonal changes in the absolute amounts of carbohydrate, protein, lipid, and ash contained in the digestive gland are represented in Fig. 36. One annual peak occurred during spring (May) of each year, corresponding to the more favourable food conditions of Logy Bay. All components then decreased rapidly from May to August, after which there was little change apart from a further decline in lipid content throughout the fall and winter.

III.5.3. Seasonal Cycle in Energy Content

The annual cycle of energy content ($kJ.g^{-1}$) calculated on the basis of the biochemical composition of the somatic tissue, gonad and digestive gland is shown in Fig. 37. The energy content of the somatic tissue (Fig. 37a) was maintained constant during the fall and early winter of 1986-87, decreasing sharply during late winter and spring (March-June 1987), followed by a rapid increase to a maximum in August. Energy content remained constant through the second fall and winter, then declined in the spring of 1988. In the gonad, organic material accumulated gradually from May to July 1987 as gamete development proceeded. The decrease in energy level observed during August appeared to be associated with a minor spawning. The energy content of the gonad showed a gradual increase from January 1988 to reach a peak during the spring, followed by a decline during June-July to increase again in August-September (Fig. 37b). The energy content of the digestive gland (Fig. 37c) showed a more clear seasonal fluctuation, with a peak during May-June of 1987, followed by a decrease during late fall and winter. A similar situation was observed during the second year, when the maximum occurred during June-July, with a decline during the fall of 1988.

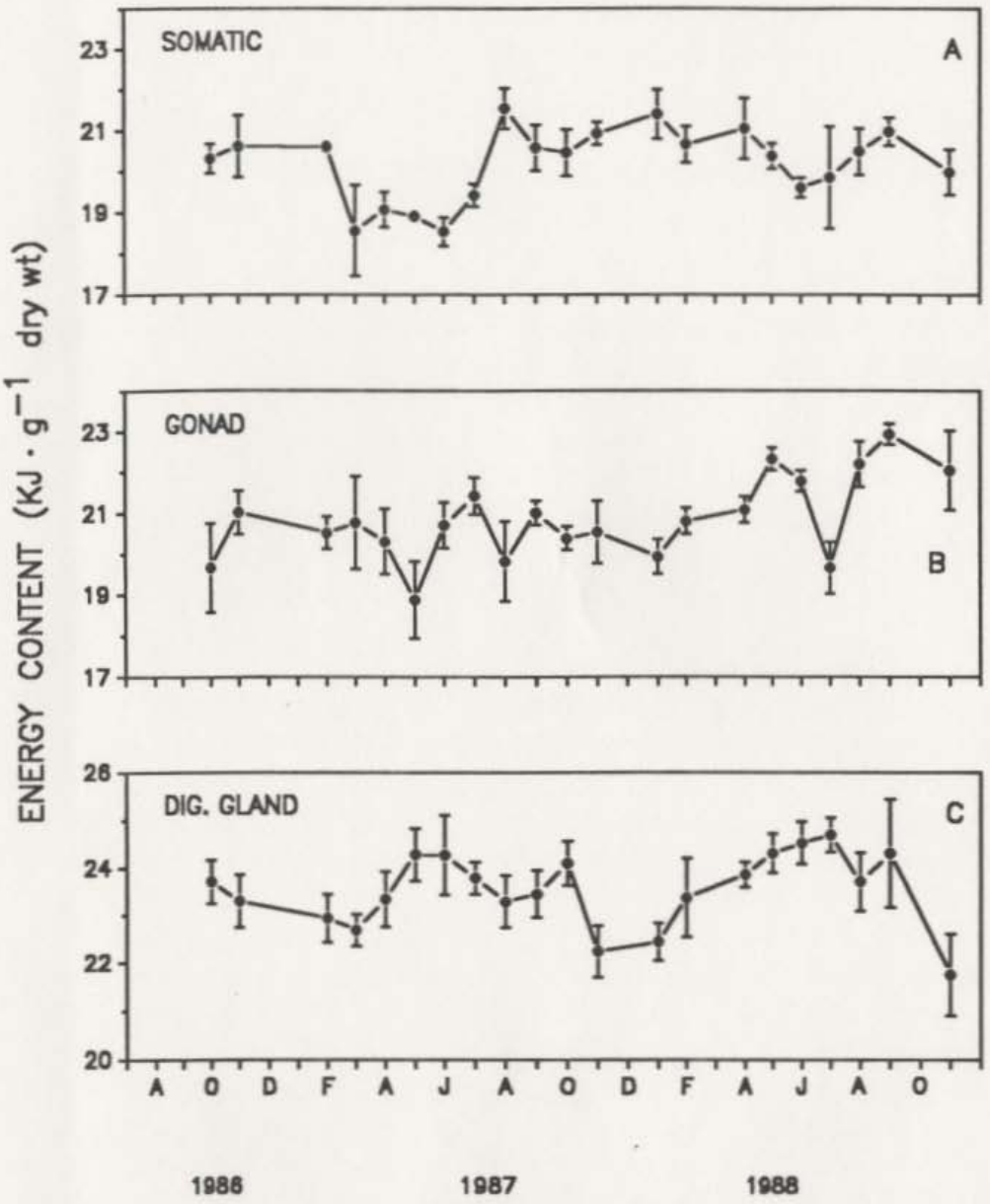


Fig. 37. Seasonal changes in the energy content of the somatic tissue, gonad and digestive gland of *Modiolus modiolus* ("standard" animal of length 10 cm). Values are monthly means ± S.E., n=5.

IV. DISCUSSION

IV.1. QUANTITY, BIOCHEMICAL COMPOSITION AND SIZE SPECTRA OF THE SESTON

Shallow marine coastal systems in cold waters have a higher biomass and a larger diversity of particles than oceanic systems, much of this diversity being associated with seasonal pulses of different classes of phytoplankton and microplankton (Malone, 1971; Mayzaud and Taguchi, 1979). The suspended particulate load (seston) in Logy Bay is lower than in many large shallow marine bays, owing partly to a negligible terrigenous input to Logy Bay, where the quantity of POM primarily depends upon phytoplankton productivity. Since phytoplankton is considered to be superior to other POM as food for filter-feeders (Jorgensen, 1975), the period April-June is the most important for the growth of filter-feeding organisms in this environment.

Seston concentrations are lower in Logy Bay than in many other environments inhabited by mytilids (Table 19), although the proportion of organic matter is among the highest reported anywhere. Widdows et al. (1979) obtained values for total seston in the Lynher estuary (southwest England) in the range of 4 to 35 $mg.l^{-1}$. Large amounts of TPM (up to 152 $mg.l^{-1}$) were reported by Griffiths (1980b) for Bailey's Cottage, South Africa, although much of it was sand and the POM fraction was considerably lower. At Tromso, Norway, Vahl (1980) recorded similar values to those obtained in the present study, with POM in the range 1-4 $mg.l^{-1}$, although TPM was considerably higher (5-12 $mg.l^{-1}$) than in Logy Bay. Newell and Bayne (1980) described a more complex seasonal pattern of seston for the Tamar estuary, southwest England, with an annual range in TPM of 3 $mg.l^{-1}$ in summer to 28 $mg.l^{-1}$ during winter. Conversely, the POM component in the Tamar is at a minimum during the winter (1.5 $mg.l^{-1}$) and at a maximum in the summer (3.0 $mg.l^{-1}$), which is slightly higher than my values for Logy Bay. Thompson (1984a) described the monthly fluctuations of TPM and POM for Bellevue, Trinity Bay, Newfoundland, with very similar values to those registered in the present study. POM varies from 1-3 $mg.l^{-1}$ at Bellevue, whereas at Logy Bay this component varies from 0.25-2.0 $mg.l^{-1}$ (Fig. 4b). TPM is greater at Bellevue (2-6 $mg.l^{-1}$) than at Logy Bay (0.3-3.0 $mg.l^{-1}$). Recently, Berg and Newell (1986) described the fluctuations in seston over an 18 month period in two inlets of Chesapeake Bay, in which TPM varied between 3.5 and 30 $mg.l^{-1}$ and POM between 1.5 and 8 $mg.l^{-1}$. From these studies it is clear that PIM is the component of the seston that shows the greatest seasonal fluctuations.

Most of the authors quoted above reported peaks in POM during the late spring or summer months, as occurs in Logy Bay, where maxima were observed

Table 19.- Total particulate matter (TPM) and particulate organic matter (POM) concentrations reported at different sites.

Place	Author	TPM ($mg.l^{-1}$)	POM ($mg.l^{-1}$)
Lynher Estuary (England)	Widdows et al. (1979)	4 - 35	2 - 4
Bailey's Cottage (South Africa)	Griffiths (1980)	2 -152	1.5 - 17
Tromso (Norway)	Vahl (1980)	5 - 12	1 - 4
Tamar Estuary (England)	Newell and Bayne (1980)	3 - 28	1.5 - 3
Bellevue, Newfoundland (Canada)	Thompson (1984)	3 - 4	1 - 3
Chesapeake Bay (U.S.A)	Berg and Newell (1986)	3.5 - 30	1.5 - 8
Logy Bay, Newfoundland (Canada)	This study	0.3 - 3	0.25- 2

during the spring season in both years of the study. The TPM maximum observed in January, 1988 was mainly due to the increase in the PIM fraction caused by resuspension during a prolonged period of rough sea conditions. A small peak in POM was also observed at this time of the year, presumably produced by resuspension of organic detritus, resulting in a low value for chlorophyll *a* and pronounced peaks in both POC and PON (Figs. 5a;6a,b).

The spring phytoplankton bloom in Logy Bay typically shows one annual peak when the concentration of chlorophyll *a* in the water increases to 50-90 times the winter level (Fig. 5a). The seasonal pattern is similar to those found by other authors in the northern hemisphere (Cadée, 1982; Mayzaud et al., 1984; MacDonald and Thompson, 1985a; Berg and Newell, 1986; Pomeroy and Deibel, 1986). The phytoplankton bloom is not suppressed by low temperature; it begins when the water temperature is still below 0°C (Figs.3,5a), confirming observations by MacDonald and Thompson (1985a) and Pomeroy and Deibel (1986). The absence of a fall bloom in Logy Bay is consistent with observations for similar environments, such as for Northern Europe (Cadée, 1982; Christensen and Kanneworff, 1985) and eastern Canada (Kranck, 1980; Thompson, 1984), suggesting that energy input to benthic filter-feeders in the form of phytoplankton is concentrated into a short period of the year in these cool temperate subarctic latitudes. Dead plant material, measured as phaeopigments and expressed in chlorophyll *a* equivalents, shows a main peak in Logy Bay coincident with that observed for chlorophyll *a*, but a second peak also occurs during July of each year (Fig. 5b), which is probably attributable to grazing of the decaying phytoplankton bloom by pelagic herbivores.

The differences in composition of the POM at various times of the year are evident from the ratio of chlorophyll *a* to phaeopigments (Fig. 5c). This ratio largely exceeds unity during the phytoplankton bloom, owing to the living nature of the organic matter at this time, compared with lower values associated with the highly degraded material observed during the rest of the year in Logy Bay. Similar results were obtained for the Bedford Basin by Mayzaud and Taguchi (1979). Wassmann and Aadnesen (1984), working in a shallow fjord system of the west coast of Norway, reported high values of the chlorophyll *a*:phaeopigment ratio during mid-April, when the phytoplankton bloom was at its maximum. Christensen and Kanneworff (1985) measured the chlorophyll *a*:phaeopigment ratio in four species of filter-feeding organisms from the North Sea, and found that it strongly reflected the proportion of living phytoplankton in the water.

Particulate organic carbon (POC) and nitrogen (PON) show a marked seasonal variation which is mainly controlled by the seasonal productivity cycle of Logy Bay (Figs. 6a,b). Such variations are to be expected for this latitude and have been reported by other authors for similar environments (Cadée, 1982; Mayzaud

et al., 1984; Pocklington, 1985). The isolated peaks of POC and PON occurring during summer 1987 were not associated with high chlorophyll *a* values, suggesting the presence of non-photosynthetic organisms or kelp detritus in the water. The unexpected high values for POC and PON in winter (January 1988) correspond with TPM but not with chlorophyll *a*. This is explained by the rough sea conditions observed in Logy Bay at this time. Thus the increase in TPM, POC and PON seems to be related to resuspension of bottom material, as well as the fragmentation of kelp. The food quality of the seston during these peaks is not as high as when the seston is mainly composed of phytoplankton. This is illustrated in Fig. 6c, where the relative detrital content of the seston is represented by the carbon:chlorophyll *a* ratio. Zeitzschel (1970) assumed that values of 100 or less for this ratio indicate that the carbon originates mainly from living phytoplankton. The values obtained in the present study exceed 100 for most of the year, suggesting a low concentration of microalgae in the water. However, during April-May of each year of the study the carbon present in the seston was primarily of phytoplankton origin, because the carbon:chlorophyll *a* ratio was usually below 100 (Fig. 6c). Similar trends were observed by Berg and Newell (1986) on the eastern side of Chesapeake Bay.

Freshly produced marine POM has a low C:N ratio (Parsons, 1975), and an increase over a ratio of 6.9 implies a contribution from terrestrial sources or an "ageing" (Pocklington and Leonard, 1979). The C:N ratio for seston in Logy Bay (Fig. 6d) is below 6.9 for most of the year, but it is not clear that the material is rich in phytoplankters. The main peak for the C:N ratio observed during August 1987 could be associated with zooplankton faeces, kelp detritus or the "ageing" of the POM after the blooms of phytoplankton and zooplankton in Logy Bay. According to Russell-Hunter (1970), animals have protein nutritional requirements which correspond to C:N ratios lower than 17. The C:N ratios obtained in the present study were never higher than 12.5, suggesting that the food supply in Logy Bay meets the nutritional requirements of the filter-feeders, at least qualitatively. This refers to protein only and it is necessary to investigate the nutritional requirements for other constituents of the seston, such as vitamins and fatty acids (Mayzaud et al., 1989).

In this study the concentrations of the three major biochemical components (carbohydrate, lipid and protein) of the seston (Fig. 7) were also measured. Variations in these constituents are primarily associated with the periods of high and low standing stocks observed in Logy Bay, their seasonal trends being very similar and highly correlated with those described for other components of the seston, such as POM, CHLA, PON and POC (Table 3). Figures 7a,b,c show that carbohydrate, lipid and protein levels are highest during April-May. This confirms that the nutritional character of the seston of Logy Bay is highly dependent on the phytoplankton bloom occurring during April-May of every year. However, a

secondary peak in protein was observed during late June of 1987, suggesting the presence of non-photosynthetic organisms such as bacteria and protozoans during the decaying bloom. Conversely, lower values for carbohydrate, lipid and protein occur during the rest of the year, when the concentration of the phytoplankters is low in this environment.

When all these biochemical components are combined, they account for 10-45% of the POM during winter, which is considerably lower than during the phytoplankton bloom, when they represent 50-90% of the POM measured in Logy Bay. This is not consistent with other studies (Widdows et al., 1979; Soniat et al., 1984; Poulet et al., 1986), which found that the sum of these biochemical constituents represents only 10-15% or less of the organic fraction of the seston. However, the present study was carried out in an environment in which the supply of POM primarily depends upon the phytoplankton bloom, and terrigenous input of SPM and resuspension are probably negligible. Conversely, the authors mentioned above were working in environments characterized by high loadings of seston originating from terrestrial sources or from resuspension of the bottom sediment, where a significant portion of the organic particulate matter is likely to be refractory.

The sum of carbohydrate+lipid+protein has been termed "food material" by some authors. Maita and Yanada (1978) found that the two major components of the food material (carbohydrate + protein) occur at maximum concentrations in the winter and minimal levels in the summer at Funka Bay, Japan. A similar seasonal variation has been recorded by Widdows et al. (1979) for the Lynher estuary in southwest England. These observations are inconsistent with my data which are, however, in good agreement with those reported by Soniat et al. (1984) for Galveston Bay, USA, where the "food material" is higher during spring-summer and lower in the winter months. The present study shows that the "food material" in Logy Bay reaches values as high as 700 $\mu g.l^{-1}$ during April-May, whereas values around 200 $\mu g.l^{-1}$ are more usual for the rest of the year (Fig. 8a).

Widdows et al. (1979) developed a food index based on the ratio food material to total seston. This index is based on the assumption that feeding is non-selective, so that PIM "dilutes" the food available for filter-feeding organisms. However, Newell and Jordan (1983) showed preferential ingestion of organic matter by the suspension feeding bivalve *Crassostrea virginica*. The main peaks in the food index for Logy Bay occur during the spring-summer, with values as high as 55% (Fig. 8b). Lower values are typical of the winter months, where the food index drops to values below 10%, indicating that the seston is of low nutritional quality. Soniat et al. (1984) also found the highest food index during these seasons (spring and summer) in Galveston Bay, but its value never exceeded about 11%, demonstrating a nutritionally dilute environment caused mainly by the high loading

of PIM. On the other hand, Widdows et al. (1979) found an inverse relationship between "food material" and "food index", whereby food material in the Lynher estuary is higher in winter and lower in summer, but the food index (food material expressed as a percentage of the total seston) is only 6% in winter, rising to 25% in summer. The food material is diluted by PIM in the seston, but low values for the food index are not necessarily associated with a low amount of food material. Thus in order to determine the availability of the food resources in a given environment, it is necessary to know both the food material content and the food index.

The seasonal fluctuation in the size frequency distribution of the SPM in Logy Bay is primarily influenced by certain biological and physical factors, such as the productivity cycle and resuspension of the bottom sediment. This is reflected in Fig. 9, where the SPM expressed in total particles per ml as well as in total volume ($mm^3.l^{-1}$) shows maximum values during spring, corresponding with the phytoplankton bloom. All the minor peaks are related to rough sea conditions and resuspension of the bottom sediment.

Kranck (1980) distinguished four basic types of particle populations in the marine environment. In the present study all four were found in Logy Bay at various times of the year. In March 1987, the size spectrum could be described as a type D or flat spectrum, characterized by low total concentrations with similar volumes of particles of all sizes, i.e. no pronounced peaks. This type of particle distribution is normally associated with living cells or detritus in low concentration. Kranck (1980) described the type D spectrum in terms of particles forming the background of the "bloom spectrum" (type A). The type A or bloom spectrum recorded in May 1987 (Fig. 10) was primarily a result of the phytoplankton bloom superimposed on a low background of about the same volume in all size classes (type D). Microscopic analysis of the samples showed that the peak is composed predominantly of single as well as chain forming diatoms (*Fragilaria* sp., *Nitzschia* sp., *Chaetoceros* sp., *Thalassiosira* sp. and *Coscinodiscus* sp). Flagellates 8-12 μm in diameter are also present. The particle size distribution for June-September 1987 corresponds to the type D or flat spectrum, whereas the peaks observed during the winter months correspond to the type B or floc spectrum (Fig. 11), which contains very few plankton cells and is mainly composed of suspended bottom sediment with a high proportion of inorganic matter.

The peaks registered in the particle size spectra during April and May of 1988 (Fig. 12) were caused by the diatoms and flagellates of the phytoplankton bloom, as in 1987, but in 1988 particle concentrations did not attain the values of May 1987, as a result of weather conditions in Logy Bay. The spring of 1988 was cloudy and stormy, and relatively low values were recorded for many of the nutritional components of the seston, such as chlorophyll *a*, PON, and POC. The

bloom spectra observed in 1987 and 1988 coincided with the times of seasonal chlorophyll *a* maxima. Thus the particle size frequency distributions described in the present study are very similar to those described by Kranck (1980) in Nova Scotia and by MacDonald and Thompson (1985a) in Sunnyside, Newfoundland, where the size spectra can display types A,B,C or D, depending on the biological and physical conditions prevailing at a given time of the year, particularly productivity cycles, kelp fragmentation, erosion, storms and resuspension.

IV.2. PHYSIOLOGICAL PROCESSES

Variability in clearance rate (CR) has been commonly reported in bivalves (Morton, 1969; Winter, 1969, 1973; Schulte, 1975; Griffiths, 1980a; Palmer, 1980; Higgins, 1980). *Modiolus modiolus* has proved to be no exception, exhibiting short-term (daily) as well as long-term (seasonal) fluctuations (Figs. 13, 14, 15). During spring and early summer *Modiolus modiolus* remains open a significantly greater proportion of the time, with a higher and more constant clearance rate (Fig. 13) than during fall and winter, when feeding activity fluctuates greatly (Fig. 14), with some mussels either not filtering or filtering at minimum rates. This behavioural pattern in winter is arhythmic, the initiation of periods of activity and quiescence being apparently random and specific to each experimental mussel, showing no consistency among individuals. These results are similar to those obtained for *Crassostrea virginica* by Epifanio and Ewart (1977) and Palmer (1980), where periods of activity alternating with relative quiescence in filtration occurred in oysters exposed to unchanging environmental conditions.

Higgins (1980) found a clear relationship between food availability and feeding rate of juvenile *Crassostrea virginica*, which is in good agreement with my observations on the feeding behaviour of *Modiolus modiolus*, i.e. there is more activity when the food supply is greater (spring and summer). The lowest and most variable CR values observed in *Modiolus modiolus* during fall and winter seem to be associated more with the low nutritive value of the food rather than with the low temperatures, because clearance rates are high during early spring, when the temperature is approximately 0°C and the nutritive value of the seston is high owing to the phytoplankton bloom. Thompson (1984a) also reported the remarkable ability of *Mytilus edulis* from Bellevue, Newfoundland, to maintain a high CR at very low temperatures, and Widdows (1976) has shown that this species has a high capacity for acclimation to temperature change.

During spring and early summer the organic component of the seston consists primarily of living cells, this being reflected in the concentrations of POM, chlorophyll *a*, PON, POC, lipid and carbohydrate, which are all several times higher than during the rest of the year. The intermittent feeding behaviour characteristic

of *Modiolus modiolus* may represent an adaptive mechanism to conserve energy by reducing the time spent filtering seston of low nutritive value. Worrall et al. (1983) also described a seasonal pattern in CR for three different populations of the bivalve *Scrobicularia plana*, with reduced values during winter and maxima during summer. Newell and Bayne (1980) described a similar feeding behaviour for the cockle *Cardium edule*, in which CR was at a minimum during winter when the organic seston was only half the summer level. This was described as a "dormant condition", although the authors concluded that this should not be confused with the "cold coma" reported by Newell (1979), since the temperature of the water was never below 8°C. Hummel (1985a) found that *Macoma balthica* quickly reduces its feeding activity when the concentration of available food diminishes, thereby eliminating the high cost of respiration associated with enhanced feeding activity. Riisgard and Randlov (1981) demonstrated that *Mytilus edulis* can also adapt to a reduced food supply by reducing the CR considerably, and Widdows et al. (1979) reported high seasonal variability in the CR of *Mytilus edulis* from the Lynher Estuary, some of which was attributable to high particle loads, conditions not observed in Logy Bay.

The differences in CR between seasons observed in *Modiolus modiolus* are not easily explained, and the relationships between food availability and clearance rate may depend on the nature of the particulate matter. The lowest ingestion rate of organic and total seston is observed during winter and the highest ingestion rate during the spring (Fig. 16), when food availability and nutritional value are greater. These results are in good agreement with those of Taghon (1981), which suggest that the reduction of feeding rate caused by a decrease in food quality, as is normally experienced by *Modiolus modiolus* during winter in Logy Bay, represents an optimal behaviour under poor food conditions. MacDonald and Thompson (1986), working on two populations of *Placopecten magellanicus* from Sunnyside, Newfoundland, reported minimal clearance rates during the winter months and maximal rates in September, when the temperature was highest. This is consistent with my observations on *Modiolus modiolus*.

Although it is possible to describe a slight seasonal pattern for CR in the horse mussel, this physiological process is not correlated with temperature or any other environmental or physiological variable. Similar results have been recorded for *Mytilus edulis* from Newfoundland (Thompson, 1984a) and for *Cardium edule* from England (Newell and Bayne, 1980). On the other hand, Bayne and Widdows (1978) described a significant negative correlation between CR and total seston when data from two populations of *Mytilus edulis* were considered together over a range of SPM from 7 to 42 $mg.l^{-1}$.

Foster-Smith (1975) mentions that pseudofaeces production in bivalves is not only related to the food concentration but also to its composition. *Modiolus*

modiolus produces abundant pseudofaeces at a very low food concentration (≈1.5-2.0 $mg.l^{-1}$) during a short period of the year, coinciding with the bloom of large diatoms and/or diatom chains (e.g. *Coscinodiscus* sp., *Fragilaria* sp., *Chaetoceros* sp.). Widdows et al. (1979) also found pseudofaeces production in *Mytilus edulis* at low particle concentrations, owing to high silt levels rather than to large particles. Similar results were obtained by Robinson et al. (1984) on *Spisula solidissima*. Presumably *Modiolus modiolus* is unable to ingest these large particles present in the seston, which has implications for the transfer of energy from the pelagic to the benthic environment.

Absorption efficiency (AE) in *Modiolus modiolus* is not affected either by seasonal changes in the physiological state of the mussels or by acclimation temperature. Similar results were reported by Widdows (1978b) for *Mytilus edulis*. Two low values obtained for *Modiolus modiolus* during fall 1986 are difficult to explain given that the food availability and the physiological responses were constant at that time. Presumably these values resulted from the unusually high clearance rates and ingestion rates compared with those observed in the fall of 1987.

The mean absorption efficiency for the entire study was 76.5%, which is very high when compared with other studies for different species (Widdows, 1978a; Bayne and Widdows, 1978; review by Bayne and Newell, 1983). However, my results are in good agreement with those of Winter (1969), who also reported very high values of AE (82-90%), using a different analytical procedure, in *Modiolus modiolus* fed with an algal monoculture. The high value of AE in *Modiolus modiolus* from Logy Bay is probably attributable to low particle loads (usually below 2.0 $mg.l^{-1}$), as well as the high digestibility of the food present in this environment. Under these conditions, some organisms are able to compensate by increasing the gut residence time, resulting in a higher AE (Bayne et al., 1984). This ability to increase AE when the food supply decreases has also been observed in *Mytilus edulis* (Thompson and Bayne, 1972; Widdows, 1978b) and in *Mytilus chilensis* (Navarro and Winter, 1982). In the latter AE is inversely correlated with food ration, increasing from 49.8% at 2.4 $mg.l^{-1}$ to 73.4% at 0.8 $mg.l^{-1}$ with *Dunaliella marina* as food. Bayne et al. (1984) related food supply, CR, gut residence time and AE in three mytilid species and found a negative relationship between CR and gut residence time. These authors also described a strong positive relationship between gut residence time and AE in the three species investigated, and similar results were obtained by Calow (1975, 1977) for two freshwater gastropods and by Hawkins and Bayne (1984) for *Mytilus edulis*. These results are consistent with those obtained for *Modiolus modiolus* from Logy Bay, where most of the time the total particle concentration ranged between 1 and 2 $mg.l^{-1}$, with values as low as 0.4 $mg.l^{-1}$ during winter.

In common with many other studies on various bivalves (Winter, 1969, 1970; Thompson and Bayne, 1972; Widdows, 1978a; Navarro and Winter, 1982; Shumway and Newell, 1984; Navarro, 1988), no significant effect of body size was found on AE in *Modiolus modiolus* (Table 5), probably because the processes controlling AE, such as ciliary and enzyme activity, are size-independent. Absorption efficiency in horse mussels was not correlated with any environmental variable, although a slight correlation ($P \leq 0.05$) was observed with SFG. Winter (1969) found no difference in AE at different food levels. Previous studies on *Cardium edule* and *Mytilus edulis* also showed that AE was not correlated with total seston or POM (Newell and Bayne, 1980; Thompson, 1984a), in contrast to those results reported for *Mytilus edulis* from the Lynher estuary by Bayne and Widdows (1978), where AE showed a significant correlation with POM (expressed as a proportion of TPM).

The seasonal changes of oxygen uptake (VO_2) in bivalves have been studied by many authors, with a variety of results. In some cases VO_2 has been related to temperature, food availability and/or gametogenesis. Thus Widdows and Bayne (1971), Gabbott and Bayne (1973), Widdows (1978b), Bayne and Widdows (1978), and Newell and Bayne (1980) have recorded a relationship between VO_2 and gametogenesis, e.g. high VO_2 values in *Mytilus edulis* at low temperature in the North Sea, caused by the metabolic demands of gametogenesis.

The oxygen uptake of *Modiolus modiolus* exibits pronounced seasonal changes which generally follow the fluctuations in ambient temperature (Table 9; Fig. 18). Furthermore, there is a strong correlation ($P \leq 0.01$) between VO_2 and gonad weight for a mussel of 5 g dry tissue weight, suggesting that the gonad weight also explains some of the variability in VO_2. It is difficult to separate the effects of temperature and gonad weight on VO_2 because they vary simultaneously, but the data suggest that the oxygen uptake cycle is not strictly driven by temperature, and may be intimately linked with the gametogenetic cycle as has been demonstrated for several other species of molluscs (Bayne and Newell, 1983; Hummel, 1985b).

Worrall et al. (1983) also found a relationship between VO_2 and temperature in three populations of the bivalve *Scrobicularia plana*, although gametogenic activity also explained a significant part of the variability in VO_2. On the other hand, Vahl (1978) monitored the changes in the metabolic rate of the Iceland scallop *Chlamys islandica* and found that VO_2 is not greatly influenced by the seasonal temperature cycle, suggesting that food availability may be responsible for most of the seasonal variability. Furthermore, there is significant seasonal variation in the dependence of oxygen uptake upon body weight in *Modiolus modiolus* from Logy Bay. Shafee (1982) reported a marked seasonal fluctuation in VO_2 for *Chlamys varia* with the highest values in August-September and the lowest values in February-March, which correspond to periods of high temperatures and peaks of gonad weight and low temperature and reduced gonad weight, respectively. As in *Modiolus modiolus* (this

study), VO_2 of the bay scallop *Argopecten irradians irradians* follows the seasonal changes of water temperature (Bricelj et al., 1987). No correlation between VO_2 and gametogenesis was observed by Thompson (1984a) and MacDonald and Thompson (1986) for the bivalves *Mytilus edulis* and *Placopecten magellanicus*, respectively, although a high correlation between VO_2 and temperature was obtained for the latter (MacDonald and Thompson, 1986). Shumway et al. (1988) showed that the VO_2 of the giant scallop *Placopecten magellanicus* exhibits pronounced seasonal fluctuations which follow the cycles of temperature and gonad maturation, the highest rates being recorded during summer when the gonads are ripe, and the lowest rates during winter when gametogenesis is just beginning.

Although *Modiolus modiolus* showed a strong positive correlation between VO_2 and temperature (Fig. 19a), negative correlations were obtained between VO_2 and PIM and PARTV, suggesting a relationship between food quality and VO_2. The inverse relationship between VO_2 and net growth efficiency (K_2) demonstrates the negative effect of respiratory losses on the growth rate of the horse mussel.

The regression coefficient (b) of the allometric equation $VO_2=aW^b$ is an expression of the effect of body size on the oxygen uptake of *Modiolus modiolus*. Considerable intraspecific and interspecific variation in the exponent b has been reported for marine bivalves, values ranging from 0.16 to 1.02, although the majority fall between 0.4 and 0.9 (Bayne et al., 1976). In the present study VO_2 was measured almost every month, and highly significant regressions were always found between VO_2 and dry tissue weight. The regression coefficients ranged between 0.61 and 1.01, excepting one lower value (0.45) during October 1986. However, very different intercepts (a) were found in the same experiments, with values lying between 0.043 and 0.354 $ml.h^{-1}$ for a mussel of 1 g dry tissue weight.

Protein catabolism leads to the formation of ammonia, which represents 60-90% of the total nitrogen excretion in several species of bivalves (Bayne et al., 1976). The energy losses associated with ammonia excretion (VNH_4-N) usually represent only 1 to 4% of the daily energy ingested by *Modiolus modiolus* of 2g dry tissue weight, and only a few values were higher than 4% (Table 8).

Ammonia excretion in the horse mussel is highly correlated with gonad weight, suggesting that mature and developing gametes in the gonad are also responsible for some of the variation in VNH_4-N, as previously reported for some species of bivalves (Widdows, 1978b; Bayne and Widdows, 1978; Worrall et al., 1983).

The seasonal cycle in VNH_4-N by *Modiolus modiolus* (Fig. 20) is similar to that described previously for VO_2 and also follows the temperature cycle. Ammonia excretion is at a minimum in the winter and increases to maximum values

in the spring and summer, when the weight of the gonad increases. Thus the seasonal cycle in VNH_4-N is not simply temperature dependent, and factors such as reproduction and biochemical energy storage cycles are known to influence the physiological responses of bivalves to seasonal environmental changes (Gabbott and Bayne, 1973; Widdows, 1978b; Bayne and Widdows, 1978; Bayne et al., 1979; Widdows et al., 1979; Bayne and Newell, 1983; Worrall et al., 1983; Thompson, 1984a).

The relationship between ammonia excretion and body size in *Modiolus modiolus* is similar to that recorded for other bivalves (Bayne, 1973a,b; Bayne et al., 1976; Bayne and Scullard, 1977; Bayne and Widdows, 1978; Widdows, 1978b; Navarro and Winter, 1982; Thompson, 1984a), where highly significant regressions have been reported.

The ratio between oxygen consumed and nitrogen excreted in atomic equivalents (O:N ratio) represents the degree to which protein is utilized by marine bivalves in energy metabolism (Corner and Cowey, 1968; Bayne and Thompson, 1970; Bayne, 1973b; Bayne et al., 1976; Widdows, 1978b; Shumway and Newell, 1984; Widdows, 1985). The values for O:N in horse mussels lie in the range reported for other bivalves in which it has been measured (Bayne and Thompson, 1970; Bayne, 1973b; Bayne and Scullard, 1977; Widdows, 1978b; Thompson, 1984a; Shumway and Newell, 1984). Highest values were found in winter (53) and lowest during spring and summer (12-25), owing to the depressed excretion rates during winter, when temperatures and food supply are low and the gonad reduced in weight. The high O:N winter values are associated with the utilization of biochemical energy reserves by *Modiolus modiolus*. Carbohydrate is used in higher proportion than protein (Fig. 32), resulting in a low VNH_4-N. On the other hand, the lower values of O:N obtained during the summer suggest that there is no significant utilization of energy reserves, and that the higher VNH_4-N is probably a result of feeding activity and growth. These observations show that the O:N ratio is a useful index of physiological integration which helps to explain the cycles of energy reserves. Crisp et al. (1981) also reported higher O:N ratios for the winter in the gastropod *Nassarius reticulatus*. Similarly, Bayne and Scullard (1977) found reduced rates of ammonia excretion in *Mytilus edulis* at low ration. Shumway and Newell (1984) observed a decrease in VNH_4-N in *Mulinia lateralis* following starvation, reflecting a decline in the overall utilization of metabolic reserves during food shortage and a high O:N ratio, which suggests that a small amount of protein is being utilized for energy metabolism. These results differ from those for other marine species in which a shortage of food availability is associated with a low O:N ratio, suggesting an immediate catabolism of proteins to support maintenance metabolism.

The overall effects of environmental factors on the horse mussel are reflected in the scope for growth (SFG) and net growth efficiency (K_2), which may be considered as two useful indices of fitness because they represent the integration of the basic physiological processes. It is therefore instructive to determine how those processes affect SFG and K_2 at any given time of the year.

The present study showed that the energy demands of respiration (VO_2) during the summer are higher than the energy absorbed, resulting in negative values for SFG and K_2 (Table 8). During this time, the temperature in Logy Bay is at its maximum (≈14°C) and rates of oxygen uptake are high. In addition, SPM is lower, resulting in reduced ingestion and absorption rates. On the other hand, the food absorbed during the spring bloom is very rich in energy, and this, together with the low VO_2 at this time, results in a positive SFG (Fig. 22) and high K_2 for *Modiolus modiolus*. Several estimates of SFG have been made for *Mytilus edulis*, with the highest values being observed during the summer for populations in southwest England (Widdows, 1978a; Bayne and Widdows, 1978; Widdows et al., 1979) and for a population from Newfoundland, Canada (Thompson, 1984a). The lower but still positive SFG values observed in smaller individuals of *Modiolus modiolus* during fall and winter are a consequence of the lower maintenance ration or food requirement during these seasons, which is advantageous at a time of the year when food availability is minimal.

Thus the high values for these indices observed in spring for *Modiolus modiolus* from Logy Bay are a consequence of the high nutritional value of the food supplied by the phytoplankton bloom. Similarly, Widdows et al. (1984) provided evidence that the variability in the physiological responses is largely determined by certain environmental factors. Of particular significance is the positive effect of the quality and quantity of particulate material on SFG in *Mytilus edulis* during the spring algal bloom. Conversely, these authors reported a low SFG when the same mussels were transplanted to a location with poor food conditions.

The value for SFG as a measure of the response of the whole organism is illustrated by data from the fall of 1986, in which high CR values were recorded, but AE was low. The net result was an estimate of SFG which fitted the seasonal pattern observed in other years. Such compensatory processes are not apparent if one relies exclusively on the measurement of individual physiological rate functions.

The seasonal pattern of fluctuations of SFG observed in *Modiolus modiolus* throughout the year is similar in the three size classes, although the smaller sizes show prolonged periods with a positive SFG (Fig. 22), largely because of the difference in slopes relating CR and VO_2 to body weight, which favours smaller individuals. Furthermore, according to Rowell (1967) horse mussels from Canadian

waters are not sexually mature until they are 4 years old, which means that small individuals are not subjected to the metabolic demands of gametogenesis, resulting in a higher SFG. Smaller mussels may also be more tolerant of summer temperatures. Similar results have been found in other species of bivalves by Widdows (1978a), Vahl (1978), MacDonald and Thompson (1986) and Navarro (1988).

Scope for growth is an estimate of production, and it is clear that the production of *Modiolus modiolus* is primarily governed by the amount of phytoplankton in the water, the spring bloom being the most important period. The lower values of SFG and K_2 observed during the rest of the year seem to be associated with food sources containing relatively little chlorophyll *a*. The results obtained in the present study are very similar to those reported by MacDonald and Thompson (1986) for the scallop *Placopecten magellanicus* and by Vahl (1980) for *Chlamys islandica*, in which the higher SFG values observed during the spring are attributable to the high nutritional content of the seston, and to a reduced VO_2 associated with low temperature and reduced gametogenesis. The highly reduced SFG observed during summer is caused by the marked drop in the phytoplankton bloom as well as by the pronounced increase in VO_2. These results suggest that SFG would be more independent of season if enough food were available to the organism, supporting the contention of Bayne and Newell (1983) that SFG and K_2 are more dependent on food availability than on temperature.

IV.3. TECHNIQUES FOR THE MEASUREMENT OF ABSORPTION EFFICIENCY

Absorption efficiency (AE) has usually been quantified by the method of Conover (1966), which assumes no absorption of the inorganic matter present in the food. However, it has been shown by Foster and Gabbott (1971) that some animals, such as Crustacea, can utilize a proportion of the ingested inorganic material. When the diet consists of a low ratio of ash:organic content, a significant proportion of the ash can be absorbed (Conover, 1966), so that AE is underestimated.

In order to validate the ash-ratio method, the present study included the use of another technique to measure AE in bivalves, utilising biogenic silica as a non-absorbable indicator (Tande and Slagstad, 1985; Conover et al., 1986). A comparison of these techniques using horse mussels feeding on natural seston in Logy Bay (Fig. 25a) demonstrated good agreement over a wide range of silica concentrations (20-240 μg silica.mg^{-1} food). The slightly lower values for AE obtained with the silica technique may be explained by the observations of Tande and Slagstad (1985), which suggest an underestimation of AE caused by a loss of

silicon during the feeding process. These authors recovered in the faecal pellets about 85% of the silica consumed, which is very similar to the amount of silica recovered by Conover et al. (1986), working with copepods. The loss of silica in the faeces may be attributable to the fragmentation of the diatom frustules into very small particles, or to fragmentation of the faecal pellets before their collection for analysis.

When pure cultures of microalgae were used, a narrower range of silica concentration was obtained (12-97 μg silica.mg^{-1} food) and there was more variation in AE values, but the agreement between the ash and silicate methods was still good, except at silicate concentrations of 30-40 μg.mg^{-1} food (Fig. 26a,b). The most reliable estimates of AE are those obtained under natural food conditions, when there is usually a large proportion of inorganic matter.

Using the rich food available during the phytoplankton bloom of 1988, several experiments were carried out in which four different methods for measuring AE were compared simultaneously. As before, ash and silicate were compared as non-absorbed components, using organic matter as the absorbable fraction. In addition, chloropigments, organic carbon and organic matter were compared as absorbable components, using the ash fraction as a reference (Tables 11, 12; Fig. 27). Values for AE from the ash ratio technique obtained during the phytoplankton bloom were slightly greater than those from the silicate and carbon techniques, but not significantly different from values from the chloropigment method (Table 12). The high values for AE from the chloropigment technique are inconsistent with the observations of Shuman and Lorenzen (1975), who reported that neither chlorophyll *a* nor its degradation products are absorbed by copepods of the genus *Calanus*. Several workers (e.g. Landry et al., 1984) have therefore estimated AE in copepods with chlorophyll *a* as a conservative tracer, using the carbon:pigment ratios in food and faecal material. In the mussel *Mytilus edulis*, however, Hawkins et al. (1985) found that total chloropigments were absorbed with net efficiencies of at least 46%, and with maximum values reaching 80%, which is consistent with my observations on *Modiolus modiolus*. Similarly, Conover et al. (1986) found that 90% of the chloropigments were absorbed or broken down to a non-fluorescing form, confirming the utility of chloropigments as a diet-specific indicator of ingested material. Conversely, it is clear that the chloropigment fraction should not be used as an indicator of the non-absorbed component for determinations of absorption efficiency.

IV.4. BIODEPOSITS

Faeces and pseudofaeces produced by benthic animals are important in sediment transport processes. The biodeposition rate (faeces + pseudofaeces) by

Modiolus modiolus was highly correlated with the phytoplankton bloom, and the highest value (40.9 mg dry weight.d^{-1}) coincided with the main peak of chlorophyll *a*, largely because *Modiolus modiolus* produces pseudofaeces only during the bloom of large diatoms in Logy Bay, and because faecal production is greater at this time. The pseudofaeces contained large diatoms such as *Coscinodiscus*, as well as many chain forms, e.g. *Thalassiosira* and *Fragilaria*. Tsuchiya (1980) reported that in *Mytilus edulis* from Japan the highest rates of biodeposition occur in the summer, although faeces production is greater than pseudofaeces production at food concentrations similar to those measured in the present study. Although faecal production in *Modiolus modiolus* always exceeds pseudofaecal production, the latter provides an important mechanism for recycling nutrients to the system. For example, chlorophyll *a* is always higher in the pseudofaeces than in the faeces, accounting for ≈90% by weight of the total pigments in the former but only 25% in the latter. The value for the chlorophyll *a* content of the pseudofaeces is very similar to that obtained for natural seston on the same date, suggesting that the pseudofaeces produced by *Modiolus modiolus* are of high nutritional value to grazers and detritivores.

Similar results were obtained for POC and PON, with values for pseudofaeces very close to those for the natural food, and values for faeces considerably lower. However, the faeces also represent a potential food source for benthic organisms, less rich in organic content than pseudofaeces but produced in more copious quantities. Furthermore, both faeces and pseudofaeces can act as substrates for microorganisms. This suggests that biodeposits probably constitute a supplementary food source (Newell, 1965) for pelagic grazers and also for bottom organisms at all seasons, the quality varying with the phytoplankton bloom.

Many other authors have mentioned the importance of the microorganisms attached to the detritus as a food source for filter-feeding organisms. Newell (1965) reported the nutritional enrichment of the faeces of the prosobranch *Hydrobia ulvae* and the bivalve *Macoma balthica* caused by the attachment of microorganisms. After three days the PON content in the faeces of *Macoma balthica* increased from 0.03% to 1.2%, while the POC dropped slightly from 8 to 7%. According to Newell (1965), the fact that the faeces were rich in carbon suggested that the animals were unable to digest the carbon in the form in which it was ingested, while the low nitrogen level suggested that the protein in the food was absorbed with high efficiency.

The organic material recovered from the faeces of *Modiolus modiolus* had a higher percentage of organic nitrogen (Table 14) than that reported for *Macoma balthica*, ranging from 0.36 to 1.1% of the dry weight of the faecal pellets. This is in agreement with other authors, who have reported high nitrogen levels for faeces of marine bivalves (Fox et al., 1952). The pseudofaeces produced by *Modiolus*

modiolus during the phytoplankton bloom (April-May) had a higher level of organic nitrogen than the faeces, ranging between 0.8 and 3.8% of the dry weight of the pseudofaeces, which is similar to values recorded for the natural seston (2.4 to 4.4% of the dry weight of the TPM; Table 14). However the data for food and pseudofaeces for the experiments 1,2 and 3 in Fig. 28 indicate preferential ingestion of organic carbon and nitrogen and the pseudofaeces represented the material which has been rejected by a selection process. These data contradict the results for chlorophyll *a* from the same experiments, suggesting that *Modiolus modiolus* cannot preferentially sort chlorophyll particles from non-algal cells, or that the gill of the mussel is not sampling the seston in the same manner as the GF/C filter used to collect seston samples. It is also probable that the large algal species rejected in the pseudofaeces have different chlorophyll *a* to C and N ratios than those which are rejected. The importance of the large diatoms in the composition of the pseudofaeces is supported by the high values of the biogenic silica found in these biodeposits (Fig. 29b) and also by microscopic observations.

Although these experiments were done only during the phytoplankton bloom, the results for SPM and microscopic observations of faeces suggest that lower concentrations of chlorophyll *a*, PON and POC would be found in the faeces at other times of the year (e.g. winter, fall), when the food supply is not as rich as during April-May. These findings are in good agreement with those published by Newell (1965).

The feeding studies on horse mussels maintained in natural seston, and observations on the biodeposits which they produce, show that this species removes particles over a wide size spectrum, recycling nutrients through the faecal pellets, which may serve as a substantial energy source for suspension and deposit-feeders. Pomeroy et al. (1984) concluded that faecal material produced by thaliaceans represents an energy source only during the first few days after production, since the faeces are soon consumed and the carbon respired by bacteria and protozoans. However, because the water is considerably colder in Newfoundland than in the lower latitudes considered by Pomeroy et al. (1984), the action of the microorganisms on the faeces may be slower, which would make the faecal matter more available to the benthos. There is some evidence for suppression of the microbial loop in very cold water (Pomeroy and Deibel, 1986), but this may be modulated by the substrate level (L. Pomeroy, University of Georgia, pers. comm.).

IV.5. TISSUE WEIGHT CYCLES

Many studies on marine bivalves have shown that the seasonal changes in tissue weight as well as the biochemical composition of the tissues are often related to reproductive cycles and to environmental conditions, especially the food supply

(both quality and quantity). *Modiolus modiolus* is no exception. Growth of the digestive gland, gonad and remaining tissues decreases during the winter, or ceases altogether (Fig. 30), whereas growth is faster during the spring, when the food supply is maximal, corresponding with the data reported by Thompson et al. (1974) for *Mytilus edulis*. It has been reported by many authors (Rowell, 1967; Brown and Seed, 1977; Seed and Brown, 1977; Comely, 1978, 1981; Brown, 1984; Jasim and Brand, 1989) that the reproductive cycle in *Modiolus modiolus* varies considerably with the environmental conditions. In this study, *Modiolus modiolus* from Logy Bay clearly spawned in 1986 and 1988, but it was not clear whether there was a spawning in 1987, when the gonad comprised a much lower percentage of the total dry weight than in 1986 and 1988. The slight increase in gonad weight during the fall of 1987 was followed by a corresponding slight decrease, but it is not clear whether this represented a minor spawning, which suggests that *Modiolus modiolus* may not spawn every year in this environment. Similar results have been reported for *Modiolus modiolus* from Norway by Wiborg (1946), who found that several years may elapse between successive spawnings. On the basis of observations of the density of gametes in the gonad and the size frequency distribution of the oocytes, Brown (1984) considered that some populations of *Modiolus modiolus* exhibit a discrete reproductive cycle with pronounced spawning periods, whereas others release gametes slowly throughout the year. In the absence of data for gonad weight, however, it is difficult to establish the cycle in these circumstances. According to Wiborg (1946), major spawnings in *Modiolus modiolus* populations take place every few years, and the mesosoma empties in most individuals. In horse mussels from Logy Bay, the gonads contained ripe or nearly ripe gametes throughout the study, but it is not possible to state whether there were intermittent "dribble" spawnings in addition to the major spawning events of 1986 and 1988, or whether these pronounced spawnings occur every two years or more irregularly. Infrequent spawning may be a consequence of the difficulty in acquiring sufficient energy for reproduction in a nutritionally dilute environment. Luxmore (1982) observed that in some polar organisms (e.g. the isopod *Serolis polita*), gonad production requires two successive summer periods to compensate for the reduced food availability during the winter. According to Clarke (1983, 1987), in polar and temperate regions in which an abundant food supply is present for a short period only, both growth and gonad production are limited to the season when food is available. This is consistent with my observations that the growth rate of *Modiolus modiolus* is determined more by food availability than by temperature, since the highest SFG values (Fig. 22) and tissue growth rates (Fig. 30A) are observed during the phytoplankton bloom, when the temperature is approximately 0°C. Bayne and Worrall (1980) and Newell et al. (1982) also assigned an important role to the food supply, and attributed the differences in the gametogenic cycle of *Mytilus edulis* to temporal and quantitative differences in food availability.

IV.6. SYNTHESIS AND UTILIZATION OF BIOCHEMICAL ENERGY RESERVES

Ansell and Trevallion (1967) defined certain features characteristic of the seasonal activities of bivalves living in boreal regions and the mechanisms which affect the seasonal cycle in biochemical composition. This cycle typically includes a period of inactivity in the winter season during which gametogenesis proceeds slowly, and stored reserves may be used to support metabolic demands. This is followed by a renewal of activity in the spring, when reserves are accumulated and growth begins, then a reproductive period during summer or early fall, when the temperature rises considerably. More recently, Bayne (1976) and Gabbott (1983) have identified other strategies in the gametogenic cycles of temperate bivalves. Some species accumulate energy reserves in one year to support gametogenesis in the next, whereas in others the synthesis of these reserves occurs immediately before gametogenesis. There may also be intraspecific variation in the relationship between the cycles of gametogenesis and energy storage (Thompson, 1984b; Thompson and MacDonald, 1990).

Modiolus modiolus follows the seasonal cycle described by Ansell and Trevallion (1967), accumulating energy reserves mainly during the spring bloom, when there is a rich nutritional food supply. The horse mussel can utilise these reserves during the spring-summer to support gametogenesis, but spawning may not occur every year in this species. There is no accumulation of reserves during winter when there are decreases in the weights of the gonad, digestive gland and remaining tissue (Fig. 30). Protein, carbohydrate and lipid decline during winter in the three different body fractions, illustrating the relationship between the biochemical composition of *Modiolus modiolus* and the poor food supply available during winter in Logy Bay (Figs. 32,34,36,37). In winter, metabolic demands are met by the utilization of stored energy reserves, particularly carbohydrate, but this is not accompanied by increasing lipid content, indicating that the carbohydrate stores are used to meet metabolic demands rather than to synthesise eggs.

Conversely, the considerable increase in tissue weight as well as in protein, lipid and carbohydrate during spring and early summer is associated with the phytoplankton bloom in Logy Bay. This observation is consistent with the measurements of scope for growth (SFG) and net growth efficiency (K_2), which both increase at this time of the year (Table 8; Fig. 22). This also supports the contention that temperature is not as important as food availability in determining the cycles of growth and biochemical composition in *Modiolus modiolus*, since the temperature was approximately 0°C at this time. Similar observations have been reported for *Mytilus edulis* (Thompson, 1984a; Emmett et al., 1987), *Ostrea puelchana* (Fernandez and de Vigo, 1987), *Chlamys septemradiata* (Ansell, 1974) and for two different populations of the giant scallop *Placopecten magellanicus* from

Newfoundland (Thompson, 1977; Thompson and MacDonald, 1990). MacDonald and Thompson (1986) also reported a very low metabolic rate and little or no gamete development during winter in the giant scallop, which is consistent with the low levels of carbohydrate reserves observed (Thompson and MacDonald, 1990). Like *Mytilus edulis* and *Placopecten magellanicus* in Newfoundland waters (Thompson, 1984a; MacDonald and Thompson, 1986), gametogenesis in *Modiolus modiolus* occurs during spring and early summer and is mainly supported by the food available at that time, with no contribution from reserves from the previous year.

In the gonad of *Modiolus modiolus* from Logy Bay, high lipid levels were observed only after the first two years of the study, suggesting that not enough energy reserves may have accumulated from the fall of 1986 to the fall of 1987 to allow gonad maturation. This may account for the irregular spawning behaviour. In Logy Bay, *Modiolus modiolus* may compensate for nutritive stress induced by poor food conditions for much of the year by prolonging the period over which energy reserves are accumulated, rather than by a reduction in both fecundity and egg quality as has been reported for other marine invertebrates (Gabbott, 1976; Bayne et al., 1979; Gabbott, 1983; Thompson, 1983). However, this strategy of *Modiolus modiolus* would lead to reduced fecundity in the long term, if not in the year that spawning takes place.

The results obtained for *Modiolus modiolus* over a period of two years support the hypothesis postulated in the present study, namely that the physiological processes as well as the biochemical storage cycles are governed primarily by food availability and to a lesser extent by the temperature cycle.

V. CONCLUSIONS

1. The suspended particulate matter load (seston) in Logy Bay is lower than in many large shallow marine bays, owing partly to a negligible terrigenous input to this environment, where the quantity of the particulate matter (POM) primarily depends upon phytoplankton productivity. The composition of the POM is different at various times of the year and this is evident from the ratio chl *a*:phaeopigments. This ratio is high during the phytoplankton bloom, owing to the living nature of the POM at this time, compared with the rest of the year, where lower values are associated with the highly degraded suspended material. This is also reflected in the seasonal fluctuation of the nutritive components of the seston which was mainly governed by the cycle of the phytoplankton. Food material (protein, carbohydrate and lipid) occurs at maximum concentrations during spring-summer, whereas minimal levels are recorded in the winter months.

2. The nutritional quality of the seston may be expressed by a food index calculated on the base of the ratio of food material (protein+carbohydrate+lipid) to total seston. This index follows the cycle of the phytoplankton bloom, the main peaks occurring during the spring-summer with values as high as 55%, whereas lower values (10%) are common during winter.

3. The size-frequency distribution of the seston of Logy Bay is highly dependent on the biological and physical conditions prevailing at a given time of the year, such as productivity cycles, kelp fragmentation, erosion, storms and bottom resuspension.

4. *Modiolus modiolus* shows its lowest and most variable feeding activity during fall and winter, which seems to be associated more with the low nutritive value of the food rather than low temperature. This intermittent behaviour shown by *Modiolus modiolus* may represent an adaptive mechanism to conserve energy by reducing the time spent filtering seston of low nutritive value.

5. *Modiolus modiolus* produces large amounts of pseudofaeces during the phytoplankton bloom, which is related to the size of the particles (large diatoms, long chains of diatoms) and not to the particle concentration in Logy Bay.

6. Absorption efficiency is high in *Modiolus modiolus*, which is probably attributable to the low particle loads (usually below 2.0 $mg.l^{-1}$) and high food quality in Logy Bay. The horse mussel may compensate for this low food concentration by increasing the gut residence time, resulting in a higher absorption efficiency.

7. Physiological processes, such as VO_2 and VNH_4-N, show clear seasonal patterns which are related to the food supply, the temperature and the gametogenic condition of the mussels.

The negative scope for growth (SFG) and net growth efficiency (K_2) observed during summer in *Modiolus modiolus* are associated with a high metabolic rate and low quality of the food supply. Conversely, higher values of SFG and K_2 result from a low metabolic rate and an energy-rich food supply provided by the phytoplankton bloom. The data support the contention that SFG and K_2 are more dependent on food availability than on temperature, suggesting that these two indices would be independent of season if enough food were available to the organism.

8. An alternative method of measuring absorption efficiency in filter-feeders was tested. The method utilizes biogenic silica as a non-absorbable indicator. A comparison with the ash-ratio technique for horse mussels feeding on natural seston demonstrated good agreement over a wide range of silica concentrations (20-240 μg silica.mg^{-1} food). Thus the ash-ratio technique was validated as a convenient method for measuring absorption efficiency in filter-feeding organisms under natural food conditions.

9. The biodeposition rate (faeces+pseudofaeces) by *Modiolus modiolus* is highly correlated with the phytoplankton bloom, largely because this species produces pseudofaeces only during the bloom of large diatoms and because faecal production is greater at this time. Thus the horse mussel removes particles over a wide spectrum and recycles nutrients through the biodeposits, which contain a large amount of nutritive material and serve as a substantial energy source for suspension and deposit feeders. *Modiolus modiolus* showed a preferential ingestion of organic carbon and nitrogen during the phytoplankton bloom. These results were contradictory to those obtained for chlorophyll *a,* suggesting that the higher concentration of chlorophyll *a* in the pseudofaeces may reflect different chlorophyll *a* to C and chlorophyll *a* to N ratios for the large algal species which make up the pseudofaeces, compared with those which are ingested.

10. *Modiolus modiolus* increases considerably its tissue weight as well as protein, lipid and carbohydrate during spring and early summer as a result of the phytoplankton bloom. Thus the growth, gonad production and biochemical composition cycle of the horse mussel are determined more by food availability than by temperature, since the temperature is approximately 0°C during the phytoplankton bloom.

11. The success of a filter-feeder in maximizing its energy gain will depend on the physiological plasticity which it can show in a given environment. *Modiolus*

modiolus is a species which is able to compensate physiologically for the poor food conditions occurring in Logy Bay during large part of the year. It does this by reducing the time spent filtering during fall and winter, when there is a poor food supply in Logy Bay. Conversely, higher values for clearance rate are registered during spring and early summer, when the seston is mainly composed of phytoplankton. Furthermore, *Modiolus modiolus* compensates for the low seston concentration by increasing absorption efficiency. Such physiological compensations minimise the reduced periods during which scope for growth is negative, and enable the horse mussel to survive in an environment characterised by an intermittent and often inadequate food supply.

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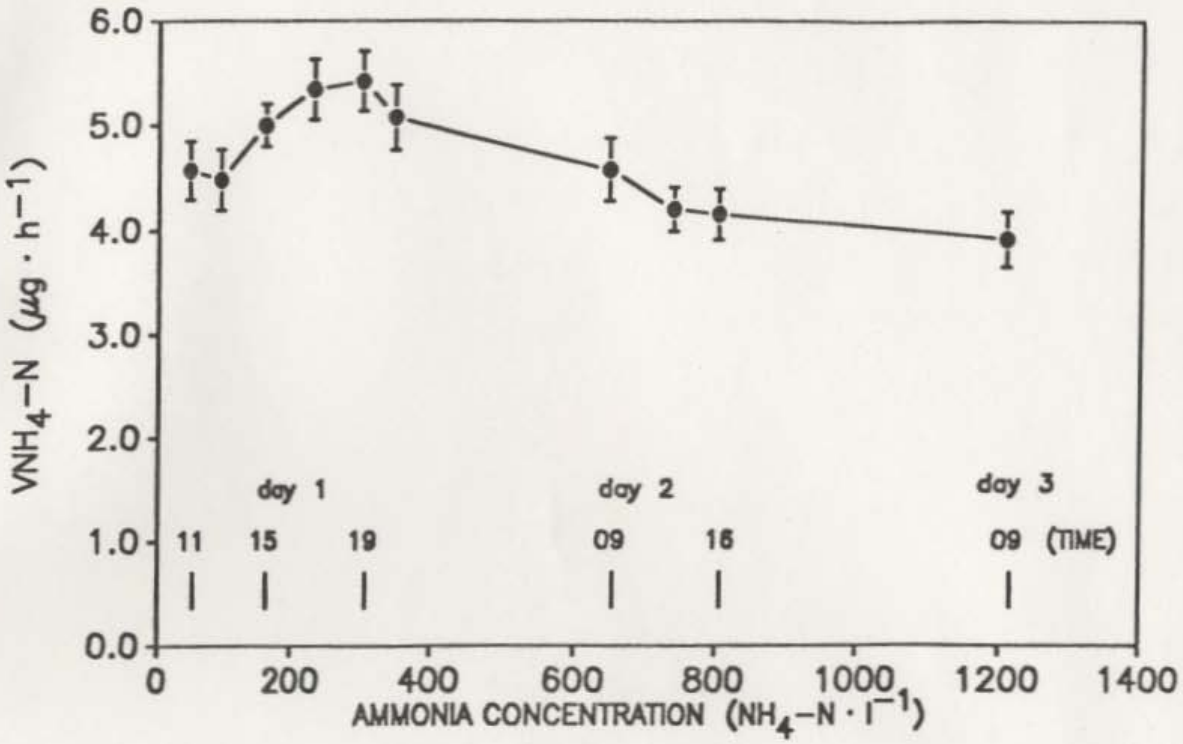
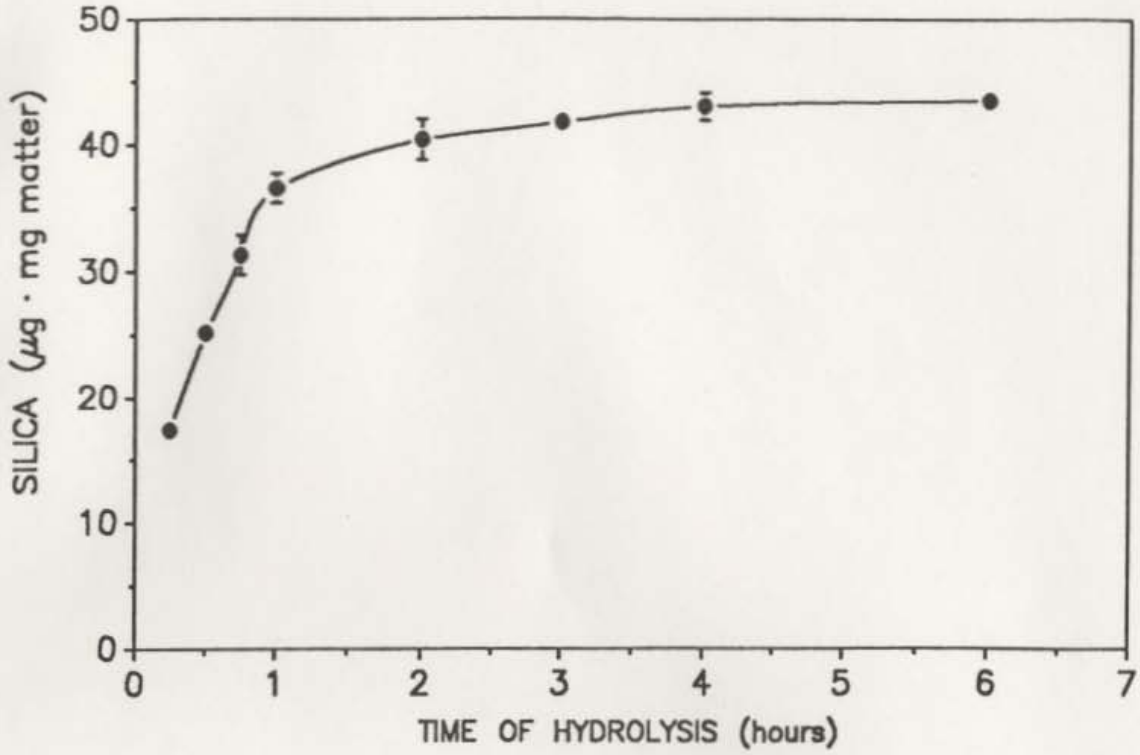
VII. APPENDICES



Appendix I. Evidence that the NH_4-N excretion rate in *Modiolus modiolus* is independent of the ammonia concentration in the experimental chambers for at least 20 hours.



Appendix II. Time course for the extraction of silica under the conditions described in the text (Material and Methods). Hydrolysis is complete within three hours.