THE INFLUENCE OF ENVIRONMENTAL FACTORS UPON THE GROWTH AND SURVIVAL OF THE PACIFIC OYSTER, *CRASSOSTREA GIGAS* THUNBERG

by

James R. Brown

B.Sc., McGill University, 1978

THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE
in the Department
of
Biological Sciences

SIMON FRASER UNIVERSITY

September 1986

Approval

Name: **James R. Brown**

Degree: Master of Science

Title of Thesis:

The influence of environmental factors upon the growth and survival of the Pacific Oyster, *Crassostrea gigas* Thunberg

Examining Committee:

Chairman:

Dr. B. Hartwick, Associate Professor, Senior Supervisor

Dr. A. Harestad, Assistant Professor

Dr. C. Levings, Research Scientist, Fisheries and Oceans

Dr. A. Chambers, Associate Professor, Faculty of Forestry U.B.C.

Dr. N. Bourne, Research Scientist, Pacific Biological Station

Date Approved Oct. 22/86

PARTIAL COPYRIGHT LICENSE

I hereby grant to Simon Fraser University the right to lend my thesis, project or extended essay (the title of which is shown below) to users of the Simon Fraser University Library, and to make partial or single copies only for such users or in response to a request from the library of any other university, or other educational institution, on its own behalf or for one of its users. I further agree that permission for multiple copying of this work for scholarly purposes may be granted by me or the Dean of Graduate Studies. It is understood that copying or publication of this work for financial gain shall not be allowed without my written permission.

Title of Thesis/Project/Extended Essay

The influence of environmental factors upon the growth and survival

of the Pacific Oyster, *Crassostrea gigas* Thunberg

Author:

(signature)

James R. Brown

(name)

OCT 24 [illegible]6

(date)

ABSTRACT

To determine the influence of environmental factors upon growth and survival of the Pacific oyster, *Crassostrea gigas* Thunberg, oysters from a common broodstock were transplanted to ten locations along the coast of British Columbia. The growth and survival of two age classes of oysters and the conditions of several environmental factors were monitored on a monthly basis from June 1984 to August 1985.

Using analysis of polynomials fitted to shell height data, the sites were categorized into high, medium and low growth groups. In areas with salinity, water temperature and available food conditions which were highly suitable to the oyster, high growth of shell weight, shell height and dry meat weight were observed. At sites with lower food concentrations, shell height and body tissue growth was significantly reduced while shell weight growth was equivalent to that of the high growth sites. Growth of all body parameters was lowest in areas with low salinity levels and widely fluctuating levels of available food.

The dry meat weight: shell weight ratio was similar for oysters at the high and low growth sites but much lower for oysters at the medium growth sites. The effect of this relationship upon two commonly used condition indices is discussed.

Through discriminant analysis, monthly levels of salinity and $\log_e$ particulate organic matter were found to best distinguish between sites in different growth categories. In multiple regression analysis, site-specific monthly instantaneous growth rates were correlated to water temperature and chlorophyll *b* concentrations.

From the literature, information on oyster-environmental interactions was used to develop a Habitat Suitability Index (HSI) model to evaluate the suitability of coastal areas for oyster culture. In the model, the effects of abiotic and biotic factors upon oyster growth and survival were quantified through the use of a relative index.

The performance of the model was evaluated using the data collected from the 10 field sites. Site-specific HSI values were found to be significantly correlated to the growth and secondary production of both year classes of oysters. Some precautions in the application of the model were discussed in view of the significant influence of seasonal variations in water temperature and food concentrations upon the output of the model.

DEDICATION

To Rose and Reema

ACKNOWLEDGEMENTS

I would like to thank my supervisor, E.B. Hartwick, for his support and encouragement during this thesis. As members of my supervisory committee, A. Chambers (UBC), A. Harestad and C. Levings (DFO West Vancouver) provided very useful advice. N. Bourne of the Pacific Biological Station kindly consented to be External Examiner. His review of the initial HSI model along with those of D.B. Quayle and F.R. Bernard of PBS and E.W. Cake of the Gulf Coast Research Laboratory, was greatly appreciated and contributed to its further refinement. W. Krane of the Dept. of Psychology at SFU was very forthcoming with statistical advice.

This research would not have been possible without the support and interest of the Marine Resources Section of the B.C. Ministry of Environment. G. Chislett took an earlier interest in this project and was instrumental in the arrangement of support from MOE. A special note of appreciation is extended to W. Roland of MRS for providing many useful discussions regarding this project and who, along with I. Sutherland, was responsible for a significant portion of the data collection and sample analyses. The work of L. Wells resulted in the fine map of the study sites. The assistance of two other MRS staffers, K. Albrecht and T. Pobran, is also gratefully acknowledged.

This project was supported by a GREAT Award from B.C. Science Council, a grant from MOE and a NSERC grant to E.B.

Hartwick.

P. Irvine was very helpful in lending the support of the B.C. Oyster Growers Association. I would like to extend my gratitude to the following individuals for the use of various oyster leases and waterfront property; D. Biford (Pacific Aqua Foods), N. Bourne (PBS), W. Franke, C. Levings (DFO West Vancouver Laboratory), M. Mullins, R. North, L. Tulloch, S. Wilmot and G. Whyte.

Field work in Lemmens Inlet would not have been feasible nor as enjoyable without the hospitality of the McLorie family of Tofino. C. Usselman, W. McLorie, F. McLorie and R. Obeid worked especially hard but with enthusiasm in the field and the laboratory. At various times, several undergraduate and secondary students, worked on the project and made a considerable contribution to the end product. They were E. Dupliess, A. Gay, H. Hartwick, J. McLorie, L. Nikl, A. Hammon and M. Tammi.

Constructive discussions and good friendship were provided by R. Ambrose, D. Fyfe, F. Juanes, B. Layton, P. Ryall and M. Stanhope. The best in the future to all of them.

The time spent on this project was alternatively filled with frustration and gratification. I was sustained through it all by the love, patience and understanding of my wife, Rose. My daughter Reema also intelligently discussed my thesis with me and provided often needed comic relief.

TABLE OF CONTENTS

Approval ii

Abstract iii

Dedication v

Acknowledgements vi

List of Tables x

List of Figures xii

Introduction 1

I. Site Related Variations in the Growth and Survival of the Pacific Oyster, *Crassostrea gigas* 7

  Introduction 7

  Methods 9

  Results 14

  Discussion 33

II. The Effect of Site Upon the Relationship Between Growth and Condition in the Pacific Oyster *Crassostrea gigas* .. 42

  Introduction 42

  Methods 44

  Results 46

  Discussion 51

III. Multivariate Analyses of the Influence of Environmental Factors Upon the Growth of the Pacific Oyster, *Crassostrea gigas* 54

  Introduction 54

  Methods 56

  Results 60

  Discussion 68

IV. A Habitat Suitability Index Model for the Culture of the Pacific Oyster 79

Introduction 79

Methods 84

Results 88

Discussion 102

General Discussion 108

Appendix A 113

Literature Cited 136

LIST OF TABLES

Table Page

1.1 Survival rates of Year 0 and Year 1 oysters over 14 months 24

1.2 Day-degree, salinity and chlorophyll *a* 28

2.1 Correlations between VCI and DWCI 50

3.1 Results of discriminant analysis 62

3.2 Multiple regression equations of monthly instantaneous growth rates predicted by environmental factors and oyster initial size 67

4.1 Variables and assumptions utilized in the formulation of the model 89

4.2 Life Requisite Suitability Index (LRSI) and Habitat Suitability Index (HSI) equations 91

4.3 Production estimates for both age classes 95

4.4 Summary of data used for HSI model validation 97

4.5 Summary of correlations between HSI values and shell growth 100

A.1 Regression parameters fitted to Year 0 shell height data 114

A.2 Regression parameters fitted to Year 1 shell height data 115

A.3 Regression parameters fitted to Year 1 whole weight data 116

A.4 Regression parameters fitted to Year 1 shell weight data 117

A.5 Summary of comparisons of regression coefficients fitted to Year 0 shell height data 118

A.6 Summary of comparisons of regression coefficients fitted to Year 1 shell height data 119

A.7 Summary of comparisons of regression coefficients fitted to Year 1 whole weight data 120

A.8 Summary of comparisons of regression coefficients fitted to Year 1 shell weight data 121

A.9 Regression parameters fitted to Year 1 dry meat weight data for 1984 122

A.10 Summary of comparisons of regression coefficients fitted to Year 1 dry meat weight data for 1984 123

A.11 Regression parameters fitted to Year 1 dry meat weight data for 1985 124

A.12 Summary of comparisons of regression coefficients fitted to Year 1 dry meat weight data for 1985 125

A.13 Parameters for shell weight vs dry meat weight regressions 126

A.14 Summary of comparisons of coefficients fitted to shell weight vs dry meat weight regressions 127

A.15 Parameters for shell height vs dry meat weight regressions 135

LIST OF FIGURES

Figure Page

1.1 Location of the study sites 10

1.2 Shell height growth Year 0 16

1.3 Shell height growth Year 1 17

1.4 Whole weight growth Year 1 19

1.5 Shell weight growth Year 1 20

1.6 Dry meat weight growth Year 1 21

1.7 Mean monthly water temperatures 26

1.8 Mean monthly salinity 29

1.9 Monthly mean chlorophyll *a* concentrations 31

2.1 Volumetric condition index values 47

2.2 Dry weight condition index values 48

3.1 Plot of discriminant function 63

3.2 Instantaneous growth rates for Year 0 oysters 65

3.3 Instantaneous growth rates for Year 1 oysters 66

3.4 Fraction of Total Particulate Matter (TPM) which is Particulate Organic Matter (POM) 75

3.5 Percentage of TPM which consists of phytoplankton organic matter (FOOD). 77

4.1 Suitability Index graphs 90

4.2 HSI values vs shell growth and production 99

4.3 HSI values from Spr85 data vs Year 0 shell growth 101

A.1 Monthly mean secchi depth 128

A.2 Monthly mean dissolved oxygen levels 129

A.3 Monthly mean chlorophyll *b* concentrations 130

A.4 Monthly mean chlorophyll *c* concentrations 131

A.5 Monthly mean carotenoids concentrations 132

A.6 Monthly mean POM levels 133

A.7 Monthly mean PIM levels 134

INTRODUCTION

There are 36 species of oysters distributed worldwide several of which are of considerable economic and ecological importance (Harry 1985). The American oyster, *Crassostrea virginica* Gmelin, is the basis of an extensive fishery along the east coast of the United States and the Gulf of Mexico (Galtsoff 1964, MacKenize 1983). Oyster reefs have been shown to be significant factors in the energetics of estuarine systems (Dame et al. 1984).

The closely related Japanese or Pacific oyster, *C. gigas* Thunberg, is extensively cultivated in Japan and Korea (Mann 1979a). The rapid growth, high meat yield and relative robustness of this species has lead to its introduction in many different parts of the world for the purpose of aquaculture (Bourne 1979). Although there is a native oyster, *Ostrea lurida* Carpenter, as well as a few small aggregations of American oysters, only the Pacific oyster is commercially cultivated in British Columbia (B.C.).

A considerable amount of the information concerning the ecology and biology of the Pacific oyster in B.C. waters as well as cultivation techniques were the result of work done by Quayle (1951, 1969, 1971). The first importations of Pacific oyster seed from Japan occurred in 1912 or 1913. The oyster grows well in local waters although maximum water temperatures are generally too low (< 20 °C) to initiate spawning activity. In certain bays and inlets, such as Pendrell Sound, water temperatures are high enough to result in fairly regular annual spawning events. Every few years, water temperatures throughout the Strait of Georgia are suitable for spawning and larval survival which has resulted in the distribution of oysters throughout the Strait. In addition, oysters were introduced and became self-sustaining populations in a few locations on the west coast of Vancouver Island. The availability of an abundant wild stock of oyster seed and high transportation costs lead to the discontinuation of oyster seed imports from Japan by 1961. Currently, the industry relies upon seed collected from areas of naturally occurring spat-fall or hatchery sources (Quayle 1969, Jones and Jones 1983).

Oysters are cultivated either by spreading oyster seed over intertidal mudflats or by subtidal suspended culture using trays or longlines. Intertidal stake culture has been attempted in local waters but has generally been proven to be uneconomical (Clayton and Pobran 1981).

In 1984, the industry produced 264,100 l of oyster meat, worth approximately $ 1.6 million (B.C. Min. of Agriculture and Food 1986). Although the economic contribution of the oyster industry to the overall provincial economy is small, both oyster and finfish aquaculture appear to entering a phase of accelerated growth. By 1995, the value of oyster production will exceed $ 4.5 million according to the B.C. Ministry of Agriculture and Food (1986). Since the availability of suitable sites for intertidal culture is limited, any further increases in oyster production must come from either more efficient use of existing on-bottom culture areas or expansion of subtidal lease holdings (W. Roland, B.C. Min. of Environment, Victoria, B.C. personal communication).

The initial, and perhaps most crucial, step in establishing a viable aquaculture operation is the selection of a site which has suitable biophysical and economic characteristics. Of further concern to both the aquaculture industry and coastal management agencies, is the long term protection of the environmental quality of culture areas. The tourism and forestry industries, as well as urban developments, require the type of sheltered coastal areas which are essential to the aquaculture industry. The potential for conflicts between aquaculture and other users of coastal resources, could be reduced through the establishment of protected areas which would be reserved for aquaculture. The many unexploited fjords in B.C. waters makes the aquaculture reserve a viable option.

A basic requirement which emerges for either the siting of oyster culture operations or the establishment of aquaculture reserves is the ability to make meaningful comparisons about the aquaculture potential of unexploited coastal areas. The development of a methodology to evaluate the biophysical suitability of a coastal area for oyster culture is the primary purpose of this thesis.

Oyster seed is collected from a number of specific sources and permanent culture operations in most areas which have regular spat-fall is prohibited by provincial law. The evaluation of oyster culture areas, therefore, should be based upon the criteria of growth and survival since the introduction of juvenile oysters is largely controlled by the grower.

The growth and survival of any organism in the natural environment are functions of multiple factors. The primary environmental factors which influence bivalve production are water temperature (Kirby-Smith and Barber 1974, Mann and Ryther 1977, Bernard 1983), food concentration (Malouf and Breese 1977, Tenore and Dunstan 1978), salinity (Bernard 1983) and water movement (Walne 1972). Particulate inorganic matter (Loosanoff and Tombers 1948, Vahl 1980), dissolved oxygen (Mitchell 1912, Davis 1975) and pH (Carriker 1959) are additional factors which may have an effect upon growth and survival. Predators (Woelke 1959, Quayle 1969), fouling organisms (Quayle 1969, Michael and Chew 1976) and disease (Sindermann 1984) are also important in aquaculture.

The influence of environmental factors upon production in bivalves have been analyzed in the past using multivariate techniques (Ulanowicz et al. 1980, 1982, Appeldoorn 1983). Such techniques have not been applied to the Pacific oyster and the relationships between oyster production and environmental conditions have not been well studied. Westley (1965) reorded several oceanographic variables and the condition of oysters collected from indigenous populations in five oyster culture areas in the state of Washington. Growth and survival were not determined, however, and the data were not analyzed using multivariate techniques.

Although a multivariate statistical analysis can reveal underlying relationships between the dependent and independent variables, it is not a practical approach towards the formulation of a workable site evaluation methodology. The major drawbacks are the difficulty non-statisticians would have interpreting the results and the inability of statistical models to account for non-linear responses of the oyster to environmental factors (without resorting to complex modelling functions).

In this thesis, the approach taken to develop a site evaluation methodology was to adapt an existing habitat classification system which has significant management applications. The Habitat Suitability Index (HSI) was developed by the U.S. Fish and Wildlife Service (UNFWS) in order to document the quantity and quality of habitat available to a species (USFWS 1980, 1981). HSI models exist for many aquatic and terrestrial species but the model presented in Chapter IV, is the first one developed for the Pacific oyster and represents the initial application of HSI methodology to aquaculture. Furthermore, the field validation of the model is one of the most extensive of any HSI model. It is the first validation to utilize data on growth and survival rather than population densities.

For any model, it is essential that testing be conducted with data excluded from the initial model formulation. In this respect, the chapter sequence is the reverse of the actual chronology of events. The HSI model was formulated utilizing information which exists in the literature. Thus the model can be considered to be a hypothesis about the relationship between the environment and oyster production which was subsequently tested with field data. The HSI model and the field validation are presented in Chapter IV.

The contents of Chapters I - III are based upon further analyses of data collected in the field validation study. Chapter I deals with variations in the survival and absolute and allometric growth of oysters cultivated in different areas. The observed discrepencies in two widely used indices of oyster condition are discussed in Chapter II. In Chapter III the influence of several environmental factors upon oyster growth is analyzed through the use of multivariate statistics.

CHAPTER I

SITE RELATED VARIATIONS IN THE GROWTH AND SURVIVAL OF THE PACIFIC OYSTER, *Crassostrea gigas*

Introduction

Bivalve production in an aquaculture operation is determined by a combination of genetic and environmental factors. Experiments involving reciprocal transfers of stocks indicate that mortality in some bivalves is largely determined by genetic factors while growth is significantly influenced by ambient environmental conditions (Mallet and Haley 1983, Dickie et al. 1984, Widdows et al. 1984). Site related differences in the growth of body parameters may be expressed in terms of absolute increases or variation in allometric relationships (Dame 1972a, Seed 1973, MacDonald and Thompson 1985, Aldrich and Crowley 1986).

The Pacific oyster, *Crassostrea gigas* Thunberg, is widely cultured in many parts of the world (Quayle 1969, Aguis et al. 1978, Spencer et al 1978, Bourne 1979, Sumner 1980, Burrell 1985). An exotic species, the Pacific oyster grows well in the coastal waters of British Columbia, Canada, although production can vary greatly between locations. Quayle (1971) reported marked variations in growth among 16 sites along the coast of British Columbia. In Washington State, Sparks and Chew (1959) and Woelke (1959a) noted considerable differences in growth rates among 3 and 5 sites respectively. As extensive as these field studies were, specific shortcomings were the lack of quantatitive analyses into absolute and allometric growth and the fact that local environmental conditions were not closely monitored.

Bivalve growth has been shown to be greatly influenced by water temperature and food concentration (Malouf and Breese 1977, Incze et al. 1980). Low salinity levels can also have a negative effect upon the growth and survival of *C. gigas* (Quayle 1969, Bernard 1983). Westley (1965) reported on the water temperature, salinity, nutrients phytoplankton biomass and primary productivity in 5 oyster culture areas in Washington State. The status of the oysters, however, was evaluated through the use of a static condition index (dry meat weight: shell weight) rather than by incremental changes in particular body parameters over time. Furthermore, some adaptation of oysters to ambient environmental conditions can not be ruled out since local populations were sampled.

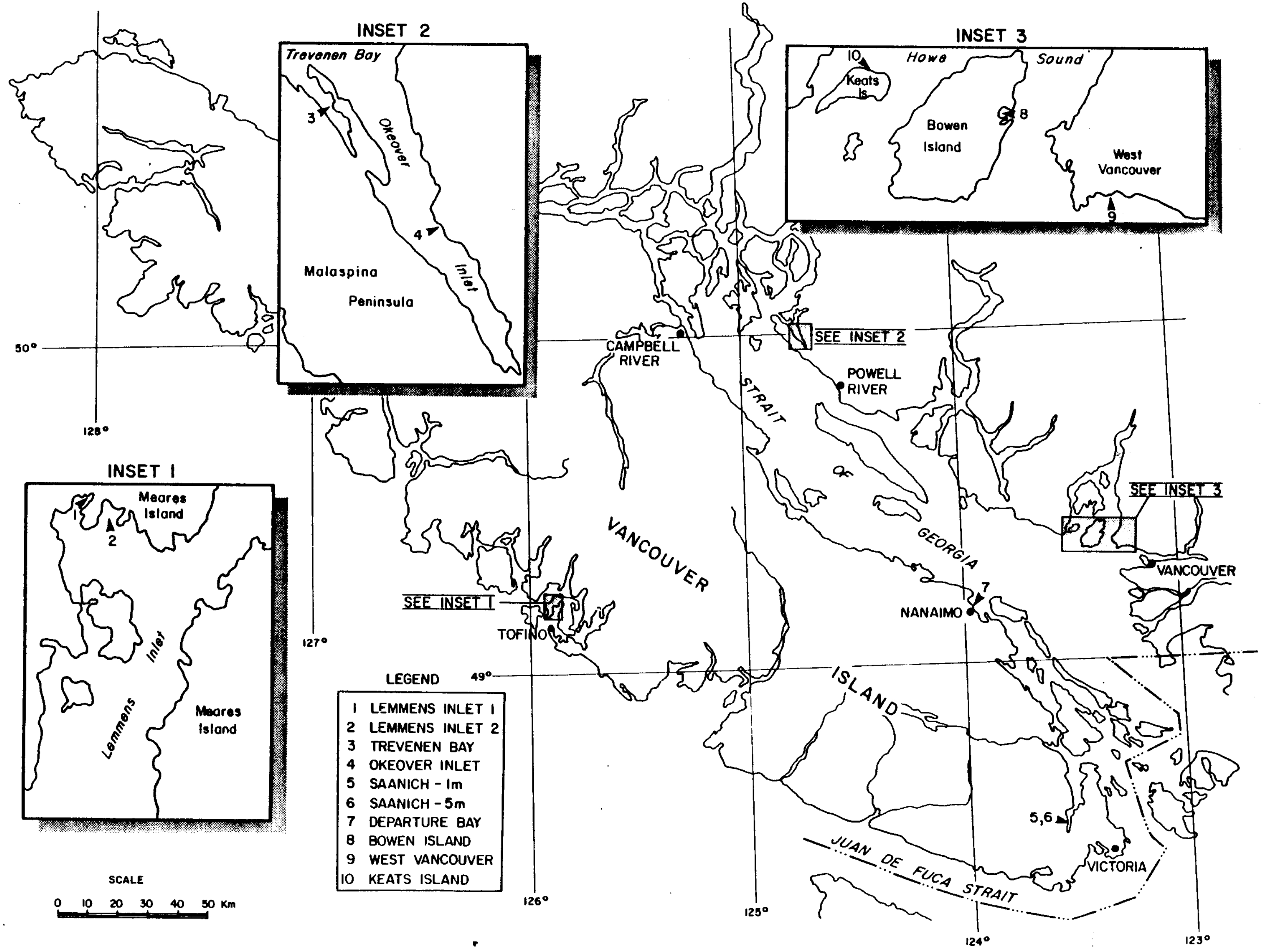
The present study examined patterns in absolute and allometric growth and survival of a common oyster broodstock grown subtidally in 10 coastal areas under different environmental conditions. Concurrently, water temperature, salinity and food concentrations were monitored in an attempt to relate variation in growth and survival to site conditions.

Methods

Ten sites along the coastline of mainland British Columbia and Vancouver Island were selected on the basis of obtaining a range of good to poor habitat conditions for oyster culture (Fig 1.1). The sites were Lemmens Inlet 1 (lat.49°12'55"N, long.125°53'03"W) and 2 (lat.49°12'38"N, long.125°53'28"W), Saanich Inlet 1 m and 5 m (lat.48°30'28"N, long.123°32'47"W), Departure Bay (lat.49°12'38"N, long.123°57'16"W), Bowen Island (lat.49°22'58"N, long.123°57'16"W), Keats Island (lat.49°24'30"N, long.123°26'36"W), West Vancouver (lat.49°20'22"N, long.123°13'53"W), Trevenen Bay (lat.50°01'21"N, long.123°44'15"W) and Okeover Inlet (lat.50°00'45"N, long.123°42'03"W). Sites were monitored monthly from June 1984 to August 1985, except during January 1985.

At each site, two age classes of cultchless oysters from the same seed-stock (purchased from Redonda Sea Farms Ltd., Vancouver, B.C.) were placed in 5 tier lantern nets (30 cm d x 1 m). The ages of the oysters in June 1984 were designated as 0 year old (20 - 30 mm shell height) and 1 year old (40 - 50 mm shell height). Age classes will be subsequently referred to as Year 0 and Year 1. Approximately 160 - 170 oysters were spread evenly among the tiers of the net in order to minimize the effects of density upon growth. All the nets were attached to floating platforms and, except for Saanich 5 m, the tops of the nets remained at 1 m below the surface throughout a tidal cycle.

Fig. 1.1. Location of the study sites.


INSET 1
Meares Island
Lemmens Inlet
Meares Island
1
2
INSET 2
Trevenen Bay
Okeover Inlet
Malaspina Peninsula
3
4
INSET 3
Howe Sound
Keats Is.
Bowen Island
West Vancouver
10
8
9
SEE INSET 1
SEE INSET 2
SEE INSET 3
CAMPBELL RIVER
POWELL RIVER
TOFINO
NANAIMO
VANCOUVER
VICTORIA
VANCOUVER ISLAND
STRAIT OF GEORGIA
JUAN DE FUCA STRAIT
7
5,6
50°
49°
128°
127°
126°
125°
124°
123°
LEGEND
1 LEMMENS INLET 1
2 LEMMENS INLET 2
3 TREVENEN BAY
4 OKEOVER INLET
5 SAANICH - 1m
6 SAANICH - 5m
7 DEPARTURE BAY
8 BOWEN ISLAND
9 WEST VANCOUVER
10 KEATS ISLAND
SCALE
0 10 20 30 40 50 Km

Nets were cleaned or changed whenever the density of fouling organisms appeared to impede water circulation.

During each visit, shell heights of 20 randomly selected oysters from each age class, were measured with a vernier caliper (±0.5 mm). Shell height is the distance from the end of the umbo to the ventral shell margin (Galtsoff 1964). Sampling was stratified such that from each level of the net an equal number of oysters were randomly removed.

All shell remains of dead oysters were removed and the left or cupped valves counted. Mortalities which occurred within the first 28 days of the study were not included because the primary cause of death could be attributed to stress from handling rather than environmental effects.

destructive

From the monthly sample of 20 Year 1 oysters, 10 were randomly chosen for laboratory analyses. Oysters were returned to the laboratory within 12 h of collection and held in a circulating, filtered seawater system for no longer than 24 h prior to analysis. Whole oyster weight (±0.005 g) was determined after fouling organisms were removed and the outer shell surface was blotted dry with paper towels. Body tissue was then separated from the shell and weighed (±0.005 g) after drying the oyster meat at 60 °C to a constant weight (24 - 72 h). Shell valves were weighed (±0.005 g) after they were dried in air (20 - 22 °C) for 24 h.

Duplicate or triplicate samples of water temperature, salinity and phytoplankton biomass were taken in conjunction with the monthly oyster measurements. Duplicate samples were taken the same day approximately 2 - 4 h apart. Whenever possible, a subsequent sample was taken within the next 24 - 48 h. Water samples were taken about 5 m up-current of the oyster nets at a depth equivalent to the mid-point of the nets. Water temperature (±0.05 °C) and salinity (±0.05 ppt) were measured using a YSI Model 33 S-C-T meter which was periodically checked against readings from a mercury thermometer and refractrometer.

Determination of chlorophyll *a* pigments followed the technique of Strickland and Parsons (1982). Water samples collected with a 3 l Van Dorn bottle were passed through a 0.30 mm^2 mesh in order to remove zooplankton and large debris. The sample (0.5 - 1.0 l) was filtered in the field through a 47 mm d Millipore© AA filter. Approximately 1 - 2 ml of 1 % $MgCO_3$ solution was added to the final 100 ml of sample in order to inhibit the decomposition of the chlorophyll molecules. Filters were immediately frozen in darkness and were stored for no more than 1 wk before analysis. Chlorophyll pigments were extracted by dissolving the filters in 90 % acetone solution for 18 - 20 h at 4 °C. Aliquot extinction coefficients were determined by spectrophotometer and the concentration of chlorophyll *a* ($\mu g \cdot l^{-1}$) was calculated using the equation of Parsons and Strickland (Strickland and Parsons 1982).

Polynomial regressions were fitted to shell height data for both year classes and to $\log_{10}$ transformed whole, shell and body weight data for Year 1 oysters using BMDP program P5R. Shell height data were normally distributed without being transformed. Polynomial equations are comparable to existing growth model such as the Von Bertalanffy equation (MacDonald and Thompson 1985). The advantages of the polynomial equation over the Von Bertlanffy model are the relaxation of the requirement for asymptotic growth and its suitability for multiple comparisons because it is a linear model (Roff 1980).

In order to reduce the multicollinearity between regression coefficients, an $\bar{x}$-x transformation was used throughout (Neter et al. 1985). The order of the polynomial was determined by testing each coefficient ($\beta_0, \beta_1, \beta_2, \beta_3 \ldots \beta_m$) against the null hypothesis of $H_0:\beta_m=0$. If the null hypothesis was accepted, then growth was described by a polynomial of the order $m-1$.

Allometric growth in terms of body dry weight and shell weight were described by fitting to site-specific data the equation:

$$\log_{10}DWT = \log_{10} A + B \log_{10}SWT$$

where DWT is dry meat or body weight (g) and SWT is shell weight (g).

Pair-wise comparisons between similar coefficients were done for all possible combinations of sites. Zar (1984) stated that the possibility of making a Type I error increases when a two sample test is used for multiple comparisons. The Bonferroni approximation was used to compensate for this, which simply divides the significance level by *n*, thereby making the test more conservative (Neter et al. 1985).

Results

Growth

Growth of shell height and weights of the whole oyster and shell followed a general seasonal pattern of high growth rates in the summer of 1984 which gradually tapered off during the fall to no growth in the winter months. Growth rates began to increase again in February-March 1985 and continued to rise into the summer months.

Growth of shell height, whole and shell weights were described by cubic polynomials (Tables A.1-4), with the exception of Year 1 shell height data from Bowen Island and whole weight data from West Vancouver where simple linear regressions (β_0,β_1) best described growth. For comparative purposes, cubic polynomials were fitted to these data, although according to the statistical method used the presence of only two coefficients would already indicate a significant difference in growth.

An examination of the regression coefficients revealed that variation in growth between sites could best be determined by comparing β_0. Since a $\bar{x}$-x transformation was used, this coefficient would be the value of y when $x=\bar{x}$. Subsequent differences were also found in comparisons of β_1 and β_2 coefficients while comparisons between β_3 coefficients were non-significant.

Shell height growth was highly variable between sites for both year classes. Final mean sizes in August 1985 for Year 0 oysters ranged from 100.2 mm at Okeover Inlet to 56.6 mm at West Vancouver (Fig. 1.2). The nets which held Year 0 oysters at Keats Island were lost 3 months into the study due to a storm. For Year 1 oysters, mean shell height at the termination of the study ranged from 108.5 mm at Okeover Inlet to 68.9 mm at West Vancouver (Fig. 1.3). In terms of shell height growth for either year class, the 10 sites could categorized into one of three groups. Within each group, the differences in growth between sites are non-significant but between groups the differences are significant (Table A.5-6). The high growth group consists of Trevenen Bay, Okeover Inlet, Lemmens Inlet 1 and 2. The growth at Departure Bay, Bowen Island, Saanich 1 m and 5 m was significantly less than that observed at the four previously mentioned sites and comprised the medium growth group. The final group consisted of Keats Island (Year 1 only) and West Vancouver which had the lowest recorded shell height growth.

These groupings were not consistent for Year 1 whole and shell weight data. By August 1985, final whole weights ranged from 139.00 g at Okeover Inlet to 47.90 g at West Vancouver (Fig. 1.4). Growth of this size parameter was not significantly

Fig. 1.2. Shell height growth Year 0 oysters.

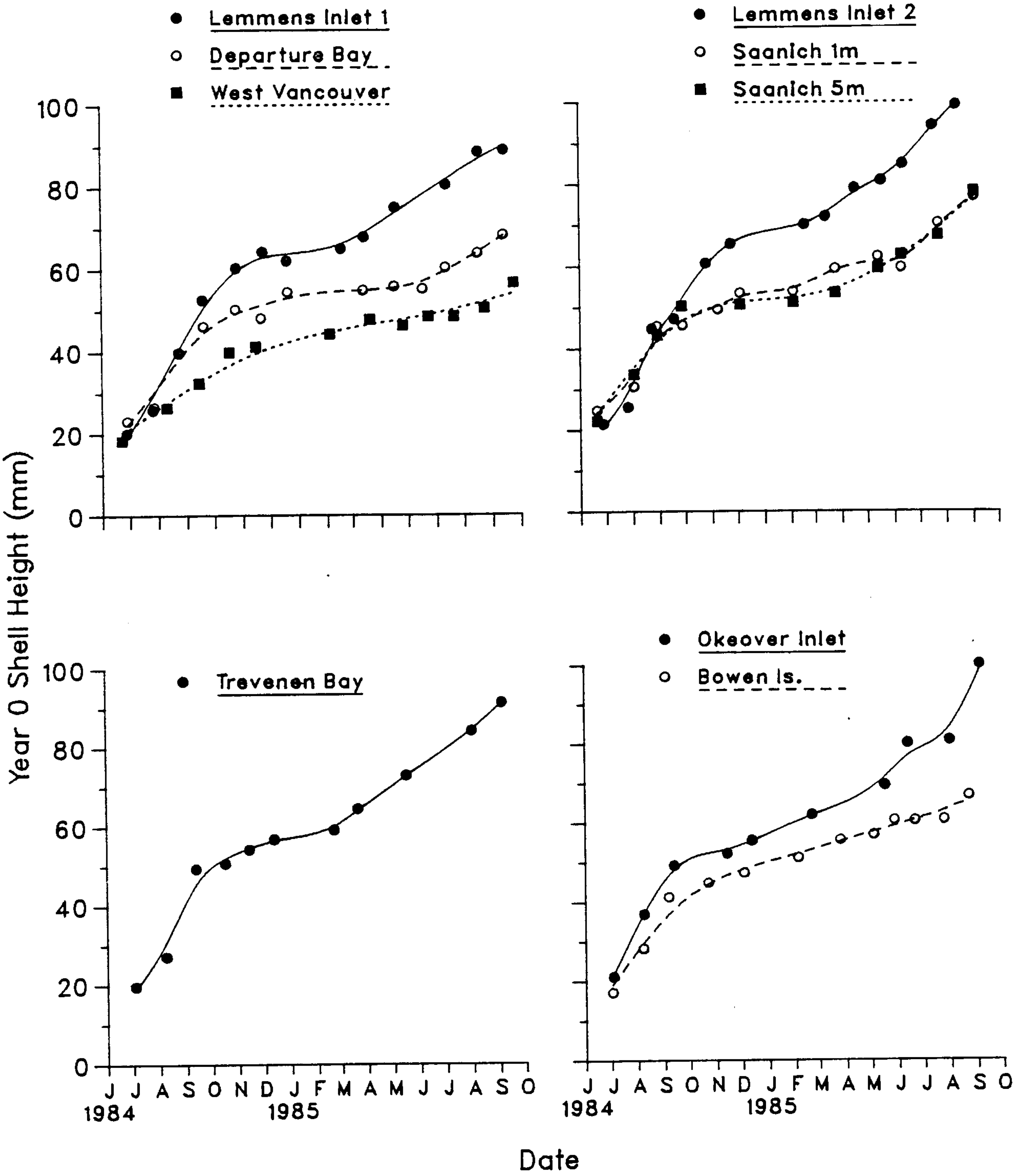
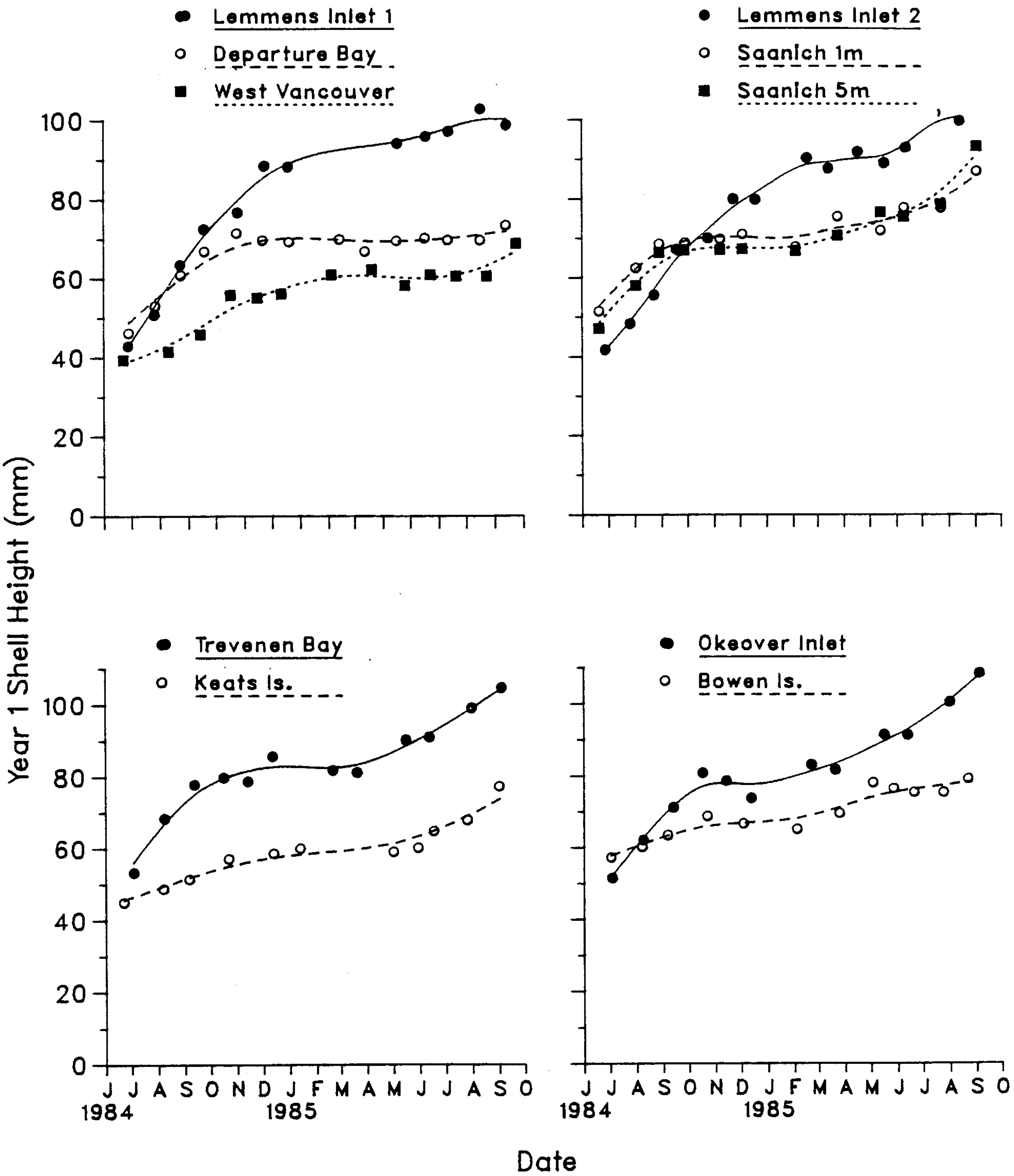

● Lemmens Inlet 1
○ Departure Bay
■ West Vancouver
● Lemmens Inlet 2
○ Saanich 1m
■ Saanich 5m
● Trevenen Bay
● Okeover Inlet
○ Bowen Is.
Year 0 Shell Height (mm)
0
20
40
60
80
100
J J A S O N D J F M A M J J A S O
1984
1985
Date

Fig. 1.3. Shell height growth Year 1 oysters.



● Lemmens Inlet 1
○ Departure Bay
■ West Vancouver
● Lemmens Inlet 2
○ Saanich 1m
■ Saanich 5m
● Trevenen Bay
○ Keats Is.
● Okeover Inlet
○ Bowen Is.
Year 1 Shell Height (mm)
0
20
40
60
80
100
J J A S O N D J F M A M J J A S O
1984
1985
Date

different between oysters at Trevenen Bay, Okeover Inlet, Lemmens Inlet 1 and 2, and Departure Bay (Table A.7). Growth at Saanich 1 m and 5 m were significantly different from all these sites, except for Departure Bay. Oyster growth at Bowen Island was similar to that observed at Saanich 1 m and 5 m but significantly less than that at Departure Bay. Whole weight growth were significantly lower at Keats Island and West Vancouver compared to the other 8 sites.

Mean shell weights in August 1985 ranged from 86.90 g at Okeover Inlet to 26.20 g at West Vancouver (Fig. 1.5). Trevenen Bay, Okeover Inlet, Lemmens Inlet 1 and 2 had similar shell weight growth (Table A.8). Growth at Departure Bay, Saanich 1 m and 5 m were significantly different from that observed at Trevenen Bay and Okeover Inlet but not from oysters at Lemmens Inlet 1 and 2. Bowen Island oyster growth was significantly less than all of the above mentioned sites but was higher than shell growth recorded at West Vancouver and Keats Island.

Oysters grown at Departure Bay, Saanich 1 m and 5 m had shells which were much shorter in height than those cultured at Trevenen Bay, Okeover Inlet, Lemmens Inlet 1 and 2. The equivalence in shell weight between these sites, however, indicates that oysters at Departure Bay, Saanich 1 m and 5 m had shells which were much thicker.

Body tissue weight data were partitioned into two periods, June-December 1984 and February-August 1985 (Fig. 1.6). These

Fig. 1.4. Whole weight growth Year 1 oysters.

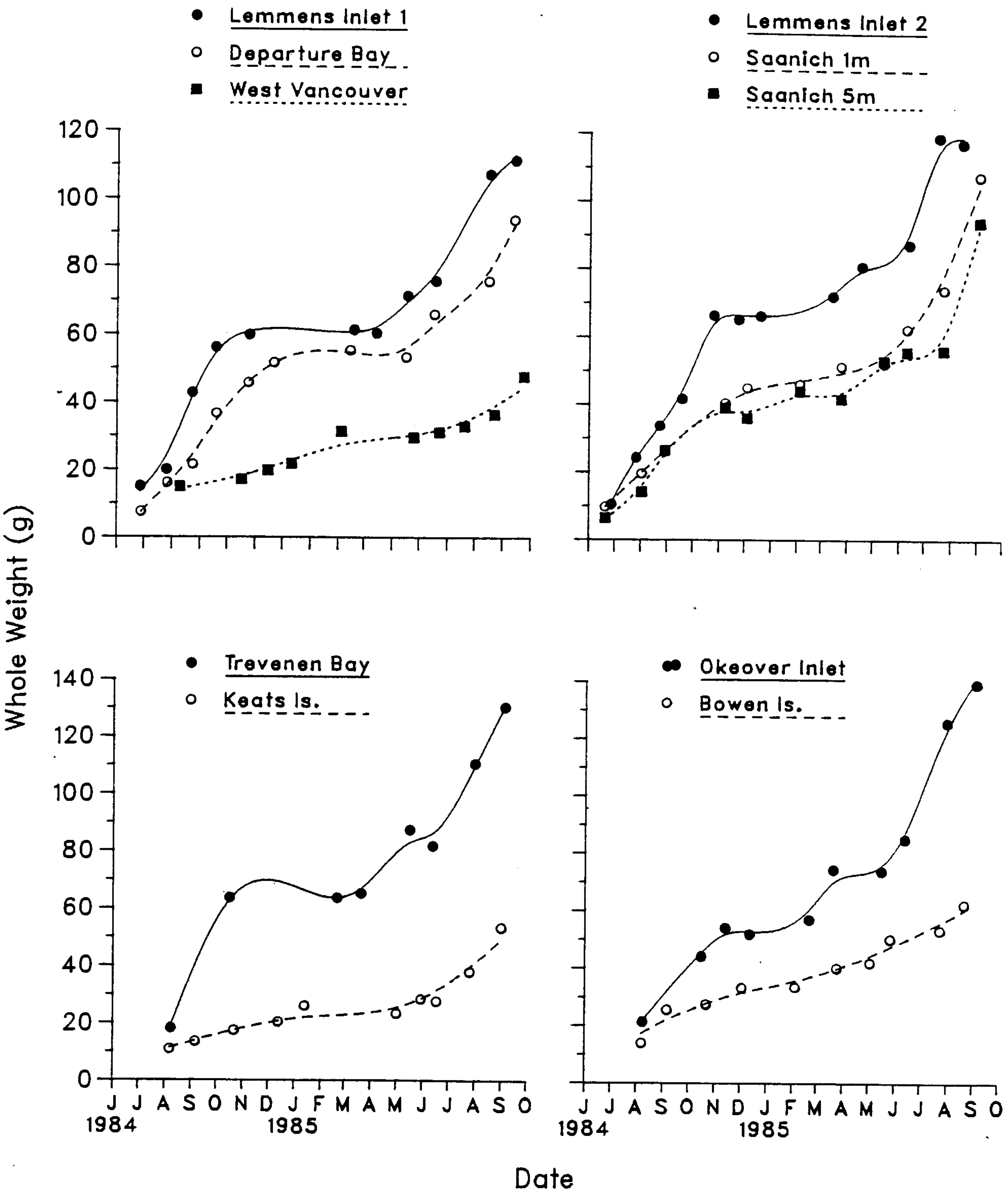
● Lemmens Inlet 1
○ Departure Bay
■ West Vancouver
● Lemmens Inlet 2
○ Saanich 1m
■ Saanich 5m
● Trevenen Bay
○ Keats Is.
● Okeover Inlet
○ Bowen Is.
Whole Weight (g)
0
20
40
60
80
100
120
140
J J A S O N D J F M A M J J A S O
1984
1985
Date

Fig. 1.5. Shell weight growth Year 1 oysters.

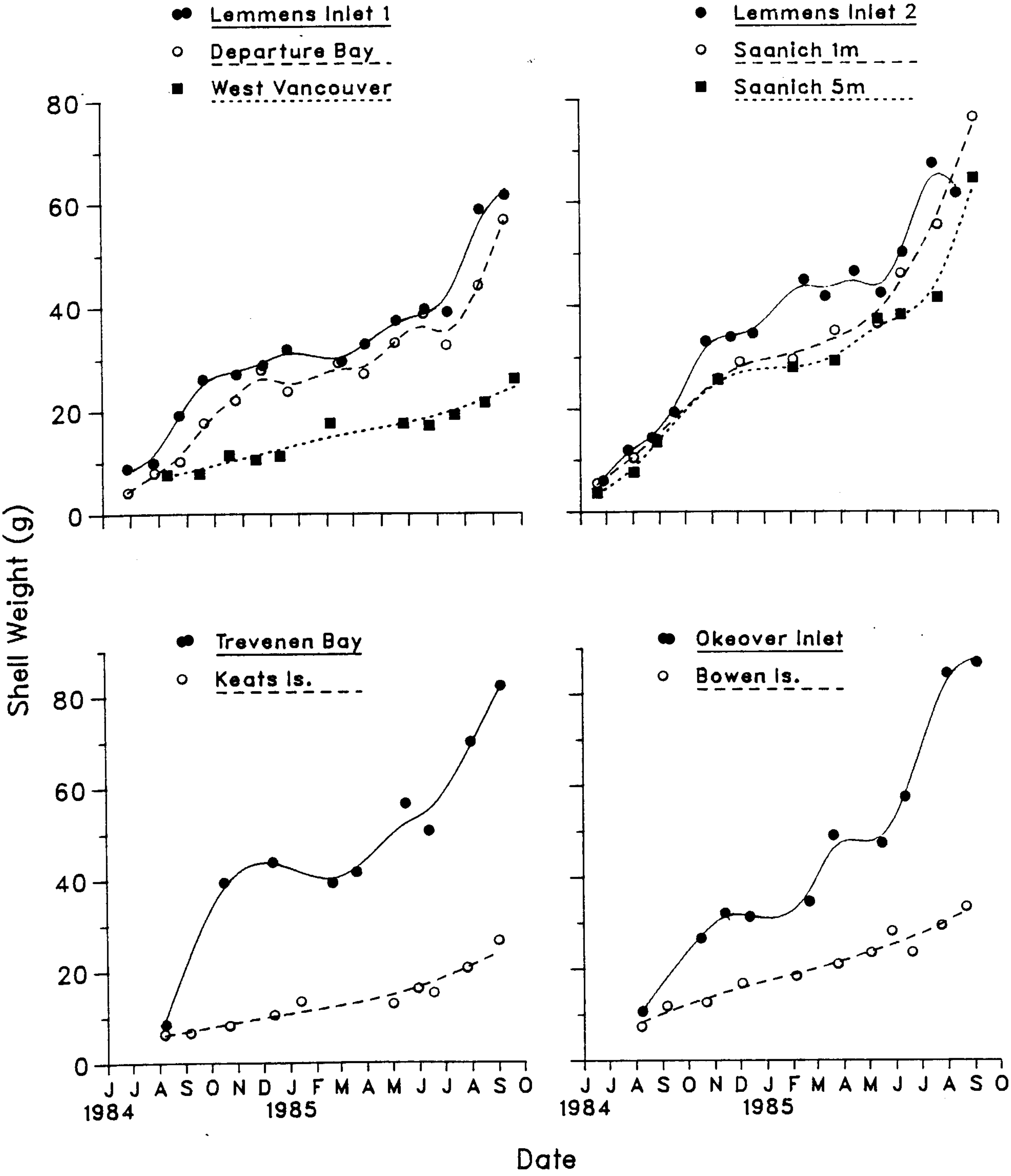
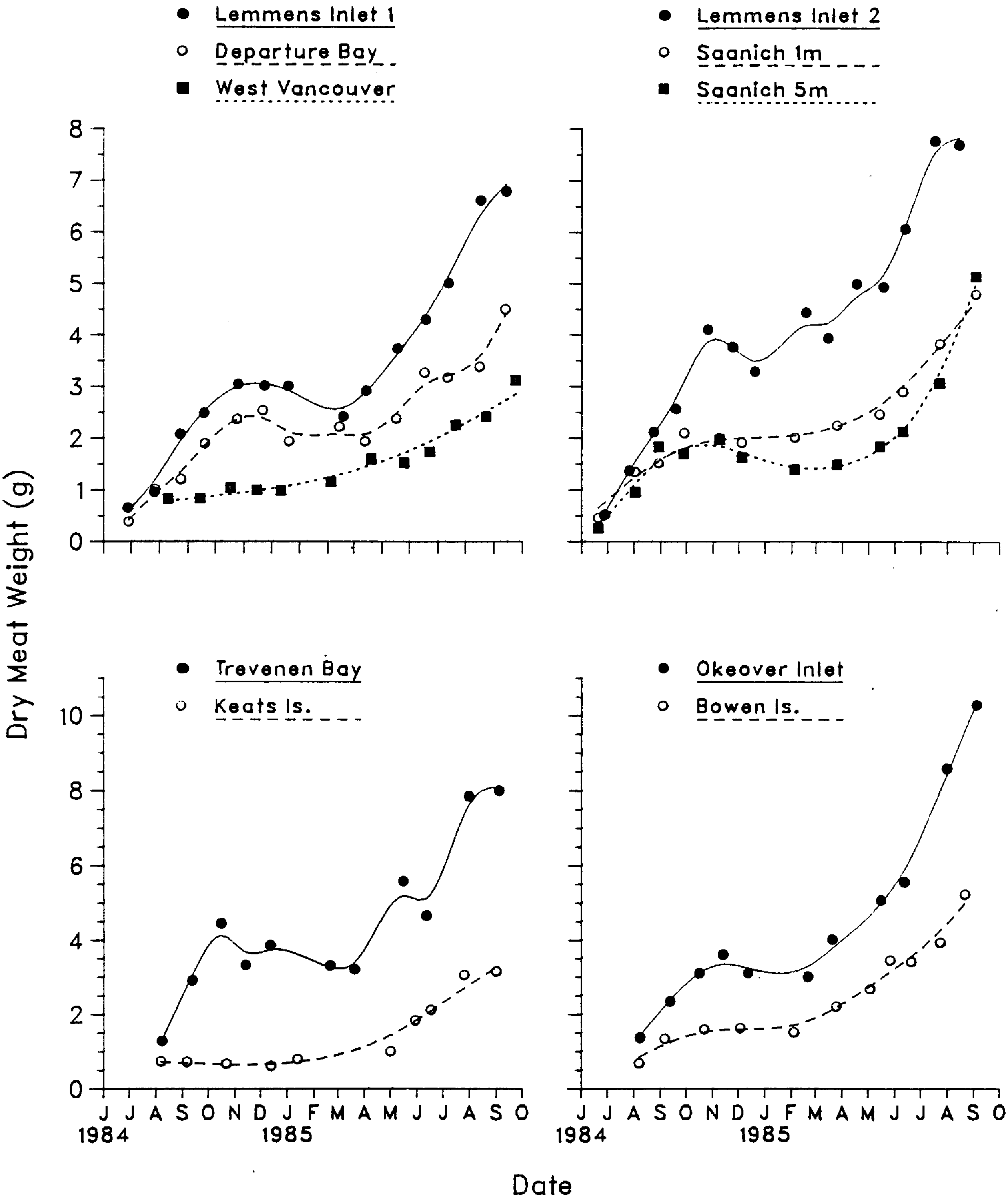

Lemmens Inlet 1
Departure Bay
West Vancouver
Lemmens Inlet 2
Saanich 1m
Saanich 5m
Trevenen Bay
Keats Is.
Okeover Inlet
Bowen Is.
Shell Weight (g)
0
20
40
60
80
J J A S O N D J F M A M J J A S O
1984
1985
Date

Fig. 1.6. Dry meat weight growth Year 1 oysters.


Lemmens Inlet 1
Departure Bay
West Vancouver
Lemmens Inlet 2
Saanich 1m
Saanich 5m
Trevenen Bay
Keats Is.
Okeover Inlet
Bowen Is.
Dry Meat Weight (g)
0
1
2
3
4
5
6
7
8
10
J J A S O N D J F M A M J J A S O
1984
1985
Date

groups were analyzed separately because during prolonged periods of low food availability, such as from December to February, the oyster will metabolize stored glycogen reserves resulting in a decrease of meat weight (Quayle 1969). A high order polynomial would be required to describe this winter decline of body weight which would complicate subsequent interpretation and multiple comparisons. The division of the data was not neccessary for the analysis of the whole weight data. Shell material forms the major component of whole weight and any losses in meat weight due to metabolic processes are partially compensated for by uptake of fluids into the shell cavity (Quayle 1969).

Growth of dry meat weight in 1984 was described by quadratic equations, except for Keats Island and West Vancouver (Table A.9). The poor fit of the polynomial model to data from these sites could be attributed to the relatively low rate of increase observed for dry meat weight. The fit of quadratic rather than cubic polynomials to the data from the other sites, indicates decreases in body growth which occurred in November and December 1984.

For the purposes of multiple comparsions, the β_0 coefficient was the most important (Table A.10). For 1984, differences in growth were non-significant between Trevenen Bay, Okeover Inlet and Lemmens Inlet. Growth at Departure Bay and Saanich 5 m was not significantly different from any of the above sites except Okeover Inlet which had the highest meat weight (3.11 g) in December 1984. Oysters at Saanich 1 m and Bowen Island had significantly lower increases in dry meat weight than Departure Bay and Saanich 5 m.

From February to August 1985, body weight increased linearly with time (Table A.11). The growth curves clearly separated, which resulted in a test of significance pattern similar to that encountered with shell height data (Table A.12). The highest growth rate occurred at Okeover Inlet which by August had a mean dry meat weight of 10.30 g. Growth at Trevenen Bay, Lemmens Inlet 1 and 2 were lower but not significantly different. There were no significant differences in body growth between Departure Bay, Bowen Island, Saanich 1 m and 5 m, although growth at these sites was significantly lower than the four areas mentioned above. Finally, Keats Island and West Vancouver have the lowest overall body tissue growth.

Comparisons of allometric growth regressions fitted to shell weight and dry meat weight data revealed that the low and high growth sites have similar shell to dry meat weight relationships (Table A.13-14). For given shell weights, oysters at Departure Bay, Saanich 1 m and 5 m have lower body tissue weight than the other sites. This is consistent with the generally thicker shells observed at these sites.

Survival

The percent survival calculated over the entire study (14 months) was lower for Year 0 oysters compared to Year 1 oysters (Table 1.1). For both year classes, the majority of the

Table 1.1. Survival rates (%) of Year 0 and Year 1 oysters over 14 months.

Age Class	Lemmens Inlet 1	Lemmens Inlet 2	Trevenen Bay	Okeover Inlet	Departure Bay	Saanich 1 m	Saanich 5 m	Bowen Island	Keats Island	West Vancouver
Year 0	49.0	59.1	57.3	54.6	32.0	43.5	31.5	37.1	--	48.8
Year 1	88.9	89.0	87.7	85.5	85.5	86.2	80.5	63.2	86.4	89.7

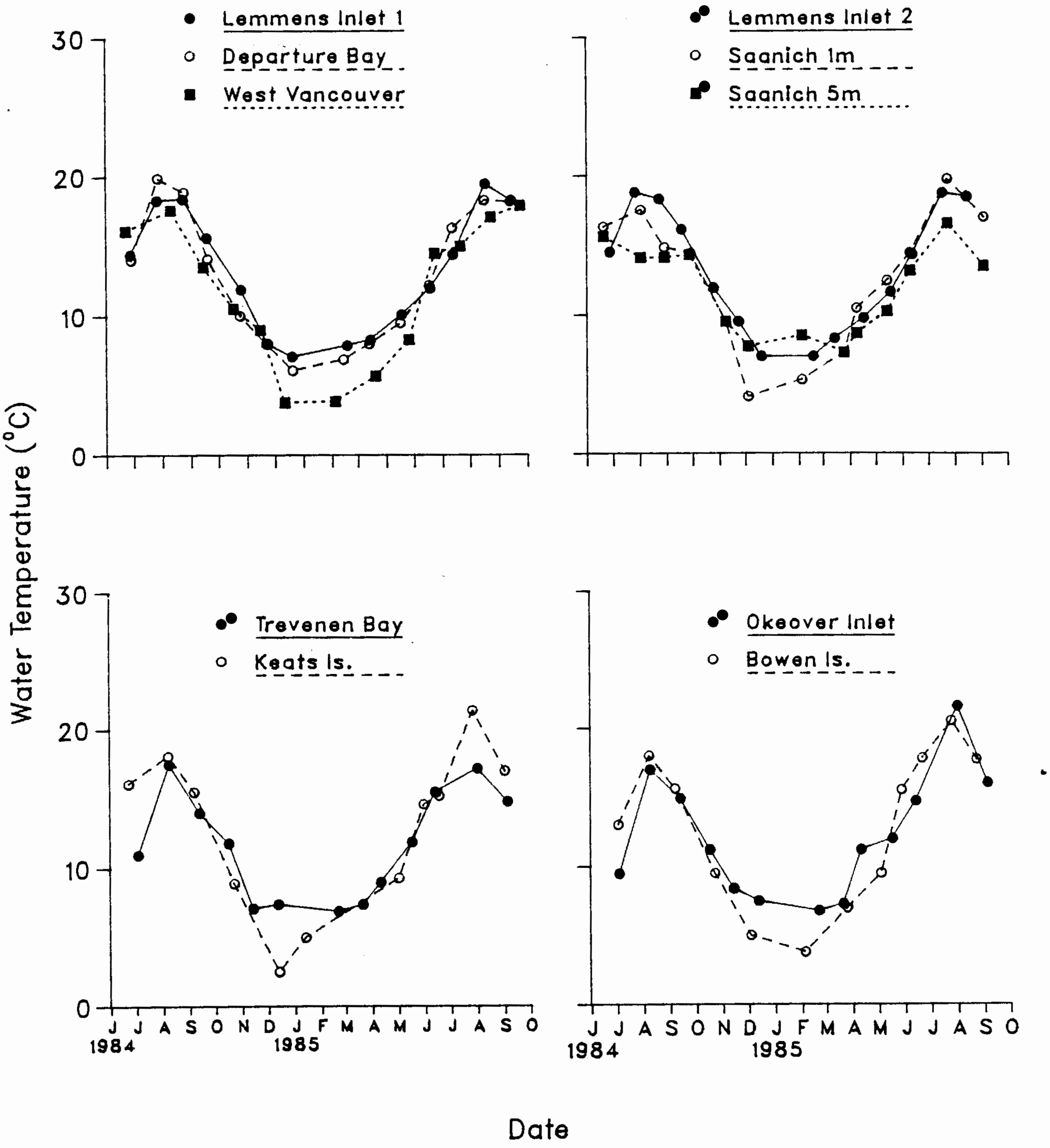
mortalities occurred during the initial 2 months of the study (July-August 1984). Very few mortalities were observed in subsequent months, except for Bowen Island, where mortalities occurred throughout the study. The survival rate of Year 1 oysters did not vary greatly between sites and ranged between 80.5 - 89.7 % with the exception of Bowen Island (63.2 %). For Year 0 oysters, survival rates at Bowen Island (37.1 %), Departure Bay (32.0 %), Saanich 1 m (43.5 %) and 5 m (31.5 %) were considerably lower than rates at the remaining sites (48.8 - 59.1 %). Despite low growth rates at Keats Island and West Vancouver, oysters at these sites did not have a rate of survival very different from that of oysters at the high growth sites.

Water Temperature

Temperature and salinity observations were similar to those reported by Thomson (1981) for Howe Sound and the west coast of Vancouver Island, Harrison et al. (1983) for the Strait of Georgia, Parsons et al. (1969) for West Vancouver, and Herlinveaux (1962) for Saanich Inlet.

Seasonal fluctuations in water temperature, as shown in Fig. 1.7, were greatest at sites in the vicinity of Howe Sound (West Vancouver, Bowen Island and Keats Island). For example, temperatures at Keats Island ranged from 2.5 °C in December 1984 to 21.4 °C in July 1985. Minimum temperatures (6.9 - 7.5 °C) were somewhat higher at Trevenen Bay, Okeover Inlet, Lemmens

Fig. 1.7. Mean monthly water temperatures (°C).


Lemmens Inlet 1
Departure Bay
West Vancouver
Lemmens Inlet 2
Saanich 1m
Saanich 5m
Trevenen Bay
Keats Is.
Okeover Inlet
Bowen Is.
Water Temperature (°C)
30
20
10
0
J J A S O N D J F M A M J J A S O
1984
1985
Date

Inlet 1 and 2. The maximum temperatures attained during both summers at Trevenen Bay, Lemmens Inlet 1 and 2 stayed below 20 °C. Water temperatures in Okeover Inlet briefly rose to 21 °C in July 1985 in contrast the maximum of 17 °C during the previous summer.

Winter minimum temperatures at Departure Bay, Saanich 1 m and 5 m were slightly higher than those reached at the Howe Sound sites. Overall summer temperatures were also lower and closer to the range observed at Trevenen Bay, Okeover Inlet, Lemmens 1 and 2. Monthly day-degrees were calculated from the average temperature between two months multiplied by the number of days separating the visits. For a particular site, the sum of the monthly values was the cumulative total over 14 months (Table 1.2). While seasonal fluctuations at a particular site were distinct, there were relatively minor differences between sites in total number of day-degrees.

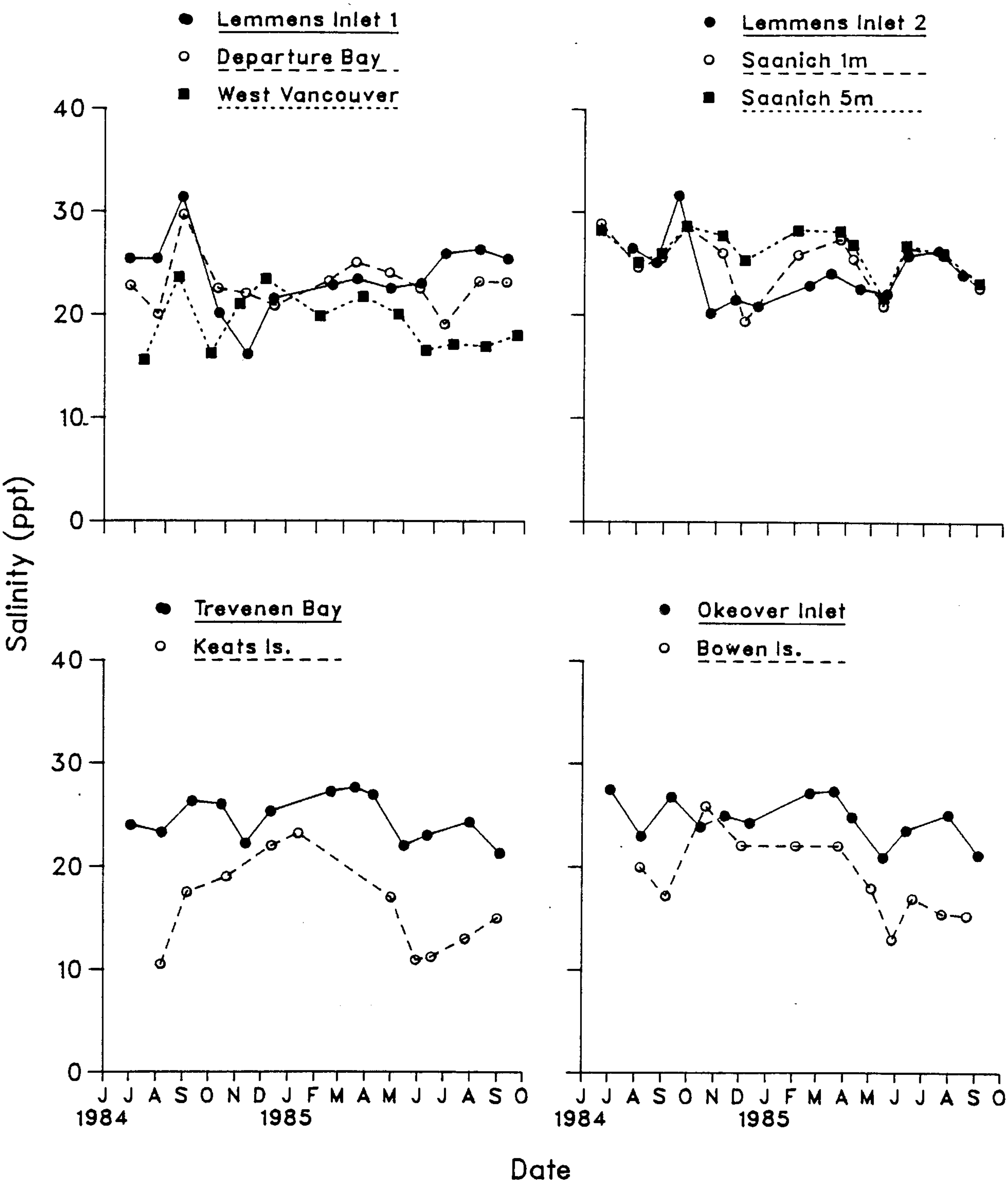
Salinity

Salinity fluctuated seasonally and also varied greatly between certain sites (Fig. 1.8). Sites in the area of Howe Sound had lower salinities through most of the year but particularly low values were observed from April to August 1985. Spring run-off events from the near-by Squamish and Fraser Rivers were largely responsible for the depressed salinity regime (Thomson 1981).

Table 1.2. Day-degree, day-salinity and day-chlorophyll *a* cumulative totals for 14 months.

	Lemmens Inlet 1	Lemmens Inlet 2	Trevenen Bay	Okeover Inlet	Departure Bay	Saanich 1 m	Saanich 5 m	Bowen Island	Keats Island	West Vancouver
Day-degree	5192	5066	5101	5550	5029	5263	5073	4710	5411	4742
Day-salinity	9063	9205	11735	10810	8872	9919	10498	6841	6802	7202
Day-chlorophyll *a*	2910	3645	1990	1464	1273	1243	1353	2224	1329	3088

Fig. 1.8. Mean monthly salinity (ppt).



● Lemmens Inlet 1
○ Departure Bay
■ West Vancouver
● Lemmens Inlet 2
○ Saanich 1m
■ Saanich 5m
● Trevenen Bay
○ Keats Is.
● Okeover Inlet
○ Bowen Is.
Salinity (ppt)
40
30
20
10
0
J J A S O N D J F M A M J J A S O
1984
1985
Date

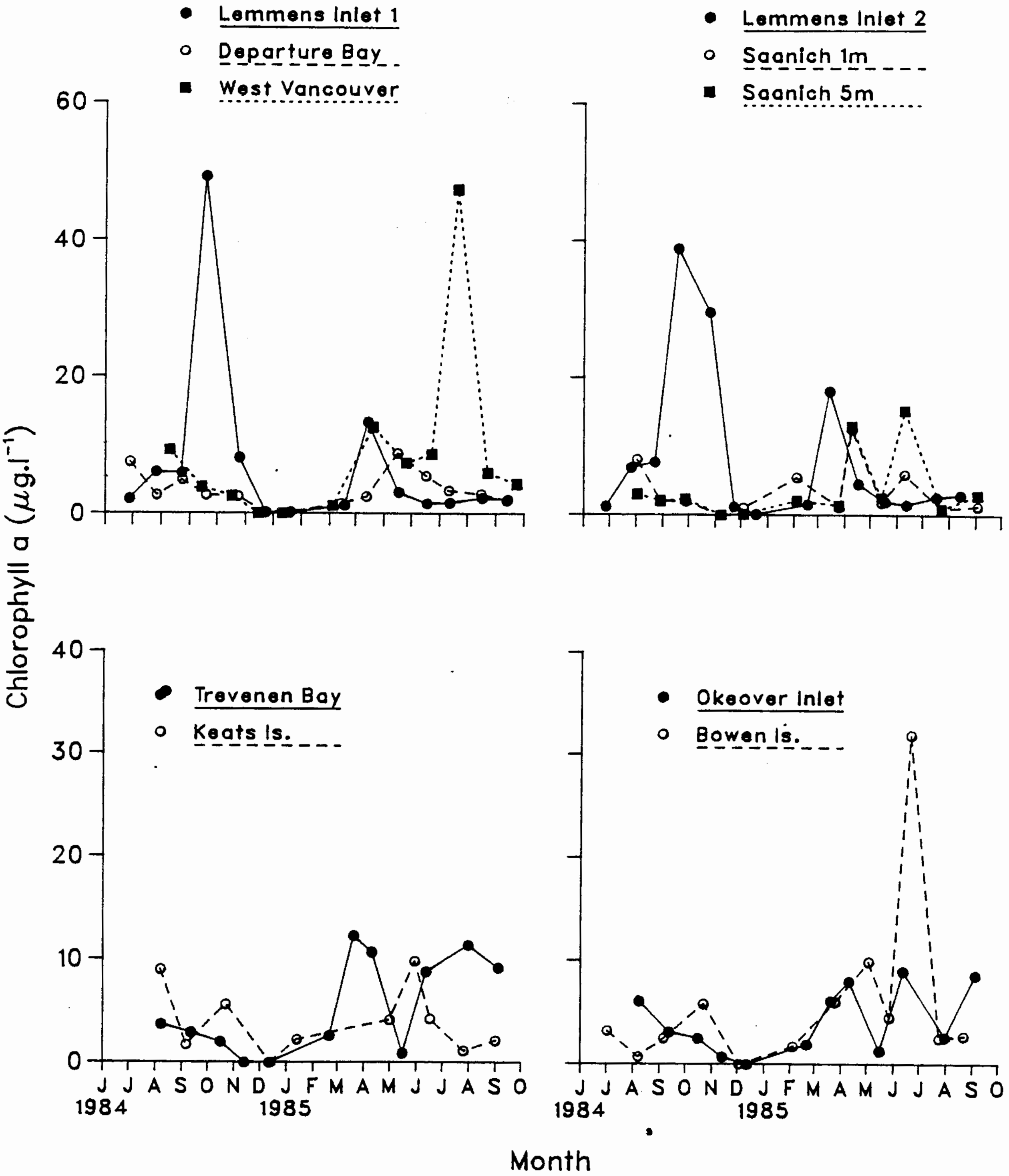
In contrast, monthly mean salinity at the remaining sites were rarely lower than 20 ppt. Cumulative day-salinity were calculated for each site, in order to compare the salinity regimes. Cumulative day-salinity ranged from 6802-7202 for Howe Sound sites compared to 8870-11734 day-ppt for the remaining 7 sites (Table 1.2). Salinity levels above 20 ppt are considered to be best for promoting the growth of the oyster (Bernard 1983). For a consistent monthly mean of 20 ppt, the cumulative day-salinity would be approximately 7780 day-ppt therefore, salinity regimes at West Vancouver, Bowen Island and Keats Island were generally in the suboptimal range for oysters.

Chlorophyll a

At most sites, phytoplankton blooms occurred twice a year, once in late summer or early fall (August-October) and again in early spring (March-May)(Fig. 1.9). The highest levels of chlorophyll *a* occurred during September-October at Lemmens Inlet 1 (49.09 $\mu g \cdot l^{-1}$) and 2 (38.93 $\mu g \cdot l^{-1}$). At both of these sites, a subsequent bloom of lesser intensity, was observed in March-April 1985. A review of the literature did not reveal any past data on phytoplankton biomass in Lemmens Inlet.

Elevated levels of chlorophyll *a* were also recorded at West Vancouver, Keats Island and Bowen Island. Peaks at these sites (9.79 - 47.28 $\mu g \cdot l^{-1}$) occurred in May-June which coincided with periods of low salinity. Nutrient inputs associated with freshwater discharges from nearby river systems were probably

Fig. 1.9. Monthly mean chlorophyll *a* concentrations ($\mu g \cdot l^{-1}$).


● Lemmens Inlet 1
○ Departure Bay
■ West Vancouver
● Lemmens Inlet 2
○ Saanich 1m
■ Saanich 5m
● Trevenen Bay
○ Keats Is.
● Okeover Inlet
○ Bowen Is.
60
40
20
0
40
30
20
10
0
Chlorophyll a (μg.l^{-1})
J J A S O N D J F M A M J J A S O
1984
1985
Month

responsible for increases in phytoplankton populations (Parsons et al. 1969, Stockner et al. 1979).

Chlorophyll *a* fluctuations in the vicinity of the Fraser River plume were observed by Parsons et al. (1969) although absolute biomass levels recorded in the present study were much higher. Chlorophyll *a* levels in the present study, however, were in close agreement to the two year mean of 54.7 $\mu g \cdot l^{-1}$ reported by Stockner et al. (1979) for Station 5 which is slightly west of the West Vancouver site and south of the Bowen Island site. Discrepencies between the phytoplankton biomass estimates of Parsons et al. (1969) and Stockner et al. (1979) are discussed at length by Harrison et al. (1983) and increased nutrient concentrations in the Fraser River was suggested as one possible cause.

The multiple phytoplankton blooms recorded in Saanich Inlet were in close agreement with observations of Takahashi et al. (1977). In that study, small peaks (5 - 10 $\mu g \cdot l^{-1}$) were reported to occur throughout the summer months. For stations located approximately 8 km north of the oyster study site, maximum blooms in the spring of 1974 in the upper 10 m of the water column were between 10 - 20 $\mu g \cdot l^{-1}$ chlorophyll *a*. In 1985, spring blooms at Saanich 1 m and 5 m had mean concentrations of 12.48 and 12.91 $\mu g \cdot l^{-1}$, respectively.

There is no previous information on the phytoplankton community in Trevenen Bay and Okeover Inlet. Summer maximum at

Trevenen Bay and Okeover Inlet were 11.36 and 8.96 $\mu g \cdot l^{-1}$, respectively.

At West Vancouver, Keats Island and Bowen Island, phytoplankton levels during the spring run-off period were major contributing factors to the cumulative day-chlorophyll *a* values calculated for these sites (Table 1.2). Lemmens Inlet 1 and 2 also had high day-chlorophyll *a* values. Values for Trevenen Bay and Okeover Inlet were slightly higher than those determined for Departure Bay, Saanich Inlet 1 m and 5 m but lower than values for Lemmens Inlet 1 and 2, Bowen Island and West Vancouver.

Discussion

A wide range of oyster growth rates were observed in this study. Direct comparisons with previous studies are conditional due to the lack of standardized growth methodology. In addition, oyster growth can be affected by the time of year that seed is transplanted and the culture method employed. Nonetheless, growth rates recorded in this study were in general agreement with those reported earlier for oysters in suspended culture.

Sparks and Chew (1959) reported that raft cultured oysters, which had an initial size equivalent to Year 1 oysters, increased in height 77.5 - 115.8 % from March to January. In a comparable 11 month period (June 1984 - May 1985), growth of Year 1 oysters ranged from 34.0 (Keats Island) to 120.1 % (Lemmens Inlet 2). Oysters grown by Quayle (1971) were about the same initial size as Year 0 oysters in this study. The growth rates calculated from Quayle's data are approximate since the exact day of the month upon which sampling took place is unknown. From mid-January to November, the highest growth rate in Quayle's study occurred at Okeover Inlet where oysters increased in height by 394 %. In the same study, oysters grown at Quait Bay, which is in the general vicinity of Lemmens Inlet, increased by 212 %. When calculated over a period roughly equivalent to that of Quayle's study, the maximal increases in shell height for Year 0 oysters occurred at Okeover Inlet (278 %) and Trevenen Bay (298 %). The lowest growth rate in Quayle's study was 100 %. In the present study, the lowest growth rate was 163 % at West Vancouver.

In the Sea of Japan, Kurcheryavenko (1985) calculated a daily increase in dry meat weight for one year old oysters during August to be 3.0×10^{-4} $g \cdot day^{-1}$. For Year 1 oysters, August body growth ranged from 4.0×10^{-2} $g \cdot day^{-1}$ at Lemmens Inlet 1 to a negative growth rate at Keats Island of -3.3×10^{-4} $g \cdot day^{-1}$. Growth rates recorded in this study are in agreement with previous works and covered a broad spectrum of growth rates.

Differences between sites in absolute and allometric growth appear to be related to salinity, temperature and available food. The high growth rates of Lemmens Inlet 1 and 2, Trevenen Bay and Okeover Inlet, were associated with elevated abundances of phytoplankton and non-stressful salinity regimes. In an LD_{50}

test, Bernard (1983) determined the critical salinity for the oyster to be between 8 - 12 ppt while a decrease in ventilation function was observed to occur around 18 ppt. Salinity levels generally remained above 20 ppt at Lemmens Inlet 1 and 2, Trevenen Bay, Okeover Inlet, Departure Bay and Saanich Inlet 1 m and 5 m. At Keats Island, Bowen Island and West Vancouver, salinity levels below 20 ppt occurred over a substantial portion of the year. Furthermore, salinity readings in July taken at West Vancouver, were found to fluctuate between 12.5 and 21.5 ppt over a tidal cycle (J.R. Brown, unpublished data). Bernard (1983) found that an oyster exposed to variations in salinity exceeding 10 % may require an acclimation period of several days.

Maximum phytoplankton abundances in the vicinity of Howe Sound, during May and June, coincided with low mean salinity readings which were highly variable over a tidal cycle (J.R. Brown, unpublished data). This overall salinity stress probably had a negative effect upon ventilation and osmo-regulatory functions of the oyster thus placing restrictions on food ingestion and assimilation. In addition, stressful levels of one variable can lower the tolerance of the oyster to conditions of another variable, such as temperature (Medcof and Needler 1941, Bernard 1983).

At Departure Bay and Saanich Inlet 1 m and 5 m, temperature and salinity regimes were suitable for oysters but available food concentrations were low. The highest phytoplankton biomass at Departure Bay and Saanich Inlet 1 m, occurred in early spring. Water temperatures (6 - 10 °C) during that period were near the lower thermal limit of the oyster's zone of metabolic function which is generally estimated to be between 8 and 10 °C (Quayle 1969, Bernard 1983). Malouf and Breese (1977) also found the assimilation efficiency of oysters to be limited at this temperature.

At Saanich 5 m, peak phytoplankton abundances occurred in the spring and summer of 1985 but not during the summer of 1984. High water temperatures during the first summer combined with the low levels of available food may have had a negative impact upon growth (Winter 1978). In fact, growth may be inversely related to high water temperatures if food availability is low (Malouf and Breese 1977). The combination of low food availability and high water temperatures at the Saanich Inlet sites, may have caused the high rate of mortality among Year 0 oysters during the summer of 1984.

Phytoplankton biomass was highest at Lemmens Inlet 1 and 2 in the late summer and early fall of 1984. Coinciding with the high water temperatures, the timing of the blooms was optimal for oysters. In addition, the high availability of food in the early fall would increase the metabolic reserves of the oyster prior to the winter months (Quayle 1969).

Chlorophyll *a* concentrations were also elevated at Trevenen Bay and Okeover Inlet although not to the extent of the levels at Lemmens Inlet. Despite this fact, site-specific growth rates were not significantly different. One explanation could be that for a given temperature, assimilation efficiency in bivalves is asymptotic beyond a certain concentration of food particles (Kirby-Smith and Barber 1974, Bayne and Newell 1983, Bernard 1983). Malouf and Breese (1977) hypothesized a temperature mediated plateau in growth rate at a certain level of food availability. Tenore and Dunstan (1973) found that between 19 and 21 °C, *Crassostrea virginica* removed a constant percentage of carbon from seston when carbon levels reached 300 - 350 $\mu g \cdot l^{-1}$. Using a ratio of carbon:chlorophyll *a* equal to 26 (Strickland 1960 in Parsons and Takahashi 1973), this carbon level converted to 11.5 - 13.5 $\mu g \cdot l^{-1}$ chlorophyll *a* which is close to the seasonal peaks at Trevenen Bay and Okeover Inlet. Water temperatures at these sites were 2 - 3 °C lower than those in the experiment of Tenore and Dunstan which could mean that food rations at high growth sites were in excess of the oysters' requirements.

Although water movement was not measured in this study, sites at Trevenen Bay and Okeover Inlet appeared to have higher current velocities than sites in Lemmens Inlet. The number of food particles which came in contact with the oyster per unit of time could have been equivalent among high growth sites.

Significant differences in the allometric relationship between shell and body growth appear to have been mitigated by site-related factors. At the medium growth sites (Departure Bay, Saanich 1 m and 5 m) oysters have shells which were of shorter height but equivalent weight to oysters at high growth sites. It appears that oysters at medium growth sites secreted shell material to increase shell thickness rather than height. Furthermore, the significantly lower body weight of medium growth site oysters could be interpreted as the allocation of resources to increase shell thickness over body weight.

Aguis et al. (1978) noted that specimens of *C. gigas* grown at one site in Malta had signficantly thicker shells compared to oysters from the same broodstock grown elsewhere on the island. The specific cause of this phenomenon was not conclusively ascertained, although high copper concentrations, high calcium levels, elevated suspended sediment loadings and limited water exchange in the bay were cited as possible agents.

In the mussel, *Mytilus edulis*, dry meat weight to shell weight ratio increased as the order of habitats progressed from intertidal, subtidal bottom to suspended culture (Aldrich and Crowley 1986). With reduced submergence time over a tidal cycle, hence limited feeding opportunities, intertidal mussels were in a less favourable habitat than mussels grown in suspended culture. There appears to be an inclination in some bivalves towards the advancement of shell growth at the expense of body tissue growth when habitat conditions are adverse.

The reduction of cavity volume through increases in shell thickness could be a mechanism to improve the efficiency of food intake. As the proportion of internal cavity filled by body tissue increases the amount of fluid filled space is reduced. It may be possible to maintain a higher flow of water over the gills at a lower energy cost because of the reduction in cavity volume through which water is circulated. Eventhough shell deposition may require up to one-third of the total energy for growth (Dame 1976, Wilbur and Saleuddin 1983) the subsequent maintenance costs are minimal. While internal volume could also be reduced by expansion of body tissue, in conditions of low food availability it may be more energtically efficient in the long term to add shell material.

The similar shell to body weight allometry for oysters at low and high growth sites could have been caused by reduced salinity levels at low growth sites. The rate of shell formation is partially dependent upon the supply of calcium to the mantle by the blood or external medium (Wilbur and Saleuddin 1983). Calcium concentrations in water is related to salinity and ranges from 1500 $\mu g \cdot l^{-1}$ in fresh water to 4.22×10^5 $\mu g \cdot l^{-1}$ in ocean water with a salinity of 35 ppt (Riley and Chester 1971). The mechanism of preferentially promoting shell growth over body growth may have been operative in the oysters grown at Keats Island and West Vancouver with its expression suppressed due to limited availability of basic shell-building substrates. Similarities in allometric relationships between low and high growth categories were the result of reduced or non-existent growth of all measured body parameters in oysters at low growth sites.

Mortality rates were higher for Year 0 oysters compared to Year 1 and showed greater variation among sites. The lower survival rate of younger oysters could be the result of their great suspectability to stress. Oyster larvae have been shown to broaden their tolerance to temperature and salinity as they age (Lough and Gregory 1975). Higher survival rates of Year 1 oysters may be indicative of increased robustness in older oysters.

The lower survival rates at Bowen Island can not be explained. The inner surfaces of shell remains of dead oysters from this site were characterized by patches of extreme thinness which, in severe cases, resulted in a hole through the shell. This condition was also occasionally found in oysters grown in Departure Bay, West Vancouver, Keats Island and Saanich Inlet 1 m and 5 m (J.R. Brown unpubl. data). Shell remains of dead and dissected oysters from high growth sites were always smooth and hard with little inner surface damage. According to Galtsoff (1964), this weakening of the inner shell surface is known as blistering and is indicative of environmental stress.

The relative consistency of Year 1 survival amongst sites (except for Bowen Island) and the high degree of variability in growth rates concurs with previous conclusions that survival is genetically influenced while growth is largely controlled by the environment (Mallet and Haley 1983, Dickie et al. 1984).

Furthermore, multiple interactions of environmental factors can result in changes in the allometric relationship between growth in shell and body tissue.

CHAPTER II

THE EFFECT OF SITE UPON THE RELATIONSHIP BETWEEN GROWTH AND CONDITION IN THE PACIFIC OYSTER *Crassostrea gigas*

Introduction

The physiological status of bivalves has often been evaluated through certain allometric relationships called condition indices (Galtsoff 1964, Walne 1970, Aguis et al. 1978, Mann 1979b). An index of oyster condition has been proposed for use in aquaculture (Mann 1978, Benninger and Lucas 1985) and water pollution monitoring programs (Lawerence and Scott 1982).

The relative merits of condition indices have been reviewed by Engle (1949), Mann (1978) and Lucas and Beninger (1985). A dry flesh weight:shell weight ratio was recommended in the latter two reviews as the most suitable condition index for aquaculture. A low value of this index would indicate energy loss as the result of either environmental stress or the release of gametes. This index is easily standardized since dry weights are involved. The use of dry ash weight has been suggested for the evaluation of the condition of small oyster spat (Walne and Millican 1972). The condition index based upon ash-free dry weight was found to be closely correlated with the index utilizing only dry weight (Beninger and Lucas 1984).

The second condition index frequently referred to in the literature is the dry flesh weight:internal volume ratio first proposed by Hopkins (1949). According to Quayle (1969), this index is based upon the hypothesis that the proportion of internal shell cavity occupied by body tissue is directly related to the nutritional status of the oyster. Internal volume is defined as the difference between whole oyster and shell volumes.. Volumes were originally determined by water displacement which was both time consuming and subject to experimental error (Lawerence and Scott 1982). Quayle (1951) recommended two sets of weighings, one in air and the other in water, for both whole oyster and shell halves. According to Archimedes Principle, the difference between air and water weight determinations is equal to the volume of the respective body parameter. Internal or cavity volume is the difference between whole and shell volumes.

Lawerence and Scott (1982) suggested that internal volume could be determined from the difference between whole oyster and shell weights in air alone, since the density of oyster flesh is similar to that of water. They report good correlation between condition index values determined using this method with values derived from the water displacement technique.

The consistency of condition index values is an important consideration when comparing oysters collected either from various locations or at different times of the year. Annual cycles of reproduction and food availablity can have a considerable effect upon condition indices (Quayle 1951, Askew 1972, Beninger and Lucas 1984). In studies which have involved the comparison of the condition of oysters collected from several locations, relative rankings of sites were frequently altered throughout an annual cycle (Walne 1970, Aguis et al. 1978). Recognizing the inherent variability of condition indicies derived from discrete samples, Lucas and Beninger (1985) recommended the use of dynamic indices based upon observed changes in bivalve physiology over time.

In the present study, seasonal and site-related variations in two commonly applied static condition indices were examined for a common broodstock of oysters grown subtidally. The results indicate that spatial and temporal variation in condition index values can obscure trends in oyster performance which are readily apparent from the analyses of dynamic growth data. Furthermore, under certain environmental conditions, the condition indices of slow growing oysters can exceed those of larger, more rapidly growing oysters.

Methods

Study sites and field experiment design were described in Chapter I. Condition index values were determined monthly for a sample of Year 1 oysters (n = 10) collected from each site. The collection and analyses of shell height and weights of whole oyster, shell and dry body tissue data were discussed in Chapter I.

Cavity volume was determined using the procedure of Quayle (1951) with some slight modifications. A Mettler top loading balance was placed on a sturdy wooden box (30 x 30 x 30 cm) which had an open side facing the operator. The platform had a hole cut into the top which provided access to the bottom suspension hook of the balance. A metal pan (8 cm d) attached to a wire frame, was hung from the hook. The metal pan was suspended in a 1 l beaker filled with fresh water (20 - 25 °C) which had been placed underneath the balance via the open side of the box. Air bubbles were allowed to disperse from the metal pan before the meter was levelled and set to zero.

Using a large pair of forceps, a single oyster was placed on the pan with care being taken to ensure that neither the pan or oyster were touching the side of the beaker. The oyster was positioned such that it was entirely submerged. About 30 - 60 s were allowed for the release of large air bubbles clinging the outer shell surface. After weighing, the oyster was removed and the zero of the meter was checked.

The oyster was then sacrificed and its body tissue removed for dry weight determination as described in Chapter 1. Shell halves were allowed to air dry for at least 24 hours before weighing in air and water. After being weighed in air, shell halves were weighed together in water following the procedure used for the whole oyster. Condition indices were not determined for oysters which had gaps between the valves or displayed positive bouyancy.

Whole oyster and shell volumes were the differences between the weights in air and water of the respective body parts. Volumetric condition index was calculated from the equation:

$$VCI = \frac{DMWT}{WV - SV} \times 1000$$

where VCI is the volumetric condition index value, DMWT is dry meat weight (g), WV is whole oyster volume (ml) and SV is shell volume (ml).

Dry meat weight:shell weight ratio condition index was derived from the equation:

$$DWCI = \frac{DMWT}{DSWT} \times 1000$$

where DWCI is the dry weight condition index and DSWT is dry shell weight (g).

The correlation between VCI and DWCI were determined for each site as well as for all sites combined. Regression analyses were performed using BMDP program P6D.

Results

Both VCI and DWCI values showed marked seasonal fluctuations for all (Fig. 2.1 and 2.2). Condition indices were highest in July and August of 1984 and 1985 while the lowest values occurred during the winter.

Fig. 2.1. Volumetric condition index (VCI) values.

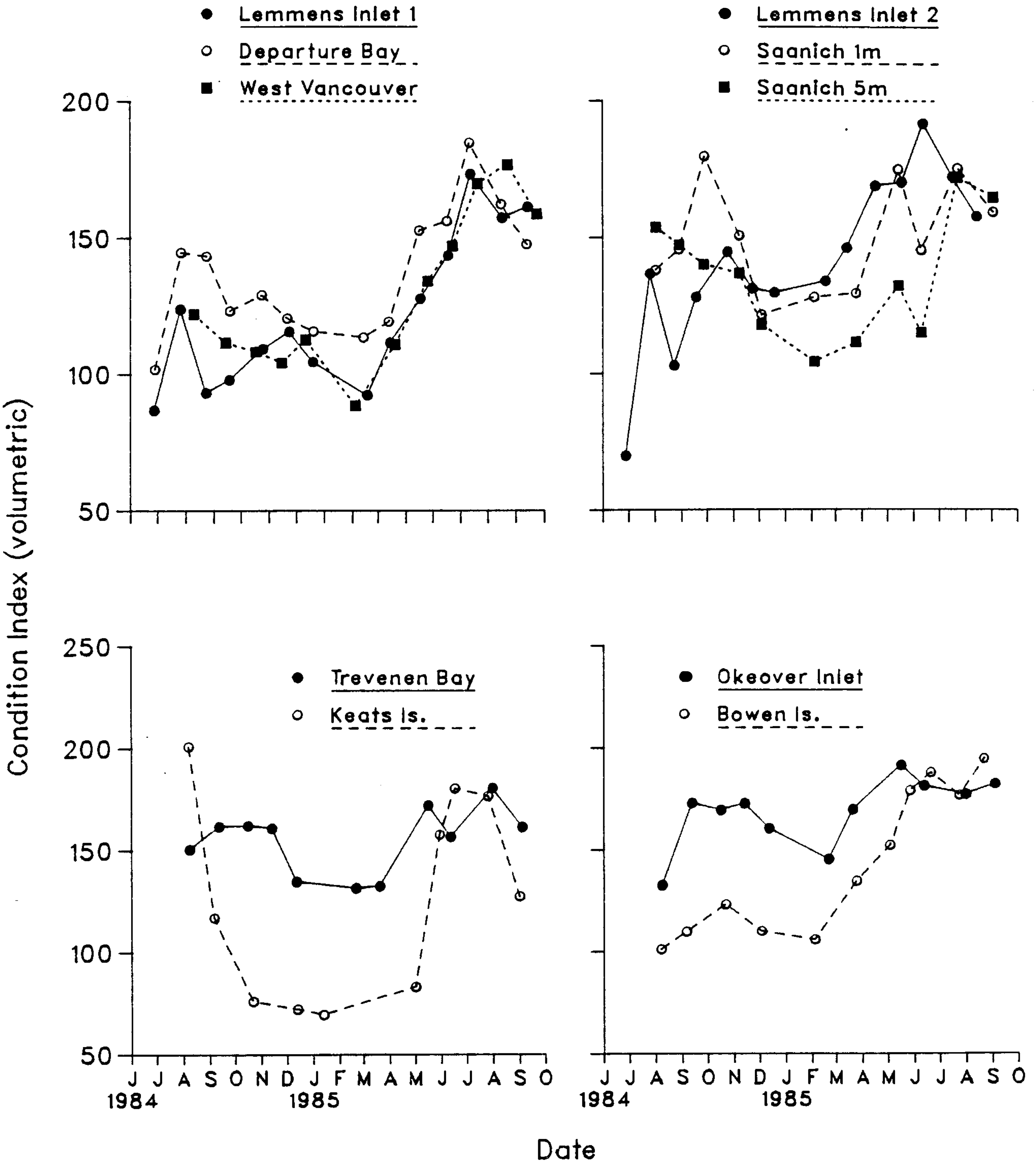
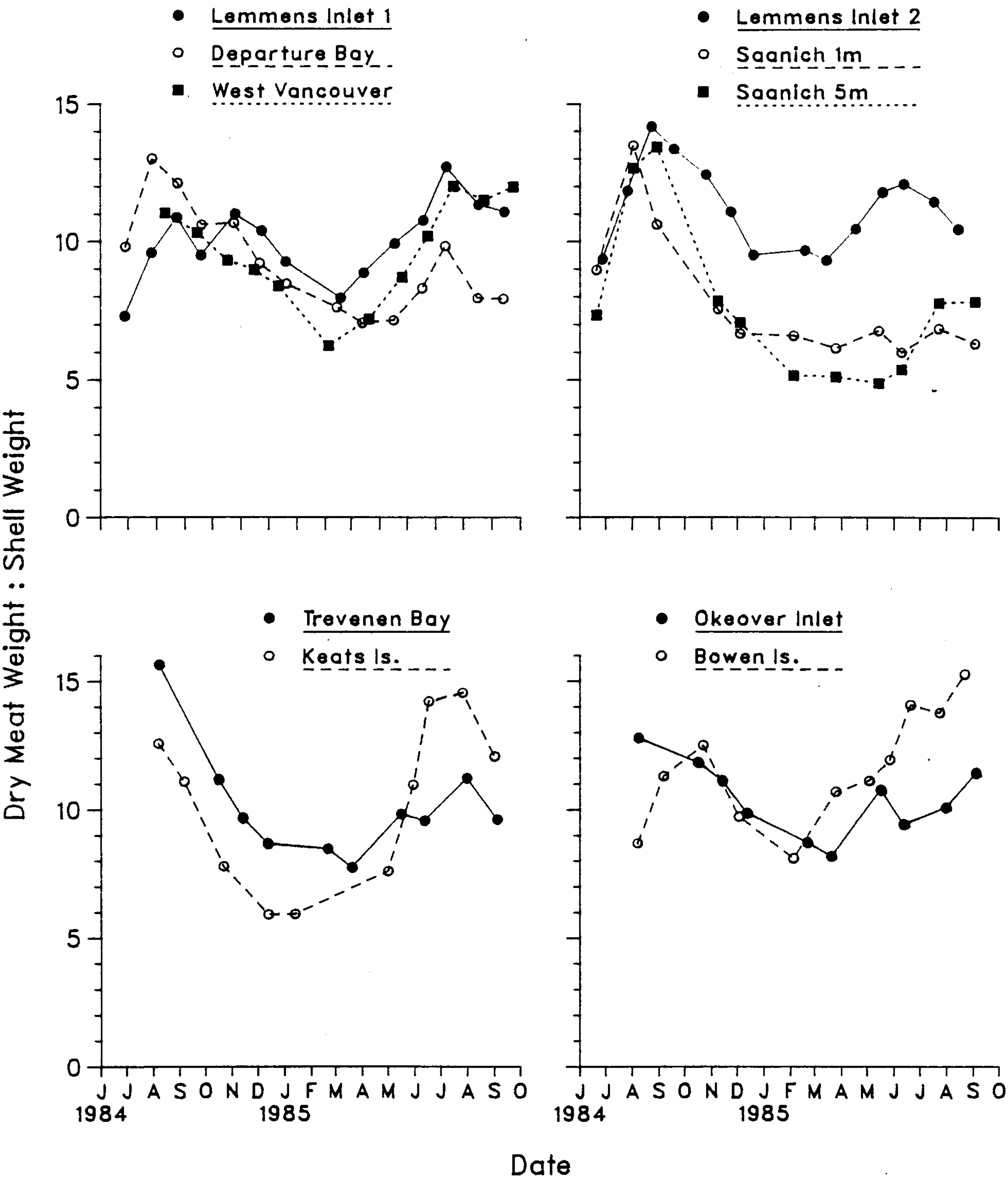

Lemmens Inlet 1
Departure Bay
West Vancouver
Lemmens Inlet 2
Saanich 1m
Saanich 5m
Trevenen Bay
Keats Is.
Okeover Inlet
Bowen Is.
Condition Index (volumetric)
200
150
100
50
250
J J A S O N D J F M A M J J A S O
1984
1985
Date

Fig. 2.2. Dry weight condition index (DWCI) values.


● Lemmens Inlet 1
○ Departure Bay
■ West Vancouver
● Lemmens Inlet 2
○ Saanich 1m
■ Saanich 5m
● Trevenen Bay
○ Keats Is.
● Okeover Inlet
○ Bowen Is.
Dry Meat Weight : Shell Weight
0
5
10
15
J J A S O N D J F M A M J J A S O
1984
1985
Date

The relative ranking of sites based upon VCI values varied from month to month. For example, Keats Island and Bowen Island oysters have the lowest VCI values amongst all the sites until May 1985 when index values for these two sites began to rise. Summer 1985 condition index values for these sites were equivalent to those of the high growth sites; Lemmens Inlet 1 and 2, Trevenen Bay and Okeover Inlet.

For oysters at Saanich 1 m and 5 m and Departure Bay, DWCI values declined as the study progressed. As shown in Chapter I, oysters at Keats Island and West Vancouver have the lowest growth rates for any body parameter yet DWCI values for these sites closely followed and, at times, exceeded those values of high growth sites.

Correlations between VCI and DWCI were determined for each site and all sites combined (Table 2.1). For each index, the combined site data were normally distributed thus the arcsin square root transformation usually applied to ratio data was unnecessary. Correlations between the two indices were generally low with the exceptions of Keats Island, Bowen Island and West Vancouver which have r^2 values between 0.46 - 0.53 ($p \leq 0.001$). For Saanich Inlet 1 m the correlation between VCI and DWCI was not significant. For all sites combined, the correlation was low but significant ($r^2 = 0.18$, $p \leq 0.001$).

Table 2.1. Correlations between volumetric condition index (VCI) and dry weight condition index (DWCI).
* = $p \leq 0.001$; ns = not significant.

	All Sites	Lemmens Inlet 1	Lemmens Inlet 2	Trevenen Bay	Okeover Inlet	Departure Bay	Saanich 1 m	Saanich 5 m	Bowen Island	Keats Island	West Vancouver
r^2	0.18	0.31	0.10	0.16	0.05	0.13	0.01	0.16	0.46	0.53	0.50
p	*	*	*	*	*	*	ns	*	*	*	*
n	1122	140	139	98	100	134	99	99	105	91	117

Discussion

The highest (201.0) and lowest (69.7) VCI values were recorded at Keats Island in August 1984 and February 1985, respectively. The VCI values were within the range of similar condition indices reported for oyster in British Columbia waters (Quayle 1969, Whyte and Englar 1982). From the literature, Pacific oysters cultivated in the northeast Pacific tend to have higher volumetric condition index values in comparison to specimens of *C. gigas* grown elsewhere in the world (Walne 1970, Aguis et al. 1978). Dry meat:shell weight ratios of *C. gigas* reported in growth experiments be Mann (1979b) were in the range of DWCI values in the present study.

Quayle (1969) and Westley (1959 in Walne 1970), rated oysters with VCI values above 100 to be in excellent condition.

Despite the low growth rates observed at West Vancouver and Keats Island, condition indices (VCI) during certain periods of the year were indicative of oysters in good condition.

The fact that oysters at high growth sites have VCI values similar to those oysters at low growth sites reduces the utility of this index. The rationale behind the VCI is that the proportion of the internal volume of the shell filled by body tissue varies directly with the nutritional status of the oyster. This relationship would not hold true if the oyster adopted a strategy of adding extra shell material to the inner surface during prolonged periods of limited food availability.

Shells of oysters cultivated at Departure Bay and Saanich 1 m and 5 m were shorter than those of oysters at the high growth sites but have equivalent weight (Chapter I). From phytoplankton biomass data, it appeared that food was less available at low and medium growth sites in comparison to high growth sites (Fig. 1.10). The trend of lower dry meat weight:shell weight ratios in oysters at medium growth sites, is further evidence of the tendency to reduce internal volume by increaseing shell thickness during extended periods of low food abundance.

Low correlations between VCI and DWCI values would indicate that the two indices can not be interpreted as describing oyster condition under similar criteria. Aldrich and Crowley (1986) noted a similar absence of correlation between ratios of meat weight:internal volume and shell weight:internal volume in the mussel, *Mytilus edulis*. These findings were attributed to differential shell and body tissue growth which is in agreement with the present study.

As previously concluded, DWCI is a better index of oyster condition than VCI (Mann 1978, Beninger and Lucas 1985, Aldrich and Crowley 1986). The underlying principle of the DWCI, however, may be disrupted if mineral elements necessary for shell formation are limited in the environment. Salinity levels at West Vancouver, Keats Island and Bowen Island were generally low (< 20 ppt) throughout most of the year. At these sites, months (May-July 1985) with the lowest salinity levels also have the highest phytoplankton abundances. Although the oysters were subjected to some salinity stress, they might have been able to convert a portion of the available food into body tissue. In comparing growth curves of shell height (Fig. 1.5) with body tissue (Fig. 1.6), a somewhat steeper slope can be discerned for the latter. From the perspective of relative growth, it would seem possible that oysters at low growth sites could maintain a similar dry meat weight : shell weight ratio as oysters at high growth sites.

Hilbish (1986) also observed uncoupled seasonal growth of shell and body tissue in *M. edulis*. In a sample of 21 habitats in Ireland, Aldrich and Crowley (1986) noted that site had a strong influence upon the meat:shell weight ratio in the mussel. They concluded that while the index has some value, any comparison of growth between stocks should be conducted at the same location.

From the present study, it is concluded that the use of DWCI is valid if factors such as salinity can be held constant and only nutritional constraints are considered. Dynamic indices, such as growth rate and those suggested by Beninger and Lucas (1985), should provide a more precise evaluation of the physiological state of bivalves.

CHAPTER III

MULTIVARIATE ANALYSES OF THE INFLUENCE OF ENVIRONMENTAL FACTORS UPON THE GROWTH OF THE PACIFIC OYSTER, *Crassostrea gigas*

Introduction

The growth response of a marine bivalve is largely determined by the interaction of several environmental variables. The Pacific oyster, *Crassostrea gigas* Thunberg, is one of the most widely cultured marine bivalves yet the relationship between oyster growth and multiple environmental factors has been the subject of very few in situ investigations.

The effects of some environmental factors upon the growth of *C. gigas* and *C. virginica* have been examined in laboratory experiments on a univariate or bivariate basis (for example Loosanoff 1958, Malouf and Breese 1977, Bernard 1983). Field studies usually describe oyster growth at one or more locations with the analyses of environmental components varying considerably in depth. Westley (1965) examined ambient environmental factors and oyster condition at 5 locations in Washington State, however, oyster-environment relationships were not analysed using rigorous statistical methods. Hall (1983) derived multiple regression equations for predicting the growth of on-bottom cultured oysters in England using temperature and initial size of the oysters as dependent variables. Dame (1972b) calculated a day-degree growth model for intertidal

C. virginica.

Multivariate analyses have been used to describe the production and growth of other marine bivalves. Appeldoorn (1983) used principal component analysis to examine the influence of environmental factors upon growth of soft clams (*Mya arenaria*) at 25 locations. Ulanowicz et al. (1982) derived predictive equations for soft clam landings in Chesapeake Bay from water temperature and salinity data. In the same region, spatfall of *C. virginica* was correlated to salinity, precipitation and harvest of previous years (Ulanowicz et al. 1980).

Since these multivariate studies tended to examine the relationship between environmental variables and indigenous populations the possibility of specific genetic adaptations to local conditions can not be dismissed. Dickie et al. (1984) demonstrated that a strain of mussels growing in their native "harsh" environment had a significant growth advantage over mussels transplanted from an area with more favourable conditions. Incze et al. (1980) found that a common broodstock of mussels transplanted at 7 different locations in an estuary exhibited site-specific growth rates. Such a transplantation represents a situation analogous to the predicament of an aquaculturist, who does not have the advantage of growing oysters which have been indigenous to the culture area for several generations. Rather, the aquaculturist must import oyster seed from another area or hatchery in the expectation that the organisms will adapt successfully to local conditions.

The purpose of the present study was to quantatitively examine the influence of environmental factors upon site-specific and seasonal growth of a common broodstock of Pacific oysters. Discriminant analysis was used to determine which variables best distinguished between sites with significantly different growth rates. Multiple regression analysis served to relate within site variation in growth to seasonal environmental conditions.

Methods

For a description of the study sites and the monitoring of oyster growth, see the Methods section in Chapter I. Shell height increases for Year 0 and Year 1 oysters were used as a measurement of growth rate for this part of the study.

Duplicate or triplicate samples of water temperature, salinity and phytoplankton biomass were taken in conjunction with the monthly oyster measurements. Duplicate samples were taken the same day approximately 2 - 4 h apart. Whenever possible, a subsequent sample was taken within the next 24 - 48 h. All water samples were taken about 5 m up-current of the oyster nets at a depth equivalent to the mid-point of the net.

Water temperature (±0.05 °C) and salinity (±0.05 ppt) were measured using a YSI Model 33 S-C-T meter which was periodically checked against readings from a mercury thermometer and refractrometer. Secchi depth was measured with a 30 cm d white disc lowered over the shaded side of the vessel or pier. Water samples for both phytoplankton pigments and weight of seston analyses were collected using a 3 l Van Dorn bottle. After collection, samples were passed through a 0.30 mm^2 mesh to remove zooplankton and large debris.

Determination of chlorophyll *a*, *b* and *c* and carotenoids followed the technique of Strickland and Parsons (1982). The sample (0.5 - 1.0 l) was filtered in the field through a 47 mm d Millipore© AA filter. Approximately 1 - 2 ml of 1 % $MgCO_3$ solution was added to the final 100 ml of sample in order to inhibit decomposition of the chlorophyll molecules. Filters were immediately frozen in darkness and were stored for no more than 1 wk before analysis.

Chlorophyll pigments were extracted by dissolving the filters in 90 % acetone solution for 18 - 20 h at 4 °C. Aliqout extinction coefficents were determined by spectrophotometer and pigment concentrations ($\mu g \cdot l^{-1}$) were calculated using the equations of Parsons and Strickland (Strickland and Parsons 1982).

Samples (0.5 - 1.0 l) for weight determination of seston were filtered in the field through pre-weighed GF/C Whatman glass microfibre filters which had been previously ashed for 2 h at 450 °C. After the sample had passed through, the filter was rinsed with 2.0 - 3.0 ml of distilled water. Suction was applied until the filter was dry, then it was removed and immediately frozen in the dark. Analysis occurred within 2 wk after collection. Total particulate matter or TPM ($mg \cdot l^{-1}$) was determined after drying the filter at 60 °C for 12 h. Weight of organic (POM) and inorganic (PIM) fractions were determined from weight loss after ignition at 450 °C for 5 h.

Dissolved oxygen concentrations ($mlO_2(NTP) \cdot l^{-1}$) were determined by Winkler titration procedure (Strickland and Parsons 1982). Dissolved oxygen samples were taken first from the Van Dorn bottle and were immediately preserved in tightly stoppered bottles (300 ml) in order to minimize the exchange of gases with the atmosphere.

Environmental variables entered into the multivariate analyses include water temperature, salinity, secchi depth, dissolved oxygen, chlorophylls *a*, *b* and *c*, carotenoids, TPM, POM and PIM. The decision to apply a $\log_e$ transformation to a particular variable was based upon the normality of the univariate frequency distribution and the patterns of residuals from the multivariate analyses (Draper & Smith 1981).

The average condition of each variable over a particular monthly period was determined from the equation:

$$V_a = \frac{V_i + V_{i+1}}{2}$$

where V_a is the average condition of the variable for a particular month and site, V_i is the mean of triplicate or duplicate field observations of the variable at the beginning of the month and V_{i+1} is the mean of the field observations of the variable at the end of the month.

Groupings of sites for discriminant analysis were based upon the comparisons of polynomials fitted to shell height data (see Methods, Chapter I). Sites which had non-significant differences in growth were grouped together. Discriminant analysis was done using BMDP program P7M.

Monthly growth rate was entered into the multiple regression analysis as the dependent variable.
After Ricker (1975), instantaneous growth was defined as:

$$\mathrm{MIGR} = \frac{\log_e H_t - \log_e H_{t-1}}{D} \times 30$$

where MIGR was the monthly instantaneous growth rate, H_t was the shell height (mm) of the current month, H_{t-1} was the shell height of the previous month and D was the number of days between observations.

Stepwise multiple regressions were calculated using BMDP program P2R. Both forward and backward stepping were used with F-to-enter and F-to-remove values set to 3.0. Since the purpose of the analysis was exploratory rather than predictive, setting a low F value was justified in order to examine all relevant environment variables (Dixon 1983).

Results

The results of the analyses of polynomials fitted to the shell height data are discussed in Chapter I and presented in Tables A.1, A.2, A.5 and A.6. Briefly, in terms of shell height growth for both year class the 10 sites were categorized into three groups. Within each group, the differences in growth between sites were non-significant but between groups the differences were significant. The high growth group consists of Trevenen Bay, Okeover Inlet, Lemmens Inlet 1 and 2. The growth at Departure Bay, Bowen Island, Saanich 1 m and 5 m was significantly less and these sites comprise the medium growth group. The final group consists of sites with the lowest recorded shell height growth which were Keats Island and West Vancouver.

Since the growth groupings were identical for both age classes, only one discriminant function was determined (Table 3.1). This function was highly significant ($\chi^2 = 75.54$, $p \leq 0.001$) and best separated the low growth group from the medium and high growth groups (Fig. 3.1). The difference between the medium and high growth groups was not as definite. Jackknifed classification revealed that cases in the low group were categorized correctly 85.0 % of the time while the percentages properly classified for the medium and high groups were 50.0 % and 69.4 %, respectively.

The relative contribution or importance of a variable to the discriminant function was evaluated by determining its correlation to the function (W. Krane, Dept. of Psychology, Simon Fraser University, Burnaby, B.C. personal communication). Salinity was the most highly correlated variable, followed by $\log_e$ POM and secchi depth. Water temperature, $\log_e$ dissolved oxygen and $\log_e$ carotenoids contributed little to the function. Variables excluded from the function were $\log_e$ transformed chlorophyll *a*, *b*, and *c*, carotenoids, TPM and PIM. Seasonal and site related variations of environmental variables are shown in Chapter I (Fig. 1.8 - 1.10) and Appendix A (Fig. A.1.1 - 1.7).

For all sites, instantaneous growth rates followed a general pattern of being high in July and August 1984 then gradually diminishing over the fall to zero levels in the winter (Fig. 3.2 and 3.3). Rates rose slightly in the spring of 1985 but summer growth rates of that year were considerably lower than those of summer of 1984.

Multiple regression equations fitted to environmental data explained 40 % and 33 % of the variation in growth for Year 0

Table 3.1. Coefficients of discriminant function and correlations of variables to first canonical variable.

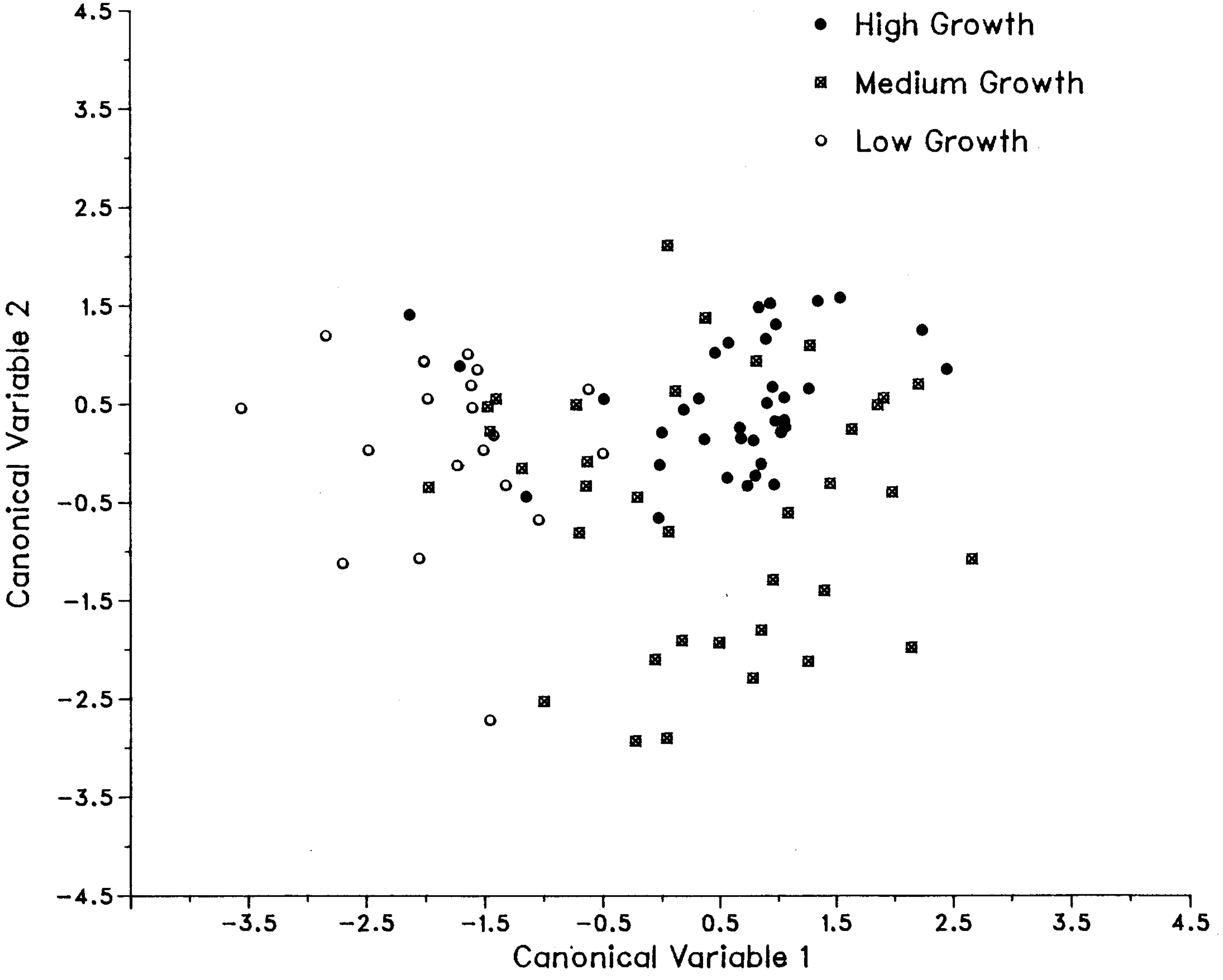
Variable	1st Canonical Variable	2nd Canonical Variable	Variable r^2 to 1st C.V.
Salinity	0.223	0.017	0.69
$\log_e$ POM	0.508	2.223	0.35
Secchi depth	0.324	-0.563	0.12
$\log_e$ Carentoids	0.332	-0.844	0.03
$\log_e$ Dissolved oxygen	2.098	-2.651	0.02
Water temperature	0.111	-0.124	0.01

Overall discriminant function: $x^2 = 75.54$; $df = 12$; $p < 0.001$

1st discriminant function: $x^2 = 19.00$; $df = 5$; $p < 0.005$

2nd discriminant function was not significant.

Fig. 3.1. Plot of discriminant function.


High Growth
Medium Growth
Low Growth
Canonical Variable 2
4.5
3.5
2.5
1.5
0.5
−0.5
−1.5
−2.5
−3.5
−4.5
−3.5
−2.5
−1.5
−0.5
0.5
1.5
2.5
3.5
4.5
Canonical Variable 1

and Year 1 oyster respectively (Table 3.2). Standardized partial regression coefficients were used to compare the relative influences of individual dependent variables upon the independent variable (Zar 1984). For both year classes, $\log_e$ chlorophyll *b* had the greatest influence followed by water temperature while the other variables were not significant.

Since oyster growth rates are known to decrease with increasing size, oyster initial size for each monthly period was included as an independent variable in a second set of regression analyses (Hall 1983). The inclusion of initial size increased the percentage of growth variation explained by both regressions for Year 0 (69 %) and Year 1 (45 %) oysters (Table 3.2). The ordering of the environmental variables entered into the regressions was also altered. For Year 0 oysters, $\log_e$ initial size had a strong negative influence on growth rate while water temperature and salinity had a lesser positive effect. Chlorophyll *b* was eliminated from the regression.

For Year 1 oysters, initial size also had a negative influence on growth rate while water temperature had a positive effect of almost equal magnitude. Chlorophyll *b* and salinity had positive but reduced influence when compared to the previous analysis without initial size.

Fig. 3.2. Instantaneous growth rates for Year 0 oysters.

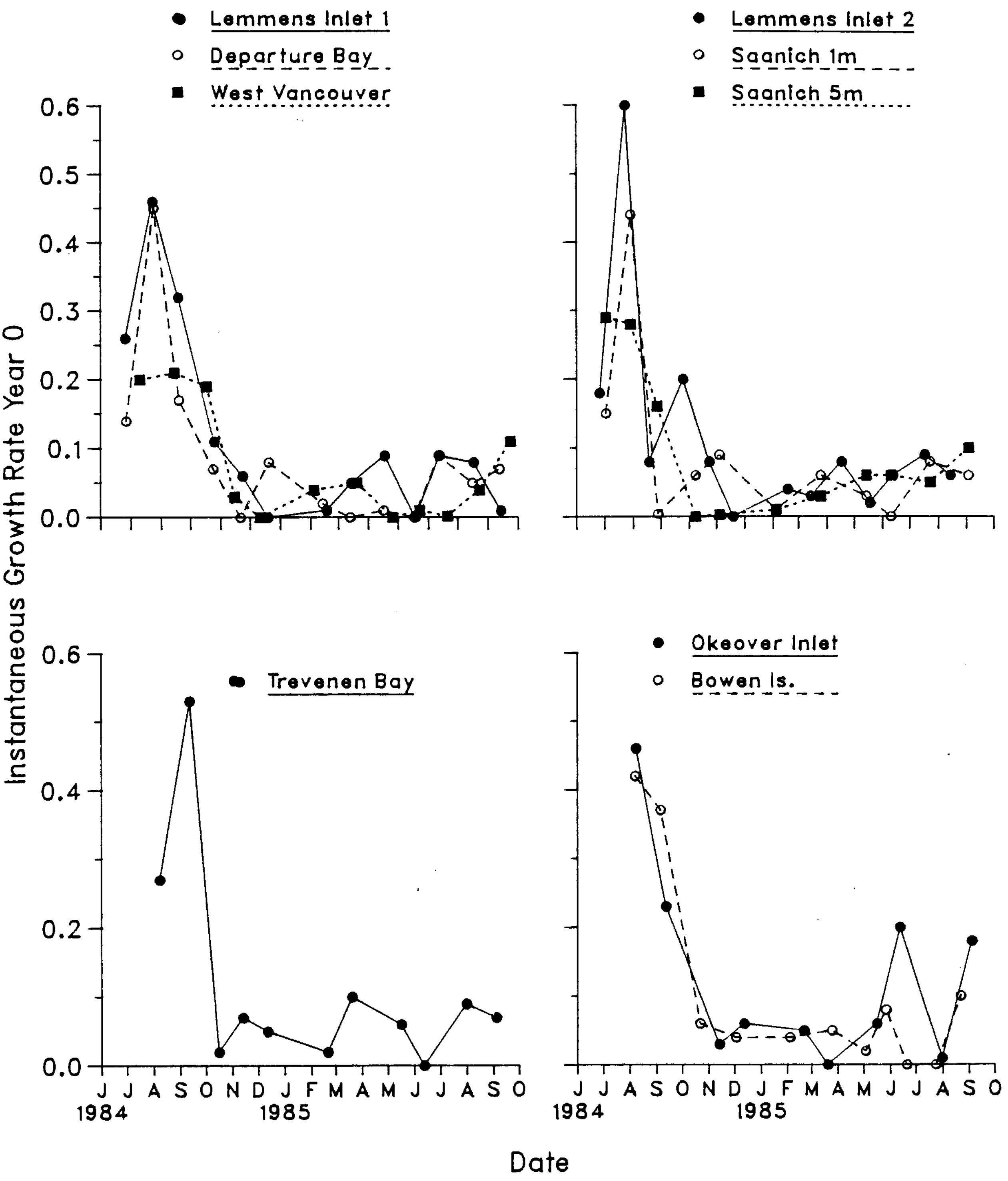

Lemmens Inlet 1
Departure Bay
West Vancouver
Lemmens Inlet 2
Saanich 1m
Saanich 5m
Trevenen Bay
Okeover Inlet
Bowen Is.
Instantaneous Growth Rate Year 0
0.6
0.5
0.4
0.3
0.2
0.1
0.0
J J A S O N D J F M A M J J A S O
1984
1985
Date

Fig. 3.3. Instantaneous growth rates for Year 1 oysters.

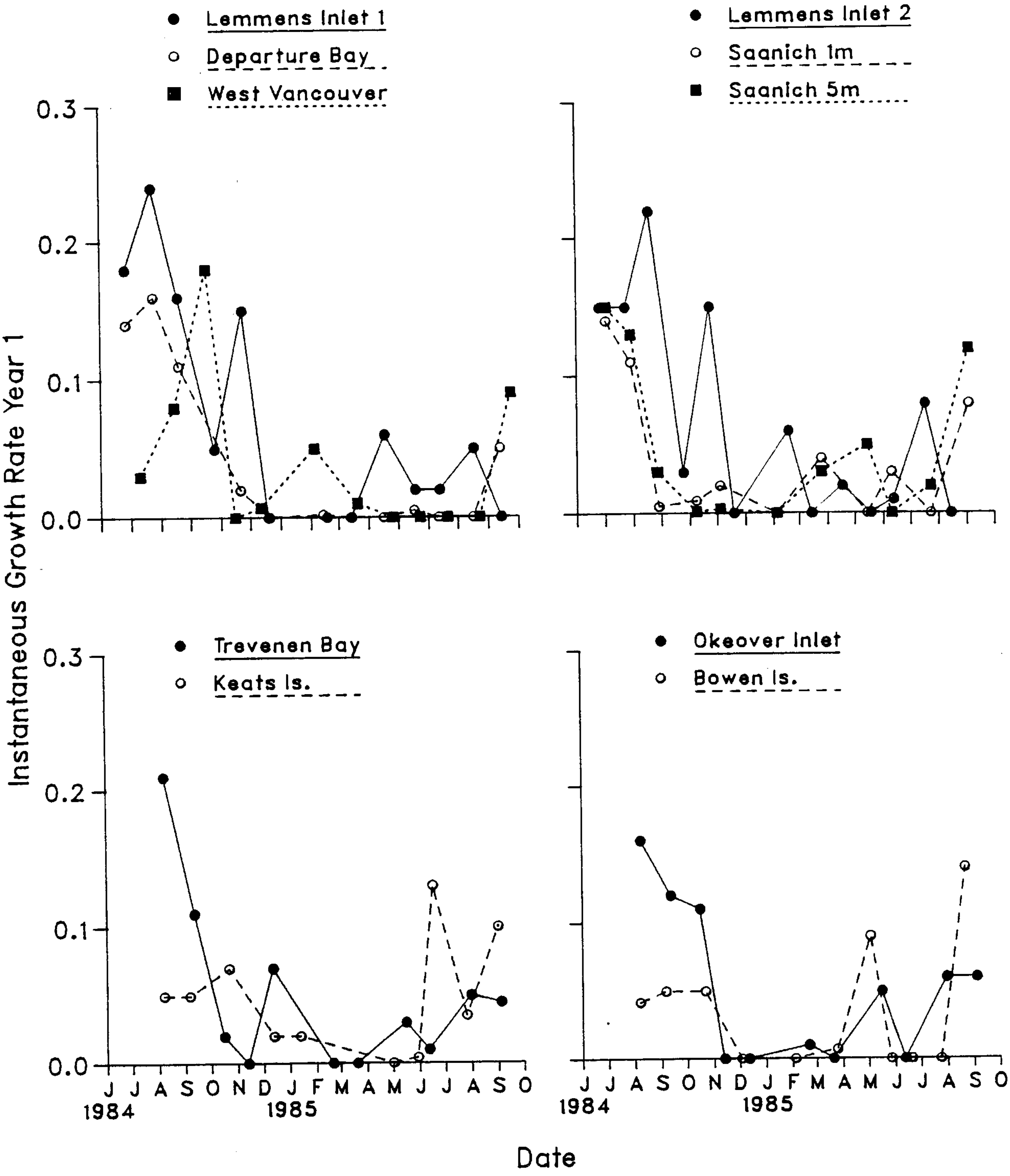

● Lemmens Inlet 1
○ Departure Bay
■ West Vancouver
● Lemmens Inlet 2
○ Saanich 1m
■ Saanich 5m
● Trevenen Bay
○ Keats Is.
● Okeover Inlet
○ Bowen Is.
Instantaneous Growth Rate Year 1
0.3
0.2
0.1
0.0
J J A S O N D J F M A M J J A S O
1984
1985
Date

Table 3.2. Multiple regressions predicting monthly instantaneous growth rates using environmental factors and initial size as dependent variables. Standardized regression coefficients are in parentheses. All regressions are highly significant ($p \leq 0.001$). CB = chlorophyll *b* ($\mu g \cdot l^{-1}$); WT = water temperature (°C); S = salinity (ppt); IS = initial size of oyster for each month (mm).

Age	β_0		Step 1		Step 2		Step 3		Step 4	r^2	n
Year 0	-0.081	+	0.129 $\log_e$CB (0.467)	+	0.007 WT (0.285)					0.40	84
	0.829	-	0.270 $\log_e$IS (-0.689)	+	0.012 WT (0.454)	+	0.009 S (0.250)			0.69	84
Year 1	-0.032	+	0.053 $\log_e$CB (0.411)	+	0.003 WT (0.287)					0.33	91
	0.395	+	0.026 $\log_e$CB (0.200)	+	0.005 WT (0.384)	-	0.113 $\log_e$IS (-0.408)	+	0.003 S (0.200)	0.45	91

Discussion

In British Columbia waters, annual oyster growth appears to be regulated by food supply and temperature. Site related growth variations were caused by differences in salinity and food supply.

For both Year 0 and Year 1 oysters, environmental factors accounted for less than half of the seasonal variation in growth. Initial size had a considerable effect on growth rates since growth efficiency in bivalves declines with age (Winter 1978). The addition of a size variable greatly increased the proportion of variance explained by the Year 0 growth regression model. The fit of the model for Year 1 growth was improved to a much lesser extent by the inclusion of the size variable. The low r^2 indicated that there were other variables affecting Year 1 growth which were not included in the analysis. A possible factor is reproductive output since the Year 1 oysters were probably capable of spawning by the second summer (Quayle 1969). As evidence, some gametic material was observed in oysters dissected during the summer of 1985. The allocation of energy from somatic growth to gametic production could be the final determinate of growth rate in mature oysters (Bayne and Newell 1983).

The fit of the regression models may have also been reduced by temporal variations in environmental factors which eluded the sampling program. Unfortunately logistical considerations limited the scope of monitoring the field sites. Regardless, the exploratory purposes of the analyses were fulfilled since the seasonal influences of food supply and water temperature upon oyster growth were distinguished.

In the regressions which involved only the environmental factors as dependent variables, available food as estimated by chlorophyll *b* concentrations was of greater importance than water temperature. This finding is in agreement with Elvin and Gonor (1979) who found for *Mytilus californianus* that food levels explained 96 % of the variance in growth while water temperature accounted for only 3 %. For two populations of *Mytilus edulis* in England, multiple regression analysis determined that food ration explained the same high proportion of seasonal variance in growth regardless whether or not temperature was included (B.L. Bayne, unpublished data cited in Bayne and Newell 1983). Kirby-Smith and Barber (1974), however, concluded that the growth of scallops in nature was temperature dependent as long as food concentrations remained above a certain level.

In fact, the two environmental variables have a combined effect upon oyster metabolism. The assimilation efficiency of bivalves rises with increasing food concentrations until an asymptote is reached which is temperature determined (Tenore and Dunstan 1973, Thompson and Bayne 1974). Ventilation function in the Pacific oyster is greatly reduced at temperatures below 8 - 10 °C which typically occur during winter in British

Columbia (Quayle 1969, Bernard 1983). Low food levels at these temperatures are not critical because the metabolic requirements of the oyster are very low (Bernard 1983). As water temperatures rise, so do the metabolic requirements of the oyster. High water temperatures combined with elevated levels of food supply result in a wide scope for growth (Mann and Ryther 1977, Bayne and Newell 1983). Such a situation occurred during the summer of 1984 at Lemmens Inlet 1 and 2 where high growth rates were observed.

Conversely, high water temperature and low food ration have been shown to cause negative growth in *C. gigas* (Malouf and Breese 1977) and *M. edulis* (Bayne and Widdows 1978, Incze et al. 1980). Chlorophyll *a* and POM levels were low at West Vancouver and Keats Island in August 1984, the month of maximum annual temperature, which resulted in very reduced oyster growth.

Temperature was not a significant factor in distinguishing between sites with different growth characteristics. Oysters were subjected to similar monthly temperatures at all sites with the exception of lower winter temperatures at Keats Island, Bowen Island and West Vancouver. Monthly water temperatures in well-mixed coastal waters are essentially the same within the narrow latitudinal range covered in the field study (Thomson 1981). In a comparison of oyster growing areas separated by wider latitudinal distances, differences in mean annual water temperatures were correlated to variation in oyster growth (Butler 1953).

The correlation of oyster growth to chlorophyll *b* rather then chlorophyll *a* is perhaps indicative of the nutritional importance of certain phytoplankton species. Chlorophyll *a* is ubiquitous to all species of phytoplankton but the chlorophyll *a* + *b* system is found only in the Classes Chlorophyceae, Euglenophyceae and Prasinophyceae (Parsons 1961, Parsons and Takahashi 1973). These small size species (< 10 μ in length), called nanoplankton, occur in low abundance in the open ocean but can be very common in nearshore areas (Sournia 1978).

Unfortunately, the majority of past surveys of phytoplankton assemblages in British Columbia fjords used net tows which permitted the escape of small nanoplankton (Harrison et al. 1983). In one of the few studies to examine the full size range of a fjord protoplankton community, Buchanan (1966) found that nanoplankton (5 - 60 μ in length) and ultraplankton (< 5 μ in length) are particularly abundant in Indian Arm. Although the number of nanoplankton taxa is small compared to other groups, such as diatoms, flagellate members of Chlorophyceae (*Pyramimonas grosii* and *Chlamydomonas sp.*) and Euglenophyceae (*Eutreptiella marina*) have considerable ecological importance. In a survey of an oyster culture area in England, Askew (1972) also reported high abundances of members of Chlorophyceae and Euglenophyceae. Incze et al. (1980) suggests that nanoplankton may be an important nutritional component of mussel diets in nature.

The retention efficiency of the filtration apparatus of *C. virginica* increases sharply as particle size increases from 1 to 4 μ (Haven and Morales-Alamo 1970). Retention efficiency then reaches a plateau which is unchanged for particle sizes up to 12 μ. For British Columbia waters, the predominant nanoplankton species associated with the chlorophyll *a* + *b* system have an average size of 3.5 μ which is in the range of optimal retention efficiency (Buchanan 1966). Further studies are required to assess the nutritional importance of small phytoplankton in oyster diets.

Salinity was an important factor in distinguishing low growth sites from medium and high growth sites. The oyster is adapted for survival in an estuarine environment but its growth is optimal in conditions closer to those of the marine environment. Bernard (1983) stated that somatic growth occurred in salinity ranging from 16 - 31 ppt with 24 ppt being optimal. Quayle (1969) estimated a similar optimal range from 20 - 25 ppt. Oysters have been successfully cultured in ponds with salinity approaching 40 ppt (King 1977). The lower end of the salinity range is more crucial and oyster growth is probably not affected when salinity conditions are above 20 - 22 ppt.

Low salinity levels can impart a significant metabolic cost upon the oyster. In adverse salinity conditions the oyster may close its shell and cease feeding activity (Pierce 1971, in Bernard 1983). Mean salinity readings at Keats Island, Bowen Island and West Vancouver were predominantly below 20 ppt throughout the study. Bernard (1983) demonstrated that salinity changes greater than 10 % are particularly stressful and that it may take several days for oysters to adapt to a new salinity regime. Acclimation to low salinity levels in the above three sites was particularly difficult since salinity conditions in July 1985, at West Vancouver, could sometimes fluctuate between 12.5 and 21.5 ppt over a tidal cycle (J.R. Brown, unpublished data). Reduced assimilation efficiency resulting from shell closures could explain the lack of growth in oysters at West Vancouver and Keats Island even in the presence of elevated food concentrations between May and July 1985.

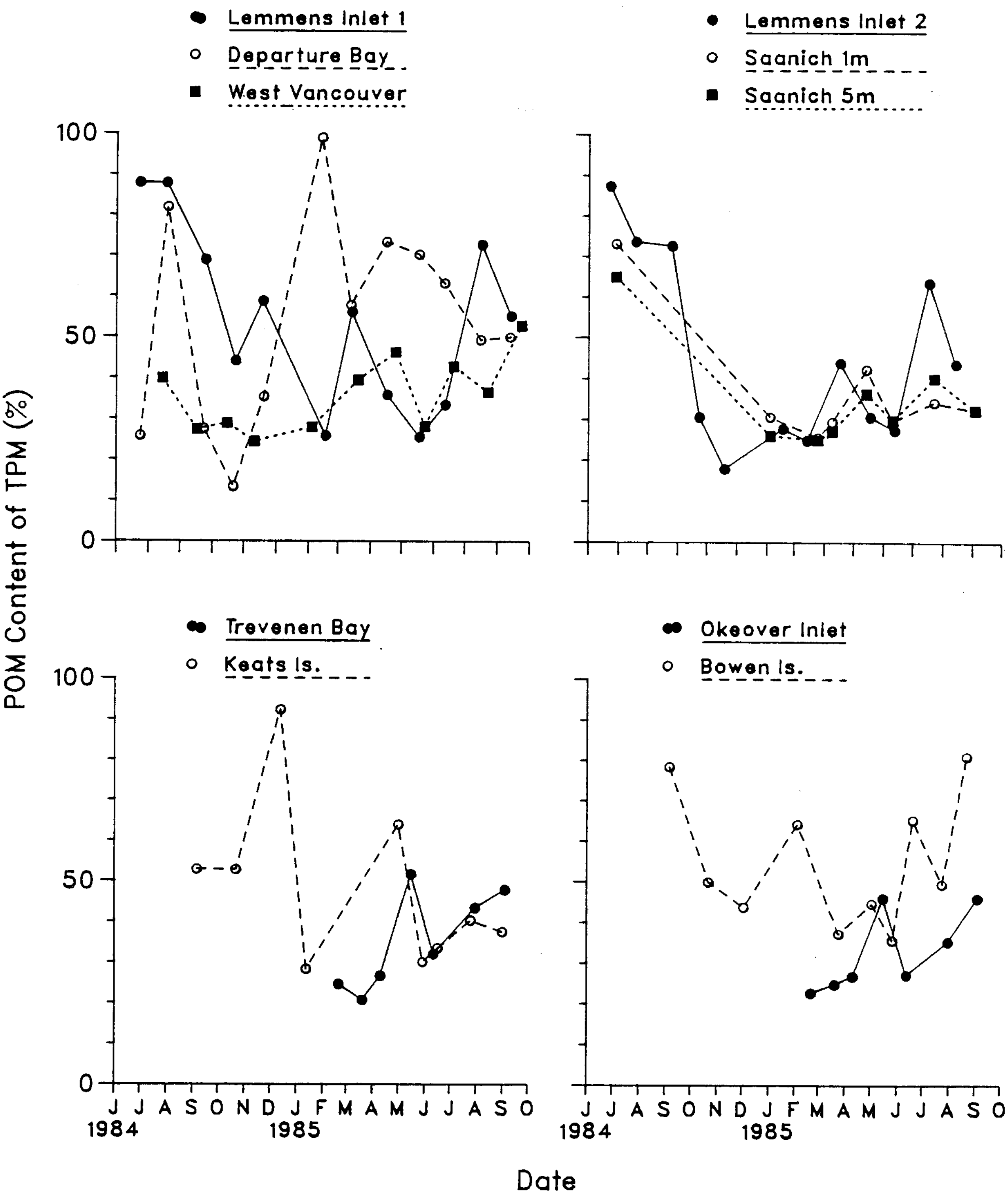
The correlation between POM and oyster growth is in agreement with previous findings (Malouf and Breese 1977, Widdows et al. 1979). Like chlorophyll *a*, POM is an estimate of food supply but it encompasses sources of particulate organic carbon other than phytoplankton. In this study, POM levels generally followed trends in phytoplankton pigment concentrations. Soniat et al. (1984) determined that lipids, carbohydrates and proteins which are commonly found in phytoplankton, may comprise only a small fraction of the POM during certain times of the year.

Widdows et al. (1979) concluded that not only the absolute amount of POM is important for bivalve growth but also the proportion of the total seston it comprises because high PIM concentrations can dilute the amount of food ingested. Vahl (1980) and Wallace and Runsen (1985) determined that growth in cultured scallops is inhibited when POM is less than 20 % of TPM. The addition of low amounts of silt to algal cultures fed to *M. edulis*, however, significantly increased growth over that of mussels feeding on pure algal solutions (Kiørboe et al. 1981). Newell and Jordan (1983) have suggested that *C. virginica* can maintain a positive energy balance even when the relative amount of food particles is low through active particle selection and ingestion.

In the present study, high POM:TPM ratios were frequently occurred at high growth sites during seasons of maximum growth (Fig. 3.4.). The POM:TPM ratio at Lemmens Inlet sites ranged from 88.0 % in summer to 25.0 % in winter. Ratios were generally reduced for low growth sites, such as West Vancouver which ranged from 39.0 - 52.0 %.

As previously mentioned, not all the POM may be food available to oysters. Though conversion factors have often been used to derive the energy content of POM, these estimates tend to be significantly lower compared to the results of wet oxidation (Newell 1982). If an indirect method must be used, the preferrable route is to convert chlorophyll *a* ($\mu g \cdot l^{-1}$) into carbon (mg) (Windows et al. 1979, Soniat et al. 1985). The carbon:chlorophyll *a* ratio in natural phytoplankton populations can vary from 25 - 60, depending upon species composition and nutritional condition (Strickland 1960, Parsons and Takahashi 1973). The predominant phytoplankton of coastal waters are members of Chlorophyceae and *Skeletenema sp.* (Stockner and Cliff

Fig. 3.4. Fraction of Total Particulate Matter (TPM) which is Particulate Organic Matter (POM).

Lemmens Inlet 1
Departure Bay
West Vancouver
Lemmens Inlet 2
Saanich 1m
Saanich 5m
Trevenen Bay
Keats Is.
Okeover Inlet
Bowen Is.
POM Content of TPM (%)
100
50
0
100
50
0
J J A S O N D J F M A M J J A S O
1984
1985
J J A S O N D J F M A M J J A S O
1984
1985
Date

1975, Stockner et al. 1979) thus a ratio of 26 is most appropriate (Parsons et al. 1961). This is the same ratio used by Soniat et al. (1984). Phytoplankton organic matter was determined from the equation:

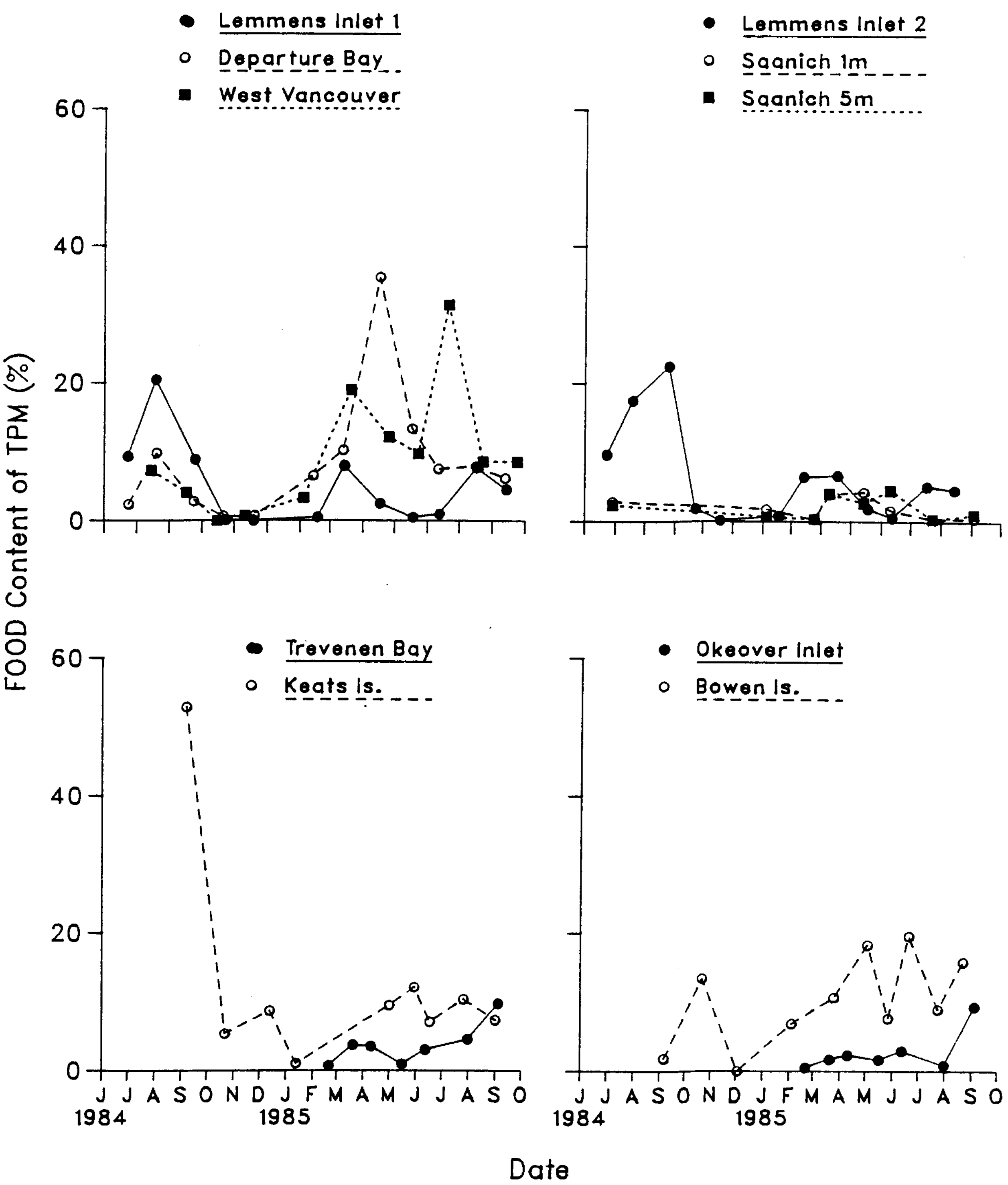
$$OM = 2.14 \times C$$

where OM is the phytoplankton organic matter (mg) and C is the amount of phytoplankton carbon (mg) (Widdows et al. 1979, Soniat et al 1984).

In Lemmens Inlet the percentage of TPM composed of OM (%FOOD) was highest (22.6 %) in fall and lowest (0.2 %) in winter (Fig. 3.5). West Vancouver had a peak %FOOD of 31.0 % in June 1985 and a low of 0.0 % in November 1984. In Galveston Bay, Texas, Soniat et al. (1985) found that %FOOD never exceeded 11.0 %. Widdows et al. (1979) using a carbon:chlorophyll *a* ratio of 54, reported maximum %FOOD of about 25.0 % in waters of southwest England. Areas of high growth in the present study, appear to have a large available food component in the seston.

The absolute levels of PIM measured in this study, were probably not at levels which would be limiting to the oyster (Bernard 1983). Kiørbore et al. (1981) found that high silt loadings ($8.0\ mg \cdot l^{-1}$) in the presence of high algal concentrations actually increased the growth of *M. edulis*. Furthermore, silt particles may be a substrate for organic compounds which are beneficial to oysters. Bernard (1983) contends that oysters have adapted to maximal particle concentrations which occur in local waters, thus their feeding

Fig. 3.5. Percentage of TPM which consists of phytoplankton organic matter (FOOD).


Lemmens Inlet 1
Departure Bay
West Vancouver
Lemmens Inlet 2
Saanich 1m
Saanich 5m
Trevenen Bay
Keats Is.
Okeover Inlet
Bowen Is.
FOOD Content of TPM (%)
0
20
40
60
J J A S O N D J F M A M J J A S O
1984
1985
Date

apparatus could handle high seasonal seston levels.

The discriminant function was not as successful in separating medium growth sites from high growth sites. This may be attributable to two variables not included in the analyses, fouling organisms and water currents. Oysters at low growth sites and Departure Bay were in areas of heavy mussel sets. Fouling has been shown to negatively impact oyster growth although the actual effects have not been quantified (Micheal and Chew 1976). Saanich Inlet and Departure Bay were protected areas subjected to limited wave action and tidal flow. Trevenen Bay and Okeover Inlet, which had high growth rates but levels of %FOOD lower than Lemmens Inlet, were areas with strong water circulation from waves and tidal currents. Water currents have been shown to increase bivalve filteration rates slightly (Walne 1972) but of greater importance is the increase in the number of food particles coming into contact with the oyster (Frechette and Bourget 1985).

CHAPTER IV

A HABITAT SUITABILITY INDEX MODEL FOR THE CULTURE OF THE PACIFIC OYSTER

Introduction

The success of an aquaculture operation is strongly dependent upon the selection of a site with the biological and physical characteristics necessary to promote the rapid growth and high survival of the cultured species. In previous chapters, it was shown that growth of oysters is significantly influenced by environmental conditions. Site-related variations in the growth and survival of marine bivalves have been demonstrated for *Mytilus edulis* (Incze et al. 1980), *Mya arenaria* (Appeldoorn 1983) and *Crassostrea virginica* (Mallet and Haley 1983).

Despite the importance of environmental factors, few attempts have been made to quantify the suitability of a habitat for aquaculture. The ability to represent the habitat requirements of aquaculture in the coastal planning process will increase in importance as aquaculture competes for the use of sheltered coastal waters with other industries such as fishing, forestry and tourism. The long-term viability of aquaculture may depend upon the establishment of coastal reserves which are protected from the environmental impacts of industrial and urban developments.

A methodology, therefore, is required to enable management agencies and aquaculturists to compare the aquaculture potential of different coastal areas. Current site evaluation criteria in British Columbia are based upon rating several environmental factors on a relative scale from which overall site suitability is the sum of individual scores (Smith 1975). Galtsoff (1964) proposed a similar system for evaluating estuarine habitat suitability for *C. virginica*. The summation approach, however, can not account for interactions between variables or the non-linear response of oysters to changes in particular variables.

Multivariate statistical models have been used to predict bivalve growth or production from environmental factors (Appeldoorn 1983, Ulanowicz et al. 1982, Hall 1983). The Morphoedaphic Index or MEI is another multivariate approach which provides estimates of fish production in fresh water lakes from data on lake bathmetry, temperature and total dissolved solids (Ryder et al. 1974, Schlesinger and Regier 1982). The development of these models necessitates large data sets and the derived model is not valid unless it is tested with additional data not used in its formulation (Holling 1978). The oyster industry in British Columbia, although it was established in 1912 or 1913 (Quayle 1969), lacks a long-term, consistent data base on either production or oceanographic conditions in culture areas. Laboratory and field experiments, however, have provided a considerable amount of information about the responses of

C. gigas and *C. virginica* to changes in different environmental factors. This information could be used to generate a general hypothesis regarding the habitat requirements of oyster aquaculture.

The U.S. Fish and Wildlife Service (USFWS) has used existing information to model the habitat requirements of several terrestrial and aquatic species (Schamberger and Krohn 1982). The Habitat Evaluation Procedures (HEP) were developed in order to document the non-monetary value of fish and wildlife resources (USFWS 1980). This methodology is an accounting system for the quality and quantity of habitat available to a selected species (USFWS 1980). The HEP utilizes the wildlife unit which is determined from the equation:

$$WU = HSI \times Area$$

where WU is the wildlife unit, HSI is the Habitat Suitability Index and Area is the amount of habitat of a particular HSI quality rating.

The HSI documents the ability of key habitat components to fulfill the requirements of crucial life requisites of a species (USFWS 1981). The HSI model is constructed from existing literature on species-environment relationships. The model compares the optimum habitat conditions for a species, as described in the literature, with existing habitat conditions. Habitat suitability is rated on a scale from 0.0 to 1.0, where 1.0 represents optimum habitat and 0.0 represents totally unsuitable habitat. The HSI is assumed to be linearly related to the ecological carrying capacity of the habitat.

The habitat requirements of many terrestrial, freshwater and marine species have been modelled using HSI techniques. Several HSI models have been constructed for marine bivalves including *C. virginica* in the Gulf of Mexico (Cake 1983). That model evaluates the suitability of subtidal estuarine areas for propagating natural oyster populations. Rodnick and Li (1983) developed a HSI model for natural populations of little-neck clams (*Protothaca staminea*).

Since the HSI methodology deals with the habitat relationships of a single species, it would appear to be an ideal frame-work for modelling the habitat requirements of mono-species aquaculture. To my knowledge, a HSI model has not been developed for the aquaculture of any invertebrate or finfish species. The purpose of this part of the study was to develop a HSI model for determining the suitability of coastal areas in British Columbia for Pacific oyster culture.

Prior to its application to aquaculture, some basic assumptions of the HSI methodology must be modified. The HSI is assumed to be linearly related to ecological carrying capacity which is usually measured by species abundance (USFWS 1981) or habitat usage by a species (Lancia et al. 1982). In aquaculture, population density is controlled by the grower. It is possible that a coastal area may be developed by aquaculture to the extent that phytoplankton are over-grazed (Incze et al. 1981) or waste products accumulate to potentially noxious levels (Kaspar et al. 1985). Modelling the aquaculture production capacity of an area may be a future objective but for the purposes of the construction of the initial habitat model, density-dependent effects were assumed to be negligible. The function of the model is to rate the habitat suitability in terms of growth or production of uncrowded oysters.

Some HSI models cover the entire life-cycle of the species. Sub-units of the model are used to take into consideration the changing habitat requirements as the animal progresses from one life stage to another (USFWS 1981). For example, the American oyster HSI model, considered the habitat requirements of both larval and adult oysters (Cake 1983). In aquaculture oysters are transplanted into the culture area after larval metamorphorsis into sessile juveniles. Oyster juveniles are either collected from areas which have a fairly consistent natural spat-fall (Quayle 1969) or hatchery sources (Burrell 1985). The HSI model, therefore, was structured to describe the habitat requirements of post-settlement oysters. Environmental variables were evaluated in regards to conditions for maximal growth and survival but not reproduction.

The completed HSI model is an untested hypothesis about the relationship of a species to its habitat (USFWS 1981). Testing the model is crucial in understanding its behaviour and in determining the conditions under which it may become unreliable (Farmer et al. 1982). The USFWS (1980) outlines a sequence of validation procedures which in ascending order of improved confidence in the model are; review by author, analyses with sample data, review by a species authority and testing with field data. The majority of the HSI models in use by the USFWS have not been field validated because of the high costs involved (Lancia et al. 1982).

Given the potential application of an oyster aquaculture HSI model by aquaculturists and management agencies, field validation was essential. In addition to testing the overall assumptions of the model in the field, an attempt was made to evaluate seasonal performance of the model by simulating a short sampling program.

Methods

From available literature on oyster-environment interactions, a HSI model was constructed following general procedures developed by the USFWS (1981). Suitability Index (SI) graphs were derived which rank the conditions of variables on a scale from 0.0 to 1.0, where 1.0 represents optimal conditions and 0.0 represents unsuitable conditions. Optimal conditions were considered those which promoted high oyster growth and survival. When quantitative results were not available for a particular variable histograms were used to derive SI values from qualitative information. Life Requisite Suitability Index (LRSI) equations were used to describe multiple variable interactions. The overall HSI was derived from a composite of LRSI values and rated habitat suitability for oyster culture on a scale from 0.0 to 1.0. Hypothetical data sets were used to initially test the model and to verify that the output reflected currently held perceptions of oyster-environment interactions (Farmer et al. 1982).

Reference should be made to the methods in Chapters I and II for description of field sites and measurements of oyster growth, survival and environmental variables. Fouling organism density and pH level were additional variables measured for validating the HSI model. A portable Beckman pH meter was used to measure pH level. Difficulties obtaining a reliable meter lead to the discontinuation of this measurement in September, however, pH levels below 7.0 which are stressful to oysters (Carriker 1959, Epifanio et al. 1975) were not recorded.

Fouling was assessed qualitatively from densities of mussels (*Mytilus edulis*) and barnacles (*Balanus glandula*) on the shell of a typical oyster. If little oyster shell was visible, then fouling was heavy (SI = 0.25). Moderate fouling was defined as partial coverage (SI = 0.50) and if only the occaisonal fouling organism was present, then fouling was light (SI = 0.75 or 1.0). Other epibiota such as tunicates and various sea weeds which are common in Northwest Pacific waters do not pose a serious fouling problem for aquaculture (Quayle 1969).

Instrumentation necessary to quantify water movement was not available so the variable was given an SI value of 1.0 for the purposes of testing the model. Model assumptions regarding intertidal exposure and substrate composition were not tested since on-bottom sites were not included in the field study. The effects of these variables upon oyster growth have been studied in depth (Gunter 1938, Quayle 1969, Spencer et al. 1978) thus the model assumptions derived from these works were considered realistic.

Oyster growth was calculated from the equation:

$$G = \frac{H_t - H_{t-1}}{D}$$

where G is the daily increase in shell height ($\text{mm}\cdot\text{day}^{-1}$), H_t is shell height (mm) at the end of the study, H_{t-1} is shell height (mm) at the beginning of the study and D is number of days between observations.

Oyster production was calculated using the growth increment summation method described by Rigler and Downing (1984). This calculation takes into account both increases in biomass as a result of growth and decreases due to mortality. For the Year 1 oysters, dry meat weight data were obtained from monthly samples. Dry meat weights of Year 0 oysters and biomass losses from mortality for both year classes were determined from regressions derived from Year 1 oyster data. For each site, dry meat weights were calculated from the equation:

$$\log_{10}DWT = \log_{10} A + B \log_{10}H$$

where DWT is dry meat weight (g) and H is shell height (mm). Total production ($g \cdot 100$ $oysters^{-1} \cdot day^{-1}$) was the summation of the monthly incremental changes in dry meat weight of an initial population of 100 oysters divided by the number of days oysters were grown at a particular site.

Environmental data were used to derive site-specific HSI ratings which were then regressed against corresponding growth or production estimates. Initial regression analysis involved HSI values derived from the mean of environmental observations over the entire study period. Then the effects of limited sampling programs upon model output were assessed by partitioning the environmental data set into "seasons" of 3 months duration. The seasons were Sum84 (Jun., Jul., Aug. 1984), Fall85 (Sept., Oct., Nov.1984), Win84 (Dec.1984, Jan., Feb. 1985), Spr85 (Mar., Apr., May 1985) and Sum85 (Jun., Jul., Aug. 1985). Environment data from each of these periods were used to derive HSI values which were regressed against whole study growth rates. Regressions were done using BMDP program P6D.

Results

The Model

From the literature, twelve variables were identified as having an influence upon oyster growth and survival (Table 4.1). For each variable a corresponding SI graph was drawn (Fig. 4.1). Multiple variable interactions were accounted for in three Life Requisite Suitability Indices (LRSI) (Table 4.2).

The first life requisite was LRSI(Growth) which encompassed those factors in which changes will elicit an incremental growth response. For both on-bottom and off-bottom culture, a composite suitability index for food and temperature was derived. Water temperature influences ventilation rate, hence assimilation efficiency in bivalves (Bernard 1983). High water temperatures during periods of low food availability can have a detrimental effect on growth (Malouf and Breese 1977). Growth is greatly curtailed or non-existent below temperatures between 8 - 10 °C (Quayle 1969).

The SI graph for available food is expressed in terms of concentration of either total particulate matter ($mg \cdot l^{-1}$) or phytoplankton pigments ($\mu g \cdot l^{-1}$ chlorophyll *a*). The functional relationship of available food to SI follows that described by Malouf and Bresse (1977) and Bernard (1983) for food concentration and assimilation efficiency. The range of particle concentrations quoted by Bernard was 10 x higher than that found in the Strait of Georgia (Harrison et al. 1983), coastal inlets

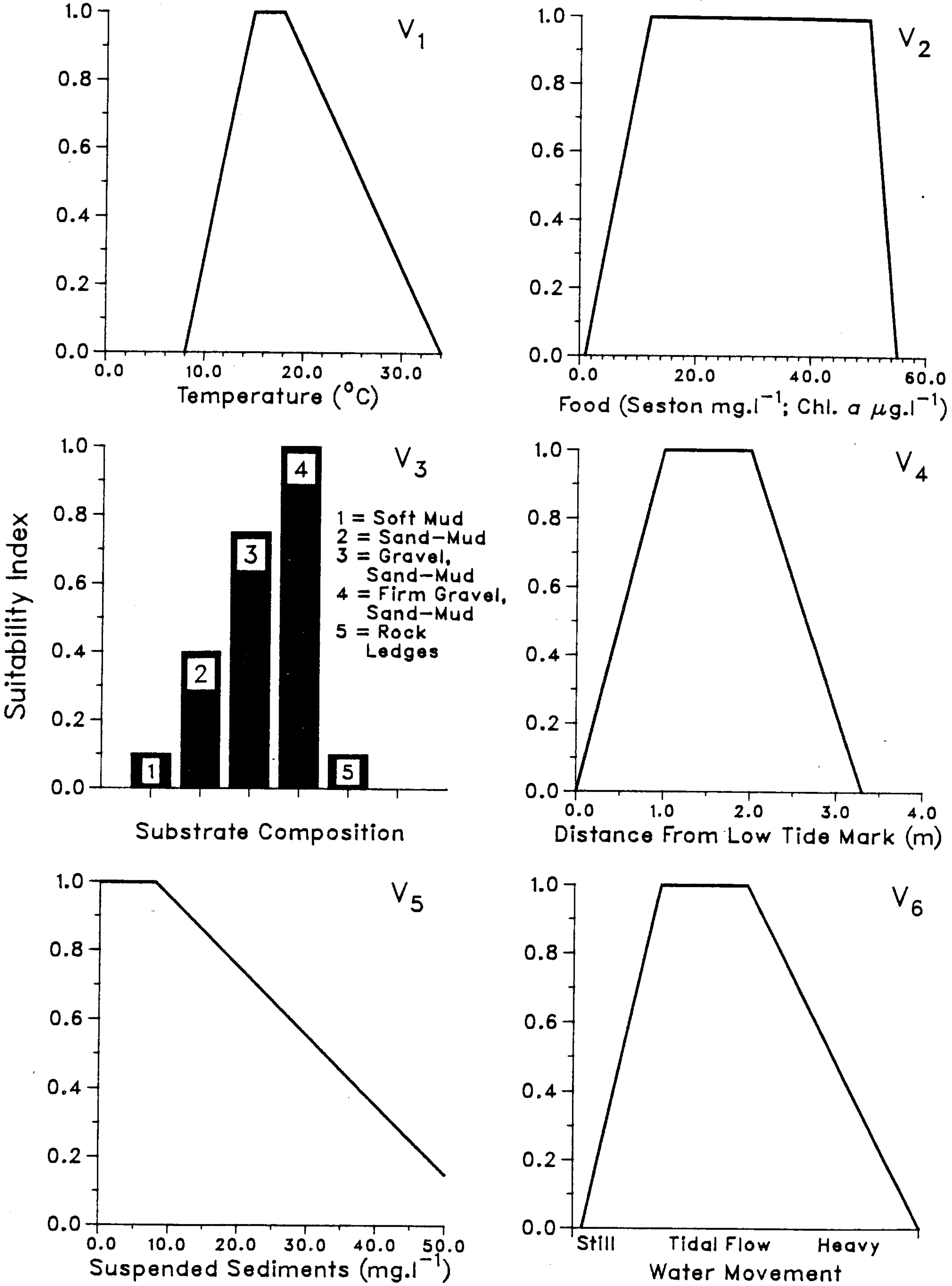
Table 4.1. Variables and assumptions used in the formulation of the model.

Variables	Source	Assumptions
V_1 Temperature	Bernard 1983 Malouf & Breese 1977 Mann & Ryther 1977 Quayle 1969	Range: 8.0 - 34.0 °C Optimum: 15.0 - 18.0 °C
V_2 Available Food	Bernard 1983 Malouf & Breese 1977 Tenore & Dunstan 1973	Range: 1.0 - 55.0 $\mu g \cdot l^{-1}$ chlorophyll *a* or $mg \cdot l^{-1}$ Particulate Organic Matter Optimum: 12.0+ $\mu g \cdot l^{-1}$ or $mg \cdot l^{-1}$
V_3 Substrate	Quayle 1969 Gunter 1938	Optimum: substrates of gravel with firm mud. Hard or silty bottoms are undesirable.
V_4 Intertidal Exposure	Spencer et al 1978 Pereya 1961 Woelke 1959a	Optimum: 0.5 - 2.0 m above the 0.0 m tide level.
V_5 Suspended Sediments	Wallace & Reinsnes 1985 Bernard 1983 Loosanoff & Tommers 1948	Range: 0.0 - 100.0 $mg \cdot l^{-1}$ Particulate Inorganic Matter Optimum: 0.0 - 8.0 $mg \cdot l^{-1}$
V_6 Water Movement	Frechette & Bourget 1985 Westley 1965 Walne 1972	Poor water circulation restricts the amount of available food and permits the accumulation of noxious waste products. Excessive wave action should be avoided.

Table 4.1 cont.

V_7 Disease	Sindermann 1984 Bourne 1979 Quayle 1961, 1969	Optimum: not present
V_8 Fouling Organisms	Humphries 1976 Michael & Chew 1976 Quayle 1969, 1971	Optimum: not present although a moderate level can be tolerated.
V_9 Predators	Bourne 1979 Quayle 1969 Woelke 1959b	Optimum: not present although a moderate level can be tolerated.
V_{10} Salinity	Bernard 1983 Hopkins 1936 King 1977 Quayle 1969	Range: 10.0 - 35.0+ ppt Optimum: 24.0+ ppt
V_{11} Oxygen	Davis 1975 Westley 1965	Not limiting at high saturation levels.
V_{12} pH	Epifanio et al 1975 Kuwatani & Nishii 1969 Carriker 1959	Range: 7.50 - 8.0+ Optimum: 7.80+

Fig. 4.1. Suitability Index graphs for habitat variables: V_1 = water temperature; V_2 = available food; V_3 = substrate composition; V_4 = intertidal exposure; V_5 = suspended sediments; V_6 = water movement; V_7 = disease (cross-hatched areas are range of SI values for V_7, V_8 and V_9; V_9 = predation; V_{10} = salinity; V_{11} = dissolved oxygen and V_{12} = pH.


V1
Temperature (°C)
0.0
10.0
20.0
30.0
V2
Food (Seston mg.l^{-1}; Chl. *a* μg.l^{-1})
0.0
20.0
40.0
60.0
V3
Suitability Index
1.0
0.8
0.6
0.4
0.2
0.0
1
2
3
4
5
1 = Soft Mud
2 = Sand–Mud
3 = Gravel, Sand–Mud
4 = Firm Gravel, Sand–Mud
5 = Rock Ledges
Substrate Composition
V4
Distance From Low Tide Mark (m)
0.0
1.0
2.0
3.0
4.0
V5
Suspended Sediments (mg.l^{-1})
0.0
10.0
20.0
30.0
40.0
50.0
V6
Still
Tidal Flow
Heavy
Water Movement

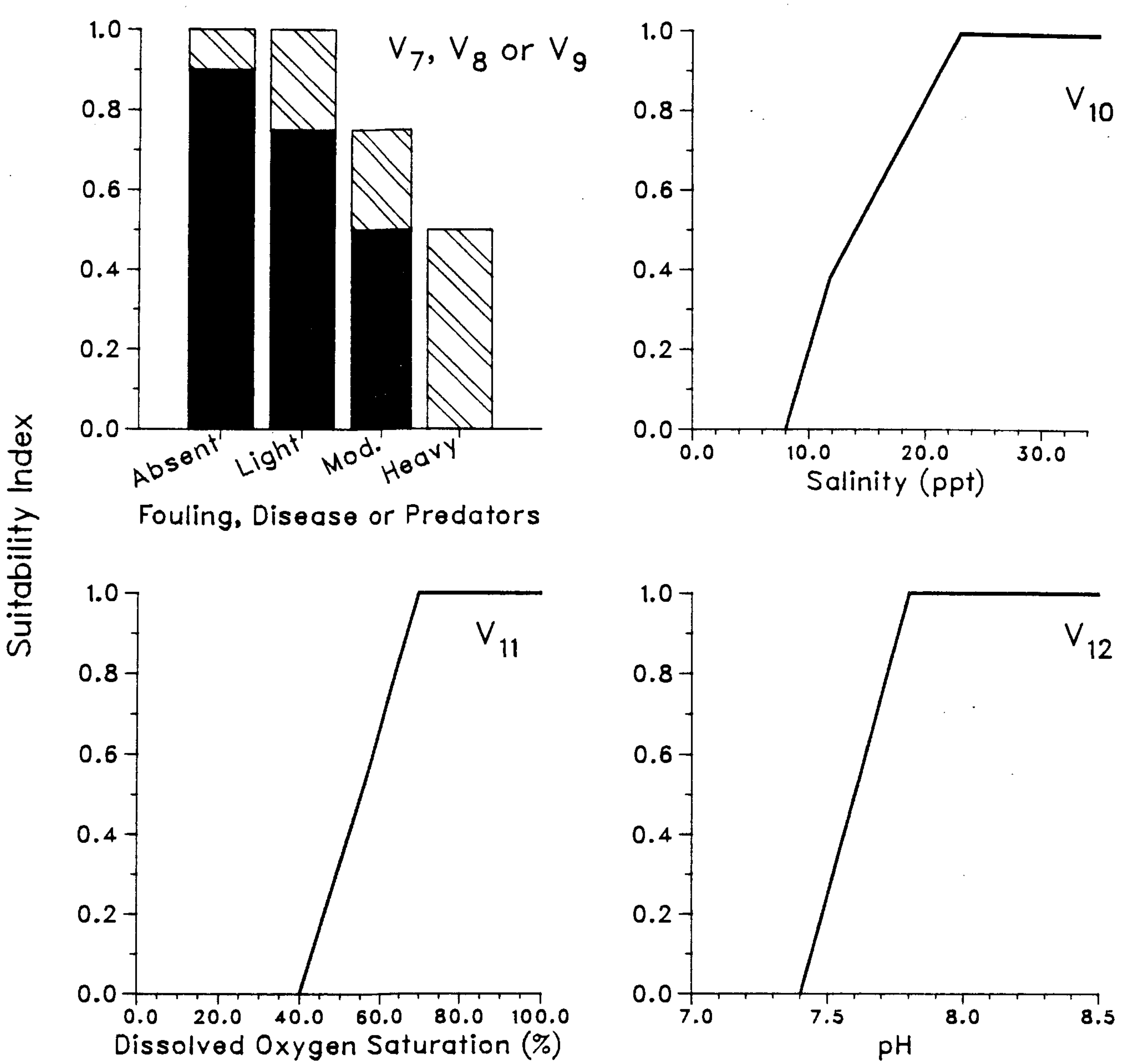

Suitability Index
1.0
0.8
0.6
0.4
0.2
0.0
V_7, V_8 or V_9
Absent
Light
Mod.
Heavy
Fouling, Disease or Predators
V_{10}
0.0
10.0
20.0
30.0
Salinity (ppt)
V_{11}
0.0
20.0
40.0
60.0
80.0
100.0
Dissolved Oxygen Saturation (%)
V_{12}
7.0
7.5
8.0
8.5
pH

Table 4.2. Life Requisite Suitability Index (LRSI) and Habitat Suitability Index (HSI) equations. The variable Suitability Index (SI) values from Fig 4.1 are denoted as V_a where a is the variable number.

Model Level	Equation	Condition
LRSI(Growth)	$(V_1 \times V_2)^{0.5}$	For off-bottom culture.
	The lesser of $(V_1 \times V_2)^{0.5}$, V_3 or V_4.	For on-bottom culture.
LRSI(Survival)	$(V_5 \times V_6 \times V_7)^{0.33}$	If both V_5 and $V_6 < 0.70$.
	$(V_b \times V_7)^{0.5}$	If only one (V_b) of V_5 or $V_6 < 0.70$.
	V_7	If both V_5 and $V_6 \geq 0.70$.
	The lesser of V_8, V_9 or the above equations.	If V_8 or V_9 are present.
LRSI(Water Chemistry)	$(V_{10} \times V_{11} \times V_{12})^{0.33}$	If both V_{11} and $V_{12} < 0.70$.
	$(V_c \times V_{10})^{0.5}$	If only one (V_c of V_{11} or $V_{12} < 0.70$.
	V_{10}	If both V_{11} and $V_{12} \geq 0.70$.
HSI	$\{\text{LRSI(Growth)} \times \text{LRSI(Survival)}\}^{0.5}$	If LRSI(Water Chemistry) ≥ 0.70.
	$\{(\text{LRSI(Growth)} \times \text{LRSI(Water Chemistry)})^{0.5} \times \text{LRSI(Survival)}\}^{0.5}$	If LRSI(Water Chemistry) < 0.70.

(Stockner and Cliff 1975) and seston samples collected in the present study (see Chapter II).

A geometric mean was used to calculate variable interactions because compensatory relationships between variables were perceived to be weak (USFWS 1980). For off-bottom culture, LRSI(Growth) was equal to the geometric mean of water temperature and available food. The least suitable of temperature-food mean, substrate composition or intertidal exposure, was LRSI(Growth) for on-bottom culture.

The second life requisite, LRSI(Survival), concerned variables which have negative effects on growth and survival. Suspended sediments, fouling organisms, predators and disease were all considered to be optimal when absent or present at very low levels. Disease is very limiting to oyster culture although the frequency and intensity of out-breaks has been low in British Columbia waters in comparison to the Atlantic oyster industry (Quayle 1961, 1969, Bourne 1979). High densities of predators (primarily the seastars, *Pisaster ochraceus* and *Pycnopodia helianthoides*) and fouling organisms (particularly *Mytilus edulis* and *Balanus glandula*) require more culture maintenance thereby increasing labour costs (Quayle 1969, 1971, Michael and Chew 1976). Suspended sediment concentrations in excess of 75.0 $mg \cdot l^{-1}$ could be harmful to the oyster (Bernard 1983) although such levels have not been reported in coastal fjords (Thomson 1981, Harrison et al. 1983). In fact, low levels of silt (> 8.0 $mg \cdot l^{-1}$) have been shown to increase the growth of mussels feeding on a mono-species culture of phytoplankton (Kiørboe et al. 1981).

Water circulation at tidal flow velocities can be beneficial through the movement of food particles and dissipation of waste products (Westley 1965, Walne 1972, Malouf and Breese 1977). Stagnant water or heavy wave action are extreme conditions which have negative effects on oyster culture (Quayle 1969). Thus water movement and suspended sediments are not included in the model unless their respective SI values are less than 0.70.

The third life requisite includes water chemistry variables which do not affect growth and survival as long as variable conditions fall within the optimal zone of the oyster. The LRSI(Water Chemistry) includes dissolved oxygen, pH and salinity. Dissolved oxygen and pH are not at limiting levels to oysters in coastal embayments which have some water circulation (Westley 1965, Kuwatani and Nishii 1969, Davis 1975). Both variables fluctuate seasonally with phytoplankton abundance (Parsons and Takahashi 1973) but remain within the tolerance zone of oysters. It is conceivable, however, that intolerable conditions of these variables could exist as the result of poor water circulation or pollution (Menzel 1979).

Salinity can vary greatly with season and location in British Columbia waters (Thomson 1981, Harrison et al. 1983). Due to seasonal influxes of freshwater, some areas have prolonged periods of salinity readings below 20 ppt which are stressful to oysters (Quayle 1969, Bernard 1983).

If LRSI(Water Chemistry) is not limiting (≤ 0.70), then the overall HSI is the mean of LRSI(Growth) and LRSI(Survival) (Table 4.2). If LRSI(Water Chemistry) is limiting then oyster growth is assumed to be reduced. The geometric mean of LRSI(Growth) and LRSI(Water Chemistry) is first calculated then the mean of this value and LRSI(Survival) is equal to the overall HSI.

Field Evaluation

Oyster growth and environmental conditions were discussed in detail in Chapters I and III. Briefly, differences in oyster growth between certain areas were shown to be significant. Salinity, chlorophyll concentrations, seston and fouling organims also showed great variation between sites. Water temperature fluctuated seasonal but differed little between sites at a given time of the year. Phytoplankton biomass and salinity also fluctuated seasonally.

Site-specific regressions were used to convert the shell height data of Year 0 oysters and shell height of mortalities of both year classes into dry meat weight (Table A.15). Using this transformed data and dry meat weight data on Year 1 oysters, production ($g \cdot 100\ oysters^{-1} \cdot day^{-1}$) was calculated for Year 0 and Year 1 oysters (Table 4.3). The production figures largely followed the observed trends in shell height and meat growth. For a given site, Year 0 production

Table 4.3. Production ($g \cdot 100\ oysters^{-1} \cdot day^{-1}$) of Year 0 and Year 1 oysters over 14 months.

Age Class	Lemmens Inlet 1	Lemmens Inlet 2	Trevenen Bay	Okeover Inlet	Departure Bay	Saanich 1 m	Saanich 5 m	Bowen Island	Keats Island	West Vancouver
Year 0	0.375	0.856	0.652	0.866	0.208	0.303	0.208	0.244	--	0.136
Year 1	1.375	1.603	1.403	1.821	0.878	0.876	0.925	0.763	0.482	0.491

(0.136 - 0.866 g·100 oysters^{-1}·day^{-1}) was lower than that of Year 1 (0.482 - 1.821 g·100 oysters·$^{-1}$day^{-1}).

The highest production of Year 1 oysters occurred at Okeover Inlet followed by Trevenen Bay, Lemmens Inlet 1 and 2. Lower levels of production were recorded for Departure Bay, Bowen Island, Saanich 1 m and 5 m. The lowest production occurred at sites with low growth which were West Vancouver and Keats Island Year 0 oyster production was highest at Lemmens Inlet 2 and Okeover Inlet. Trevenen Bay was slightly lower and production at Lemmens Inlet 1 was markedly below it but above the remaining sites. The low level of production for Year 0 at Saanich 5 m and Departure Bay contrasts with the moderate production level sustained by Year 1 at these sites and can be attributed to the low survival rates of Year 0 oysters.

A summary of growth rates, environmental variable means and derived HSI values are presented in Table 4.4. For a particular environment variable, the annual mean was calculated from monthly means, excluding data collected in December, January and February. Low water temperatures and near absence of phytoplankton biomass during these months, resulted in HSI values which were judged to be too low given the observed annual oyster growth. Dissolved oxygen, pH, disease and predation were not found at levels harmful to oysters at any site and so these variables were given SI values of 1.0.

Table 4.4. Summary of data used in model validation. Growth and environment variables are means for entire study period from June 1984 to August 1985. Data collected from November 1984 to February 1985 were excluded from calculations of environment variable means. Growth 0 = shell growth Year 0; Growth 1 = shell growth Year 1.

Site	Growth 0 ($mm \cdot day^{-1}$)	Growth 1 ($mm \cdot day^{-1}$)	Temperature (°C)	Salinity (ppt)	Chl. *a* ($\mu g \cdot l^{-1}$)	Silt ($mg \cdot l^{-1}$)	Fouling SI	HSI
Lemmens Inlet 1	0.167	0.146	14.7	24.9	8.56	6.2	0.75	0.77
Lemmens Inlet 2	0.189	0.146	14.7	25.2	10.51	6.3	1.00	0.95
Trevenen Bay	0.168	0.120	13.0	24.5	6.86	8.5	1.00	0.77
Okeover Inlet	0.185	0.133	14.6	24.4	5.25	9.2	1.00	0.74
Departure Bay	0.110	0.067	14.5	23.2	4.03	1.3	0.50	0.47
Saanich 1m	0.118	0.081	14.0	25.9	3.59	10.6	0.50	0.43
Saanich 5m	0.127	0.105	13.0	26.3	4.34	10.1	1.00	0.64
Bowen Is.	0.120	0.053	14.4	17.3	6.95	1.7	0.25	0.41
Keats Is.	--	0.074	14.6	14.3	4.69	1.6	0.25	0.36
West Vancouver	0.089	0.069	13.9	18.4	10.72	2.5	0.25	0.46

Regressions of HSI values (based upon complete study environmental data) against oyster growth were found to be highly significant for both Year 0 ($r^2 = 0.82$, $p \leq 0.001$) and Year 1 ($r^2 = 0.88$, $p \leq 0.001$) oysters (Fig. 4.2A and B). There were also significant but lower correlations between HSI values and production for Year 0 ($r^2 = 0.65$, $p \leq 0.01$) and Year 1 ($r^2 = 0.77$, $p \leq 0.001$) oysters (Fig. 4.2C and D).

Fluctuations in phytoplankton biomass strongly affected model predictions model when data from 3 month seasonal periods were used as input. Correlations between seasonal HSI values and growth of Year 0 and Year 1 oysters are summarized in Table 4.5. The patterns of correlations were similar for both year classes. Correlations between HSI values and shell growth were highest using input data collected in August 1984 and Spr85 (March-May). For Spr85 data, chlorophyll *a* concentration was a better estimate of available food than TPM. For August and Fall 1984, HSI ratings based on TPM resulted in better correlations than those derived from phytoplankton pigment data. Data from Win84 and Sum84 resulted in poor and generally, non-significant correlations. Zero HSI values occurred for all sites when Win84 data were used as input.

While the correlation between HSI ratings derived from Spr85 and oyster growth was highly significant, HSI values were slightly lower than those calculated from entire study data (Fig. 4.3.). Lower water temperatures associated with Spr85 data were primarily responsible for the uniformly depressed HSI

Fig. 4.2. Habitat Suitability Index values derived from entire study environmental data regressed against: (A) Year 0 shell growth; (B) Year 1 shell growth; (C) Year 0 production and (D) Year 1 production. Sites are coded as; 1 = Lemmens Inlet 1, 2 = Lemmens Inlet 2, 3 = Trevenen Bay, 4 = Okeover Inlet, 5 = Saanich 5 m, 6 = Saanich 1 m, 7 = Departure Bay, 8 = Bowen Island, 9 = West Vancouver and 10 = Keats Island.

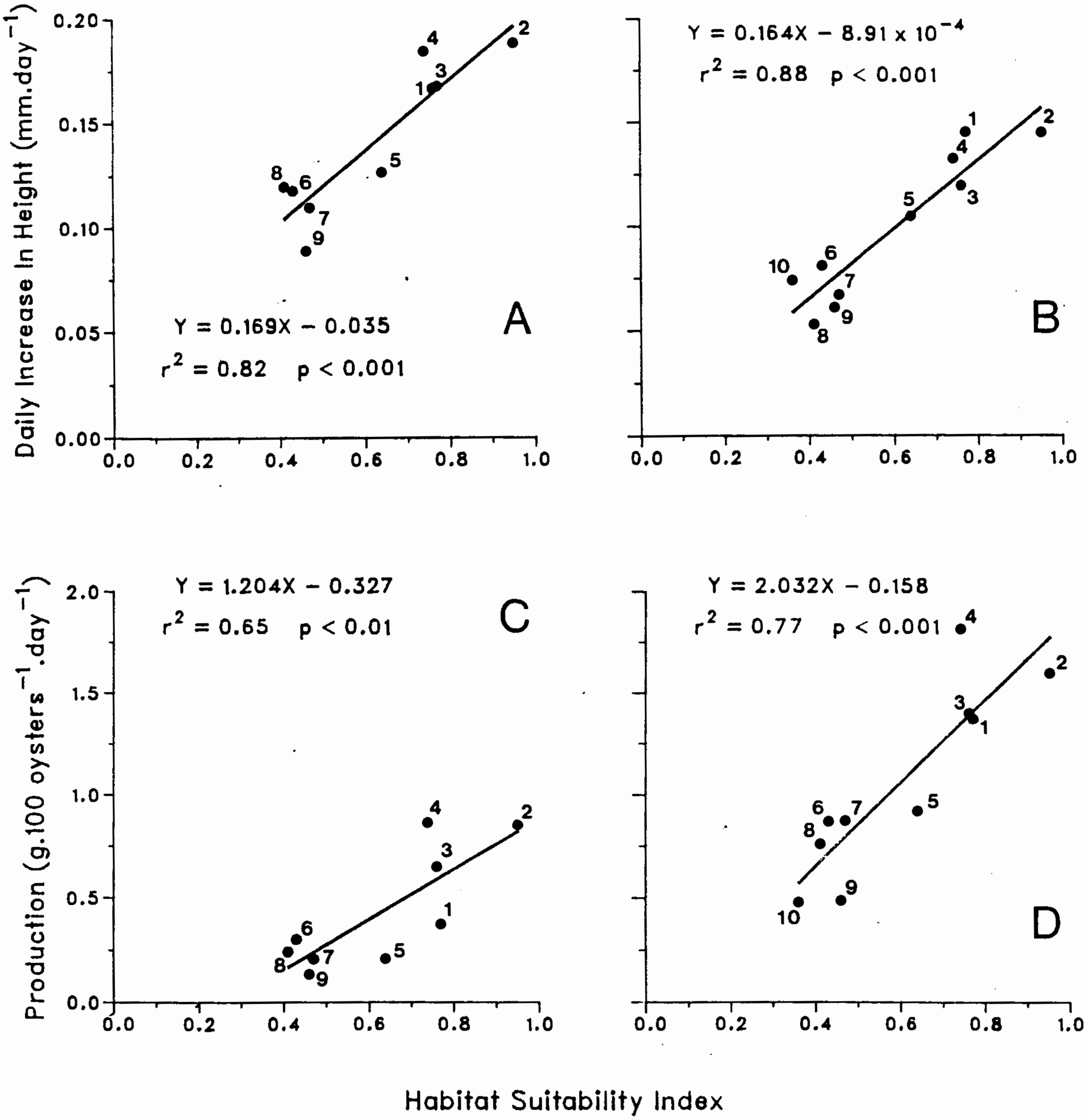
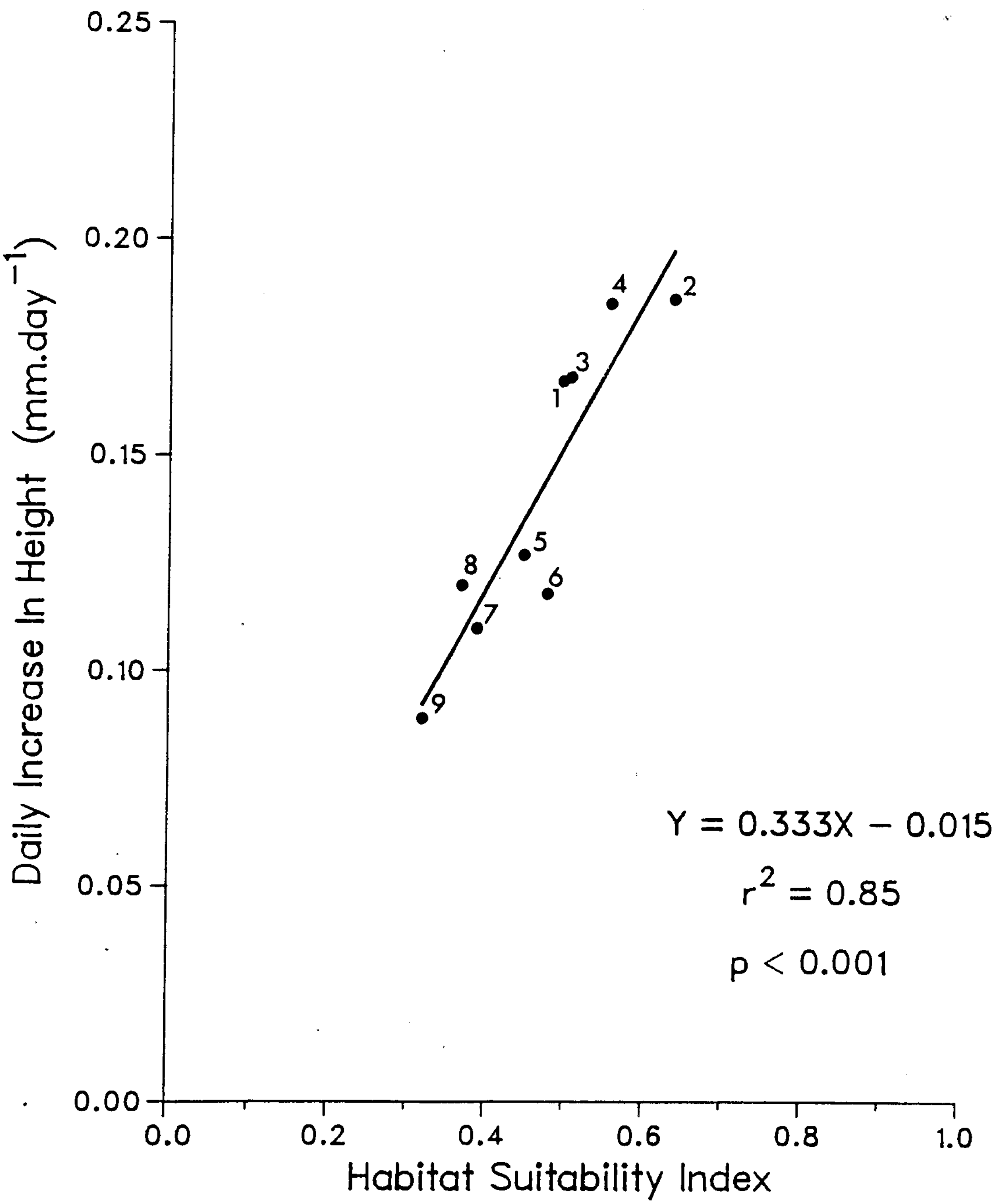

Daily Increase In Height (mm.day^{-1})
0.20
0.15
0.10
0.05
0.00
Y = 0.169X − 0.035
r^2 = 0.82 p < 0.001
A
Y = 0.164X − 8.91 x 10^{-4}
r^2 = 0.88 p < 0.001
B
Production (g.100 oysters^{-1}.day^{-1})
2.0
1.5
1.0
0.5
0.0
Y = 1.204X − 0.327
r^2 = 0.65 p < 0.01
C
Y = 2.032X − 0.158
r^2 = 0.77 p < 0.001
D
0.0
0.2
0.4
0.6
0.8
1.0
1
2
3
4
5
6
7
8
9
10
Habitat Suitability Index

Table 4.5. Coefficient of determination (r^2) for site-specific increases in shell length ($\text{mm}\cdot\text{day}^{-1}$) of Year 0 and Year 1 oysters over the entire study regressed against HSI values calculated after partitioning the environmental data set on a seasonal basis. HSI values for selected monthly observations are also included.
Except when noted, $n = 9$, where n is the number of sites. *ns* = not significant; * $P \leq 0.05$: ** $P \leq 0.01$; *** $P \leq 0.001$.

Available Food	Whole Study	Sum 84	Aug 84	Sept 84	Fall 84	Spr 85	Sum 85
<u>Year 0</u>							
Chl. *a*	0.82 ***	0.29 *ns*	0.53 **	0.53 *	0.39 *	0.85 ***	0.04 *ns*
TPM	-	0.36 *ns*†	0.83 **‡	0.41 *ns*†	0.84 **‡	0.57 **	0.49 **
<u>Year 1</u>							
Chl. *a*	0.88 ***	0.46 **	0.67 ***	0.55 *	0.39 *	0.72 ***	0.02 *ns*
TPM	-	0.16 *ns*†	0.83 ***‡	0.19 *ns*†	0.85 ***‡	0.61 **	0.52 **

† Sites are Lemmens 1 & 2, Saanich 1 m & 5 m, Departure Bay.
‡ Sites are Lemmens 1 & 2, Departure Bay, Keats Island, Bowen Island, West Vancouver.

Fig. 4.3. HSI values derived from Spr85 data regressed against increase in shell height for Year 0 oysters. Site numbering scheme is the same as Fig. 4.2.


0.25
0.20
0.15
0.10
0.05
0.00
Daily Increase In Height (mm.day⁻¹)
0.0
0.2
0.4
0.6
0.8
1.0
Habitat Suitability Index
1
2
3
4
5
6
7
8
9
Y = 0.333X − 0.015
r² = 0.85
p < 0.001

values.

Discussion

The significant correlations of HSI values to growth of both age classes and the similarity in patterns of seasonal HSI correlations, indicated that an age-specific model was unnecessary. The habitat requirements of young and adult oysters are probably similar because oysters do not have a prolonged juvenile stage. Mature sex cells appear in oyster spat just a few weeks after settlement although spawning is usually postponed until the second summer (Quayle 1969, Cake 1983).

The highest correlations between HSI values and oyster growth were greater than those obtained in previous field validation studies of HSI models. Cook and Irwin (1985) determined that HSI values from a habitat model for the pronghorn (*Atnilocapra americana*) were significantly correlated ($r^2 = 0.70$, $p \leq 0.001$) to population densities in 28 winter ranges. In a study site mapped into grids of habitat suitablity based on a bobcat (*Lynx rufus*) HSI model, there was 55.54 % agreement with habitat use by radio-collared cats (Lancia et al. 1982).

Layher and Maughan (1985) included SI values in a multiple regression model in order to predict standing stocks of channel catfish (*Ictalurus punctatus*). Regressions were significant for stream systems in Kansas ($r^2 = 0.50$, $p \leq 0.01$) and Okalahoma

($r^2 = 0.48$, $p \leq 0.01$). In a separate test, standing stocks of Okalahoma streams were predicted using the Kansas model. Correlation between predicted and estimated standing stocks was low ($r^2 = 0.27$, $p \leq 0.01$) but significant. The authors concluded that the SI curves were regionally consistent and fish biomass was related to abiotic factors.

The much higher correlations of the Pacific oyster HSI model may be partially attributed to the method of evaluation rather than the structure of the model. The social behaviour of vertebrates can result in the decoupling of the relationship between habitat and population density (Van Horne 1983). Dominant animals can force less competative individuals of the same species into habitats of secondary preference, thus affecting the results of studies into habitat selection and utilization. Inherit sampling errors associated with the census of terrestrial species may also cause incorrect estimates of species abundances (Cook and Irwin 1985).

The Pacific oyster HSI model was validated using growth and survival data which are an expression of the overall metabolic state of the organism. The response of an organism to changes in the environment is much more apparent at the individual metabolic level than at the population structure level. The metabolic assumptions of the HSI model were also evident in the near zero intercept of the validation regressions. Field validation results closely follow the hypothetical relationship between HSI and growth potential where 0.0 represents totally unsuitable habitat and 1.0 represents optimum habitat (USFWS 1981).

While it is not difficult to conceive of a habitat with 0.0 suitability for oyster culture (for example a freshwater lake) the definition of an optimal habitat is much less tangible. The paucity of quantatitive growth data on existing oyster culture areas and the large number of unexploited fjords, means that the optimum oyster growing area in British Columbia waters can not be ascertained. Lemmens Inlet 2 had the highest growth rates amongst the study sites for Year 0 (0.189 $mm \cdot day^{-1}$) and Year 1 (0.146 $mm \cdot day^{-1}$). The HSI rating of 0.95 (based on whole study data) was near the theortical optimum of 1.0. In comparison with Year 0 oysters, slightly higher growth rates were determined from the results of Quayle (1969) for oysters grown at Okeover Inlet (0.256 $mm \cdot day^{-1}$) and Quait Bay (0.196 $mm \cdot day^{-1}$) which is in the vicinity of Lemmens Inlet. These figures are approximate since the precise sampling dates of Quayle's study are not known. Furthermore, his oysters were planted in February and were able to take advantage of the spring phytoplankton bloom early during the first year of growth.

In a study by Sparks and Chew (1959), oysters approximately the same initial size as Year 1 oysters, were grown in submerged trays at 3 locations in Washington state for 11 months. Growth rates calculated from these data ranged from 0.126 - 0.200 $mm \cdot day^{-1}$ which is in close agreement with the high growth sites in the present study. In fact, growth of oysters used for the

HSI model validation may be higher because the measurements were taken over a 14 month period and oyster growth is known to decrease with age (Woelke 1959a).

Growth rates of oysters at Lemmens Inlet 2 are near the known maximum growth of Pacific oysters. Although other areas or years of higher or lower oyster growth could possibly occur, the HSI model appears to cover the range of known growth capabilities of the coastal waters of British Columbia. With some minor modifications, the geographical coverage of the model could possibly be extended to areas north and south of Vancouver Island.

Correlation of HSI values to oyster growth and production was intended to be a method of evaluating the performance of the model. At the current stage of development, it would be imprudent to attempt to use the HSI model as a means of predicting absolute yields from an oyster farm. Multivariate analyses have been used in the past to derive predictive functions for oyster harvest (Ulanowicz et al. 1980, 1982) and commercial production (Hall 1984). The HSI model rates the potential of a coastal area for oyster culture but absolute production or growth rates are not implicitly related to particular HSI values. Oyster growth at Trevenen Bay, Okeover Inlet and Lemmens Inlet 1 and 2 was not significantly different (see Chapter I) eventhough the whole study HSI values for these sites ranged from 0.74 - 0.95. The actual yields of an oyster farm are dependent upon a variety of non-habitat factors as well, such as broodstock genotype (Mallet and Haley 1983), culture technique and diligence of grow-out maintenance (Quayle 1969, 1971).

The lack of quantitative data on the causal effects of biological variables, often results in their being handled in a less satisfactory way than physical factors in the HSI model (Schamberger and Krohn 1982). Disease, predators and fouling organisms are important considerations in aquaculture and they could not be omitted simply on the basis that quantitative information was lacking. Quantification of the relationship concerning growth, water movement and nutritional value of available food could significantly improve the accuracy of the HSI model. Water movement at the velocity of tidal currents can increase the number of particles coming into contact with the oyster (Walne 1972, Frechette and Bourget 1985). High growth rates at Trevenen Bay and Okeover Inlet, despite lower levels of chlorophyll *a* in comparison to Lemmens Inlet, could be attributed to strong tidal and wind-driven currents. Researchers have also noted the need for further data on preferential selection of food particles (Newell and Jordan 1985), utilization of nanoplankton (Incze et al. 1980) and absorption of dissolved organic substances (Amouroux 1984). Information forthcoming from these areas could be incorporated into the HSI model and improve its capability.

This study has shown that in the analysis of oyster culture habitat, the importance of food supply can not be ignored. The seasonal performance of the model was strongly affected by phytoplankton abundance. Temporal variation (both inter and intra-annual) in phytoplankton populations can be high, affecting the credibility of model predictions. Since an extensive phytoplankton sampling program would be expensive, model users should priorize coastal areas in terms of the required precision of HSI values. Existing data-bases and preliminary field surveys could be used to obtain approximate HSI values for a number of areas. Coastal areas which require higher confidence in HSI values may then be selected for more detailed environmental survey extending over several months.

The utility of habitat models for management purposes can be viewed from two perspectives (Farmer et al. 1982). The first view is one of skepticism regarding the usefulness of habitat models when the knowledge of underlying species-habitat relationships is limited. From the other perspective, even incomplete habitat information can substantially improve the basis upon which land-use decisions are made. In the light of the later statement, HSI modelling techniques could prove to be useful in the representation of the aquaculture industry in the inevitable decisions regarding the allocation of coastal resources among competing development interests.

GENERAL DISCUSSION

The results of this study have relevant implications to bivalve ecology, aquaculture and coastal management.

Oyster growth was strongly influenced by environmental factors while survival was affected to a much lesser extent. Genetic factors probably have an effect upon the magnitude of growth response in a particular habitat (Mallet and Haley 1983, Dickie et al. 1984). Both absolute and allometic growth were influenced by location although allometric relationships were not always consistent among sites. If temperature, salinity and food conditions were good for oysters then high growth was observed in all body parameters (shell height, and weights of whole oyster, shell and body tissue). In habitats with good water temperature and salinity regimes but depressed food concentrations, body tissue and shell height growth were low while shell weight (hence thickness) increased. Finally in areas which had good water temperature conditions, critical salinity levels and highly variable food availability, growth of all measured body parts was low. The allometric relationships between weights of shell and body tissue were similar for both the high and low growth sites.

While habitat related variation in shell thickness has been observed in other studies, the causal mechanism and functionality of this response is unknown (Aguis et al. 1978, Aldrich and Crowley 1986). Further research into the resource partitioning in bivalves between shell and tissue growth is necessary. One approach might be to determine the separate energetic costs involved for shell, reproductive tissue and somatic tissue growth. Since the thickening of shell appears to be caused by adverse environmental conditions, shell permability and chemical composition might be worth examining. Further study could reveal whether other natural factors or pollutants affect the dry meat weight to shell weight ratio. To an oyster farmer, the selection of a site which promotes high meat growth is an obvious concern. The elucidation of factors which affect this relationship is important to aquaculture.

Closely related to the discussion of allometric relationships is the relevancy of static condition indices. The ambiguity of the volumetric condition index (VCI) would seem to affect its utility as a standard of comparison. The dry weight condition index (DWCI) is useful in this regard provided that salinity is not highly variable. The super-imposition of critical fluctuations in salinity, upon variations in temperature and food availability reduces the functionality of the DWCI. Both indices have significant seasonal variation which resulted in differential rankings of sites from month to month.

Multivariate analysis of the influence of environmental factors upon oyster growth rates did not result in strong predictive functions. As an exploratory technique, however, the main factors which affect seasonal and site-related growth were revealed. Food concentrations and salinity were significant factors in distinguishing between sites with different growth rates. Water temperature and food concentration regulate seasonal growth rates. There was evidence that nanoflagellates may be of considerable importance to oyster nutrition.

Water movement is probably an important factor which was not adequately investigated in this study. Future efforts might be directed towards the development of an index of available food which would integrate phytoplankton abundance, nutritional value of food particles and water circulation. The effects of fouling organisms upon oyster growth and survival should also be the subject of further study. This could include an examination of the effects attached sessile organisms on oysters as well as potential competition between suspension feeding epibionts and oysters for food particles.

More precise determinations of the effects of these factors upon oyster production could be incorporated into the HSI model. Significant seasonal variations in food concentrations and water temperatures exerts considerable influences upon model output. Model users should endeavour to standardize the collection of input data. The logistical and analytical factors involved with the collection of some of the input data, such as available food, might be economically prohibitive to some potential model users. Several inexpensive alternatives to phytoplankton pigment analysis are suggested in a technical report which documents the model (Brown and Roland, in prep.). The net result, however, is a trade-off between cost and confidence in the model output.

Nonetheless, HSI methodology shows potential for application to other aquaculture species. As a management tool, HSI techiques have been implemented in the assessment of environment impacts and in the mitigation of conflicts between multiple users of a common resource (USFWS 1980, Urich et al. 1986). Subtle modifications will likely occur to the Pacific oyster HSI model as it is applied by management agencies.

The identification of habitats which are valuable for oyster culture is of considerable immediate importance to the B.C. oyster industry. The establishment of a long term program for the collection of data on regional oyster production and environmental conditions could be very useful in the management of the oyster industry.

The HSI model proposed in this thesis, documents the overall suitability of a particular habitat for oyster culture. The logical progression would be the integration of the HSI model with hydrographic features in order to derive an estimate of the aquaculture carrying capacity of a coastal fjord. Inzce et al. (1980) proposed a carrying capacity model for suspended mussel culture. Factors included in the model were water circulation, energy content of the seston and particle clearance rate by successive rows of suspended mussels. Biodeposition rates and residence time of waste products also need to be considered (Kaspar et al. 1985). The end result would be the development of management procedures which would encourage sustainable aquaculture operations while minimizing the negative impacts of culture activities upon the marine environment.

APPENDIX A

Table A.1. Summary of parameters from polynomial equations fitted to Year 0 shell height data. All regressions are significant ($p \leq 0.05$).

	Lemmens Inlet 1	Lemmens Inlet 2	Trevenen Bay	Okeover Inlet	Departure Bay	Saanich 1 m	Saanich 5 m	Bowen Island	Keats Island	West Vancouver
β_0	67.93	70.56	61.35	61.52	55.05	55.35	53.46	53.94	--	45.41
β_1	0.07	0.09	0.08	0.07	0.02	0.06	0.03	0.04	--	0.03
β_2 ($\times 10^{-3}$)	-0.25	-0.17	-0.14	0.06	-0.21	-0.14	0.001	-0.14	--	-0.06
β_3 ($\times 10^{-5}$)	0.26	0.24	0.19	0.24	0.22	0.14	0.21	0.16	--	0.11
r^2	0.87	0.84	0.79	0.86	0.72	0.76	0.75	0.73	--	0.72
n	215	243	187	187	193	198	205	229	--	186

Table A.2. Summary of parameters from polynomial equations fitted to Year 1 shell height data. All regressions are significant ($p \leq 0.05$).

	Lemmens Inlet 1	Lemmens Inlet 2	Trevenen Bay	Okeover Inlet	Departure Bay	Saanich 1 m	Saanich 5 m	Bowen Island	Keats Island	West Vancouver
β_0	88.68	81.76	88.20	84.23	70.66	73.51	69.68	71.15	58.38	56.71
β_1	0.09	0.13	0.01	0.02	-0.006	0.01	0.01	0.02	0.01	0.03
β_2 ($\times 10^{-3}$)	-0.55	-0.45	-0.14	0.02	-0.31	-0.15	-0.09	-0.02	0.03	-0.08
β_3 ($\times 10^{-5}$)	0.21	0.10	0.24	0.24	0.19	0.14	0.19	0.06	0.14	0.09
r^2	0.74	0.73	0.75	0.58	0.46	0.44	0.61	0.36	0.52	0.44
n	205	190	161	189	219	191	190	166	196	214

Table A.3. Summary of parameters from polynomial equations fitted to Year 1 $\log_{10}$ whole weight data. All regressions are significant ($p \leq 0.05$).

	Lemmens Inlet 1	Lemmens Inlet 2	Trevenen Bay	Okeover Inlet	Departure Bay	Saanich 1 m	Saanich 5 m	Bowen Island	Keats Island	West Vancouver
β_0	1.86	1.86	1.84	1.82	1.75	1.67	1.67	1.57	1.35	1.40
β_1 ($\times 10^{-3}$)	0.17	0.53	0.53	0.66	0.76	0.28	0.42	0.42	0.29	0.84
β_2 ($\times 10^{-5}$)	-0.94	-1.25	-0.06	-0.004	-1.27	-0.30	-0.93	-0.18	0.03	-0.006
β_3 ($\times 10^{-7}$)	0.57	0.69	0.43	0.38	0.58	0.43	0.54	0.33	0.40	0.16
r^2	0.83	0.86	0.82	0.73	0.89	0.85	0.88	0.56	0.66	0.46
n	100	90	70	90	99	99	80	98	88	100

Table A.4. Summary of parameters from polynomial equations fitted to Year 1 $\log_{10}$ shell weight data. All regressions are significant ($p \leq 0.05$).

	Lemmens Inlet 1	Lemmens Inlet 2	Trevenen Bay	Okeover Inlet	Departure Bay	Saanich 1 m	Saanich 5 m	Bowen Island	Keats Island	West Vancouver
β_0	1.52	1.56	1.65	1.63	1.49	1.50	1.47	1.29	1.08	1.15
β_1 ($\times 10^{-3}$)	0.33	1.50	0.57	0.92	0.89	0.74	0.33	0.84	0.75	1.13
β_2 ($\times 10^{-5}$)	-0.45	-0.11	-0.19	-0.25	-0.98	-0.37	-0.52	-0.23	-0.01	-0.11
β_3 ($\times 10^{-7}$)	0.46	0.46	0.49	0.37	0.51	0.39	0.52	0.24	0.26	0.11
r^2	0.80	0.86	0.85	0.80	0.88	0.88	0.86	0.61	0.67	0.53
n	130	110	70	80	109	99	100	98	88	100

Table A.5. Summary of comparisons between polynomial equations fitted to Year 0 shell height data. * = $p \leq 0.005$; ns = not significant.

	Lemmens Inlet 1	Lemmens Inlet 2	Trevenen Bay	Okeover Inlet	Departure Bay	Saanich 1 m	Saanich 5 m	Bowen Island
Lemmens Inlet 2	ns							
Trevenen Bay	ns	ns						
Okeover Inlet	ns	ns	ns					
Departure Bay	*	*	*	*				
Saanich 1 m	*	*	*	*	ns			
Saanich 5 m	*	*	*	*	ns	ns		
Bowen Island	*	*	*	*	ns	ns	ns	
West Vancouver	*	*	*	*	*	*	*	*

Table A.6. Summary of comparisons between polynomial equations fitted to Year 1 shell height data. * = $p \leq 0.005$; ns = not significant.

	Lemmens Inlet 1	Lemmens Inlet 2	Trevenen Bay	Okeover Inlet	Departure Bay	Saanich 1 m	Saanich 5 m	Bowen Island	Keats Island
Lemmens Inlet 2	ns								
Trevenen Bay	ns	ns							
Okeover Inlet	ns	ns	ns						
Departure Bay	*	*	*	*					
Saanich 1 m	*	*	*	*	ns				
Saanich 5 m	*	*	*	*	ns	ns			
Bowen Island	*	*	*	*	ns	ns	ns		
Keats Island	*	*	*	*	*	*	*	*	
West Vancouver	*	*	*	*	*	*	*	*	ns

Table A.7. Summary of comparisons between polynomial equations fitted to Year 1 $\log_{10}$ whole weight data. * = $p \leq 0.005$; ns = not significant.

	Lemmens Inlet 1	Lemmens Inlet 2	Trevenen Bay	Okeover Inlet	Departure Bay	Saanich 1 m	Saanich 5 m	Bowen Island	Keats Island
Lemmens Inlet 2	ns								
Trevenen Bay	ns	ns							
Okeover Inlet	ns	ns	ns						
Departure Bay	ns	ns	ns	ns					
Saanich 1 m	*	*	*	*	ns				
Saanich 5 m	*	*	*	*	ns	ns			
Bowen Island	*	*	*	*	ns	ns	ns		
Keats Island	*	*	*	*	*	*	*	*	
West Vancouver	*	*	*	*	*	*	*	*	ns

Table A.8. Summary of comparisons between polynomial equations fitted to Year 0 $\log_{10}$ shell weight data. * = $p \le 0.005$; ns = not significant.

	Lemmens Inlet 1	Lemmens Inlet 2	Trevenen Bay	Okeover Inlet	Departure Bay	Saanich 1 m	Saanich 5 m	Bowen Island	Keats Island
Lemmens Inlet 2	ns								
Trevenen Bay	ns	ns							
Okeover Inlet	ns	ns	ns						
Departure Bay	ns	ns	*	*					
Saanich 1 m	ns	ns	*	ns	ns				
Saanich 5 m	ns	ns	*	*	ns	ns			
Bowen Island	*	*	*	*	*	*	*		
Keats Island	*	*	*	*	*	*	*	*	
West Vancouver	*	*	*	*	*	*	*	*	ns

Table A.9. Summary of parameters from polynomial equations fitted to 1984 (June-December) Year 1 $\log_{10}$ dry meat weight data. All regressions are significant ($p \leq 0.05$) except Keats Island and West Vancouver which are significant.

	Lemmens Inlet 1	Lemmens Inlet 2	Trevenen Bay	Okeover Inlet	Departure Bay	Saanich 1 m	Saanich 5 m	Bowen Island	Keats Island	West Vancouver
β_0	0.35	0.29	0.52	0.40	0.21	0.14	0.19	0.18	-0.14	-0.11
β_1 ($\times 10^{-2}$)	0.48	0.72	0.30	0.44	0.54	0.56	0.77	0.35	0.02	0.05
β_2 ($\times 10^{-4}$)	-0.38	-0.41	-0.51	-0.33	-0.43	-0.60	-0.84	-0.63	-0.02	-
r^2	0.71	0.78	0.52	0.46	0.81	0.72	0.89	0.39	0.01	0.02
n	60	50	40	40	59	39	40	38	28	20

Table A.10. Summary of comparisons between polynomial equations fitted to 1984 Year 1 $\log_{10}$ dry meat weight data. * = $p \leq 0.005$; ns = not significant. Regressions for Keats Island and West Vancouver are not significant.

	Lemmens Inlet 1	Lemmens Inlet 2	Trevenen Bay	Okeover Inlet	Departure Bay	Saanich 1 m	Saanich 5 m	Bowen Island	Keats Island
Lemmens Inlet 2	ns								
Trevenen Bay	ns	ns							
Okeover Inlet	ns	ns	ns						
Departure Bay	ns	ns	*	ns					
Saanich 1 m	*	ns	*	*	*				
Saanich 5 m	ns	ns	*	ns	ns	ns			
Bowen Island	ns	ns	*	ns	ns	ns	ns		
Keats Island	--	--	--	--	--	--	--	-	
West Vancouver	--	--	--	--	--	--	--	--	-

Table A.11. Summary of parameters from polynomial equations fitted to 1985 (February-August) Year 1 $\log_{10}$ dry meat weight data. All regressions are significant ($p \le 0.05$).

	Lemmens Inlet 1	Lemmens Inlet 2	Trevenen Bay	Okeover Inlet	Departure Bay	Saanich 1 m	Saanich 5 m	Bowen Island	Keats Island	West Vancouver
β_0	0.61	0.72	0.75	0.72	0.46	0.43	0.36	0.43	0.20	0.23
β_1 ($\times 10^{-2}$)	0.27	0.15	0.23	0.25	0.16	0.19	0.33	0.26	0.30	0.23
r^2	0.60	0.24	0.53	0.53	0.26	0.37	0.53	0.49	0.47	0.39
n	70	50	40	60	60	60	50	60	60	70

Table A.12. Summary of comparisons between polynomial equations fitted to 1985 Year 1 $\log_{10}$ dry meat weight data.
* = $p \leq 0.005$; ns = not significant.

	Lemmens Inlet 1	Lemmens Inlet 2	Trevenen Bay	Okeover Inlet	Departure Bay	Saanich 1 m	Saanich 5 m	Bowen Island	Keats Island
Lemmens Inlet 2	ns								
Trevenen Bay	*	ns							
Okeover Inlet	*	ns	ns						
Departure Bay	*	*	*	*					
Saanich 1 m	*	*	*	*	ns				
Saanich 5 m	*	*	*	*	ns	ns			
Bowen Island	*	*	*	*	ns	ns	ns		
Keats Island	*	*	*	*	*	*	*	*	
West Vancouver	*	*	*	*	*	*	*	*	ns

Table A.13. Parameters of regression equations for $\log_{10}$ shell weight vs $\log_{10}$ dry meat weight for Year 1 oysters. All regressions are highly significant ($p \leq 0.001$).

	Lemmens Inlet 1	Lemmens Inlet 2	Trevenen Bay	Okeover Inlet	Departure Bay	Saanich 1 m	Saanich 5 m	Bowen Island	Keats Island	West Vancouver
β_0	-1,22	-0.93	-0.75	-0.91	-0.84	-0.82	-0.93	-1.21	-1.18	-1.10
β_1	1.15	0.98	0.84	0.95	0.84	0.78	0.84	1.20	1.15	1.06
r^2	0.92	0.91	0.85	0.90	0.84	0.83	0.80	0.86	0.71	0.82
n	140	140	99	100	139	109	110	108	98	119

Table A.14. Summary of comparisons between regression equations fitted to 1985 Year 1 $\log_{10}$ shell weight and $\log_{10}$ dry meat weight data. * = $p \le 0.005$; ns = not significant.

	Lemmens Inlet 1	Lemmens Inlet 2	Trevenen Bay	Okeover Inlet	Departure Bay	Saanich 1 m	Saanich 5 m	Bowen Island	Keats Island
Lemmens Inlet 2	ns								
Trevenen Bay	*	ns							
Okeover Inlet	ns	ns	ns						
Departure Bay	*	*	ns	ns					
Saanich 1 m	*	*	*	ns	ns				
Saanich 5 m	*	*	ns	ns	ns	ns			
Bowen Island	ns	*	*	ns	*	*	*		
Keats Island	ns	ns	*	ns	*	*	ns	ns	
West Vancouver	ns	ns	*	ns	*	*	ns	ns	ns

Fig. A.1. Monthly mean secchi depth (m).

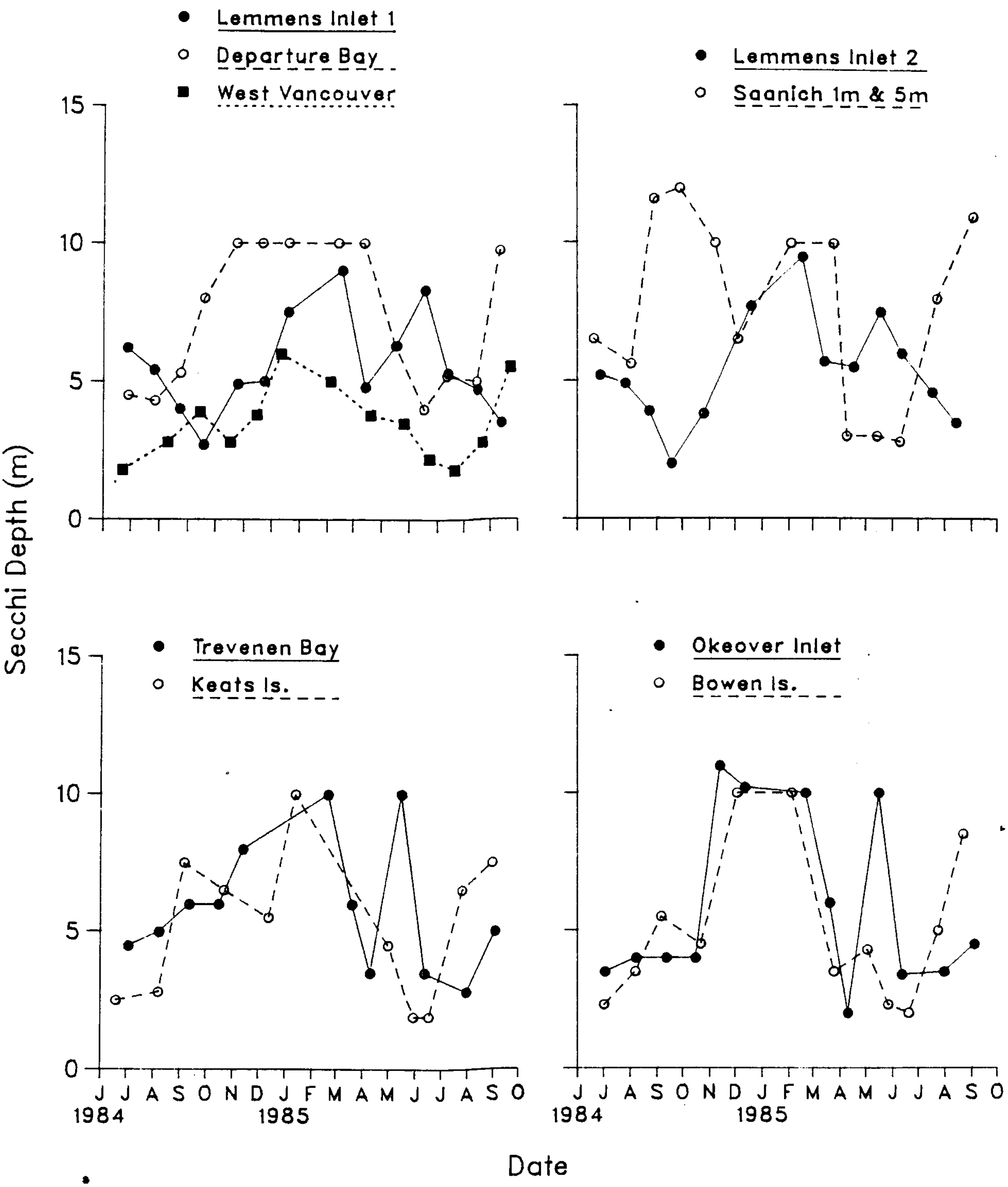

● Lemmens Inlet 1
○ Departure Bay
■ West Vancouver
● Lemmens Inlet 2
○ Saanich 1m & 5m
● Trevenen Bay
○ Keats Is.
● Okeover Inlet
○ Bowen Is.
Secchi Depth (m)
0
5
10
15
J J A S O N D J F M A M J J A S O
1984
1985
Date

Fig. A.2. Monthly mean dissolved oxygen levels ($ml\text{-}O_2(NTP) \cdot l^{-1}$).

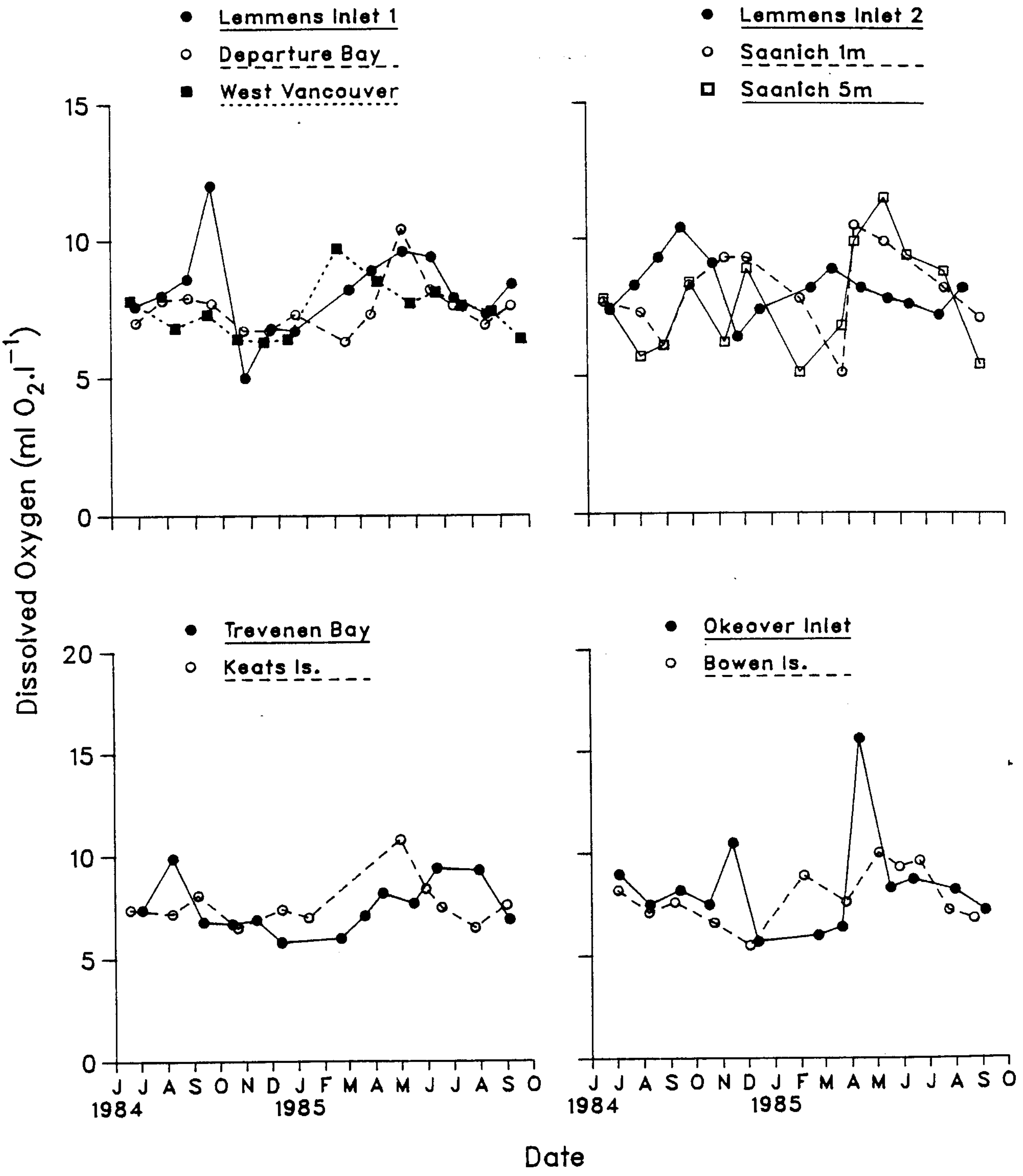

Lemmens Inlet 1
Departure Bay
West Vancouver
Lemmens Inlet 2
Saanich 1m
Saanich 5m
Trevenen Bay
Keats Is.
Okeover Inlet
Bowen Is.
Dissolved Oxygen (ml $O_2.l^{-1}$)
15
10
5
0
20
15
10
5
0
J J A S O N D J F M A M J J A S O
1984
1985
Date

Fig. A.3. Monthly mean chlorophyll *b* concentrations ($\mu g \cdot l^{-1}$).

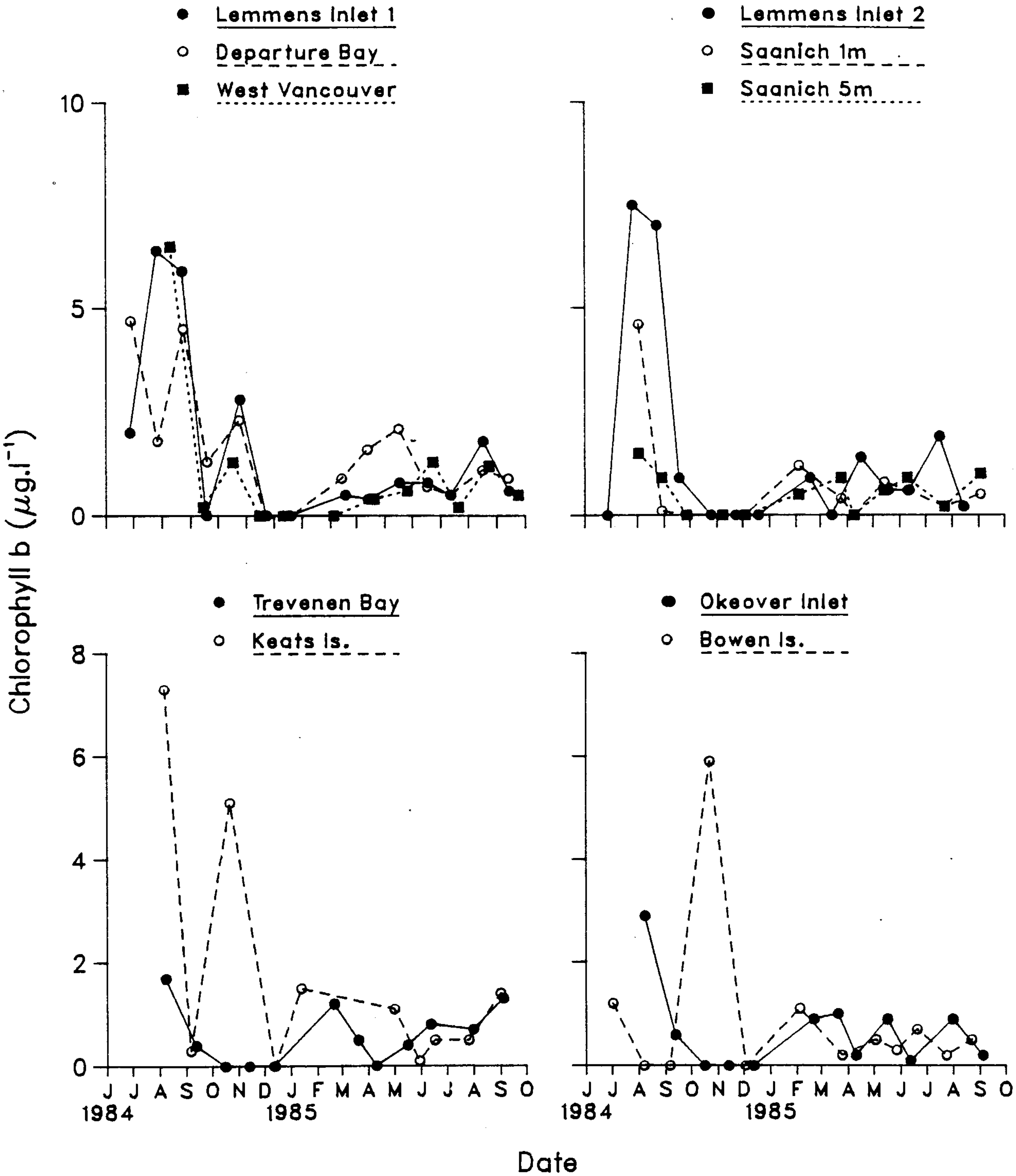

Lemmens Inlet 1
Departure Bay
West Vancouver
Lemmens Inlet 2
Saanich 1m
Saanich 5m
Trevenen Bay
Keats Is.
Okeover Inlet
Bowen Is.
Chlorophyll b (µg.l⁻¹)
10
5
0
8
6
4
2
0
J J A S O N D J F M A M J J A S O
1984
1985
Date

Fig. A.4. Monthly mean chlorophyll *c* concentrations ($\mu g \cdot l^{-1}$).

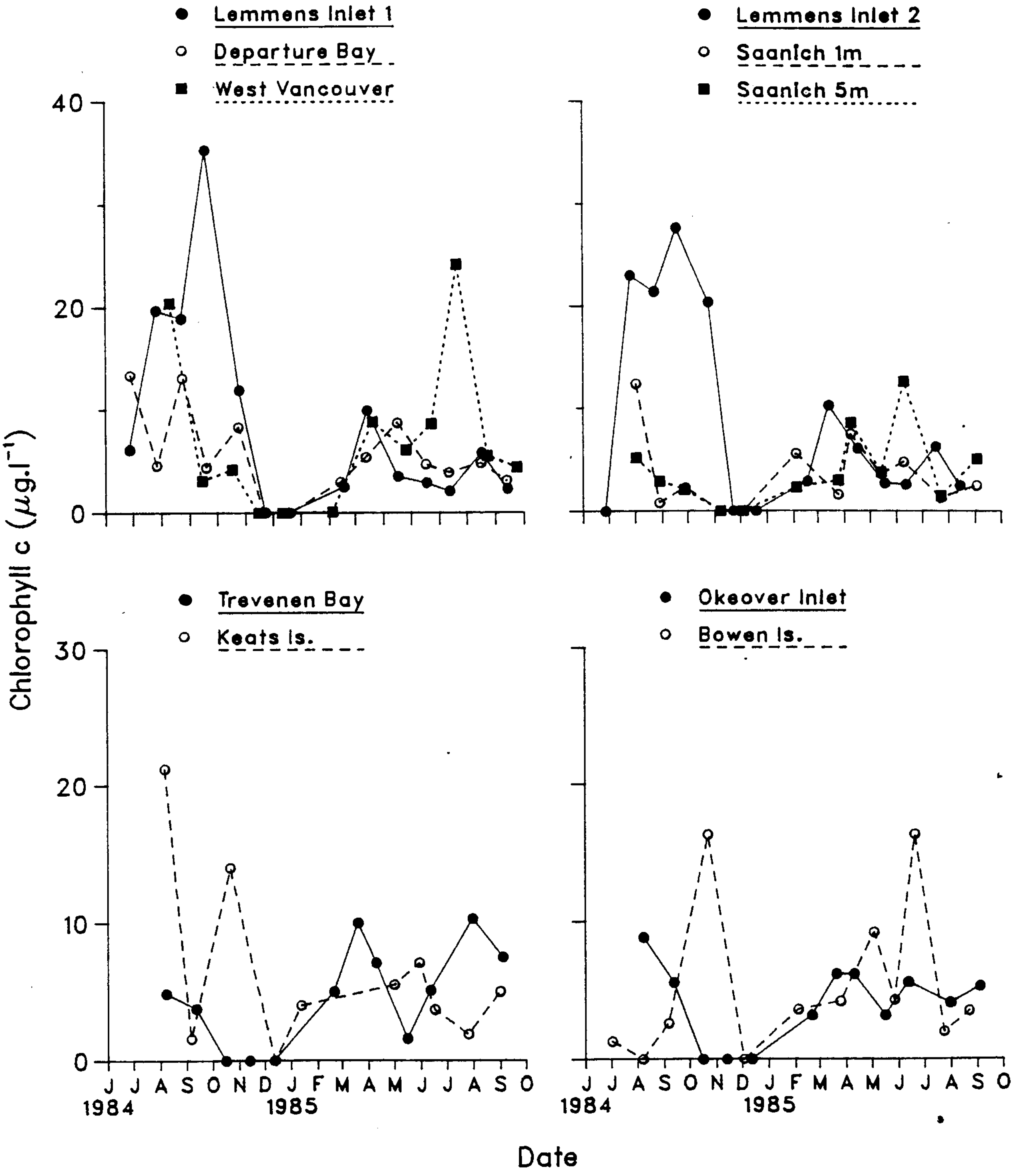

● Lemmens Inlet 1
○ Departure Bay
■ West Vancouver
● Lemmens Inlet 2
○ Saanich 1m
■ Saanich 5m
● Trevenen Bay
○ Keats Is.
● Okeover Inlet
○ Bowen Is.
40
20
0
30
20
10
0
Chlorophyll c (μg.l⁻¹)
J J A S O N D J F M A M J J A S O
1984
1985
Date

Fig. A.5. Monthly mean carotenoids concentrations ($MSPU \cdot m^{-3}$).

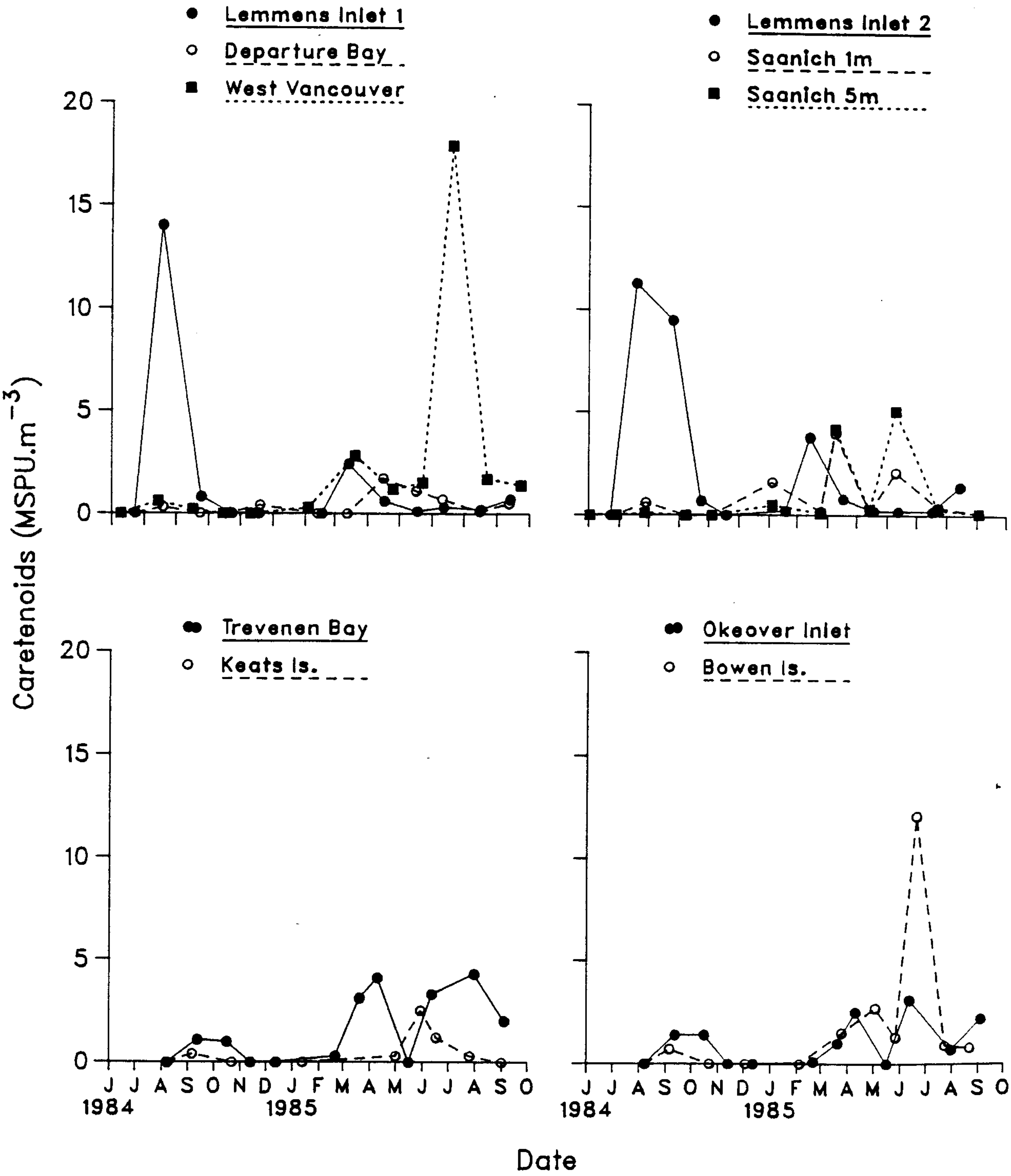

● Lemmens Inlet 1
○ Departure Bay
■ West Vancouver
● Lemmens Inlet 2
○ Saanich 1m
■ Saanich 5m
● Trevenen Bay
○ Keats Is.
● Okeover Inlet
○ Bowen Is.
Caretenoids (MSPU.m^{-3})
20
15
10
5
0
J J A S O N D J F M A M J J A S O
1984
1985
Date

Fig. A.6. Monthly mean Particulate Organic Matter (POM) levels ($mg \cdot l^{-1}$).

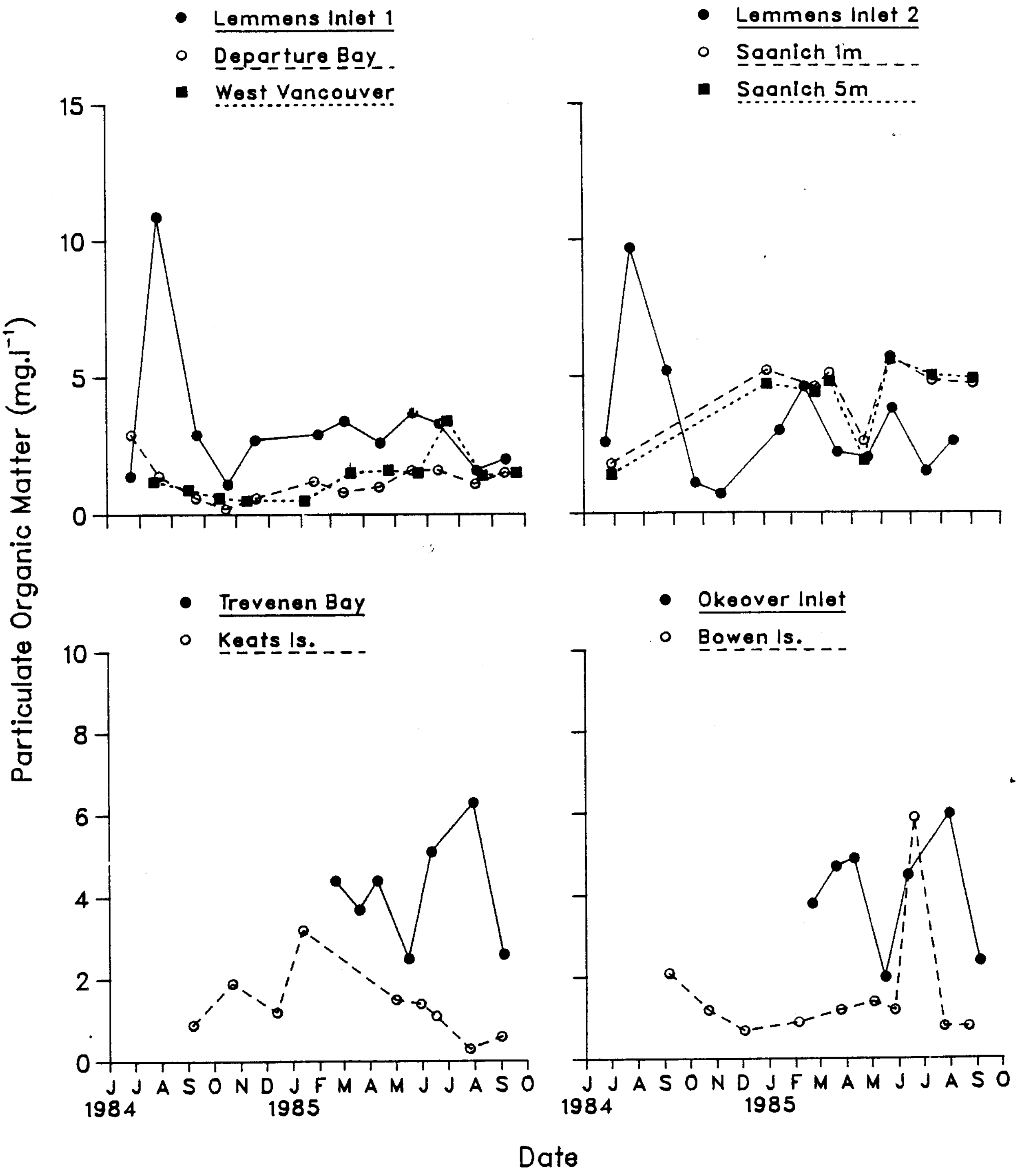

● Lemmens Inlet 1
○ Departure Bay
■ West Vancouver
● Lemmens Inlet 2
○ Saanich 1m
■ Saanich 5m
● Trevenen Bay
○ Keats Is.
● Okeover Inlet
○ Bowen Is.
Particulate Organic Matter (mg.l^{-1})
15
10
5
0
10
8
6
4
2
0
J J A S O N D J F M A M J J A S O
1984
1985
J J A S O N D J F M A M J J A S O
1984
1985
Date

Fig. A.7. Monthly mean Particulate Inorganic Matter (PIM) levels ($mg \cdot l^{-1}$).

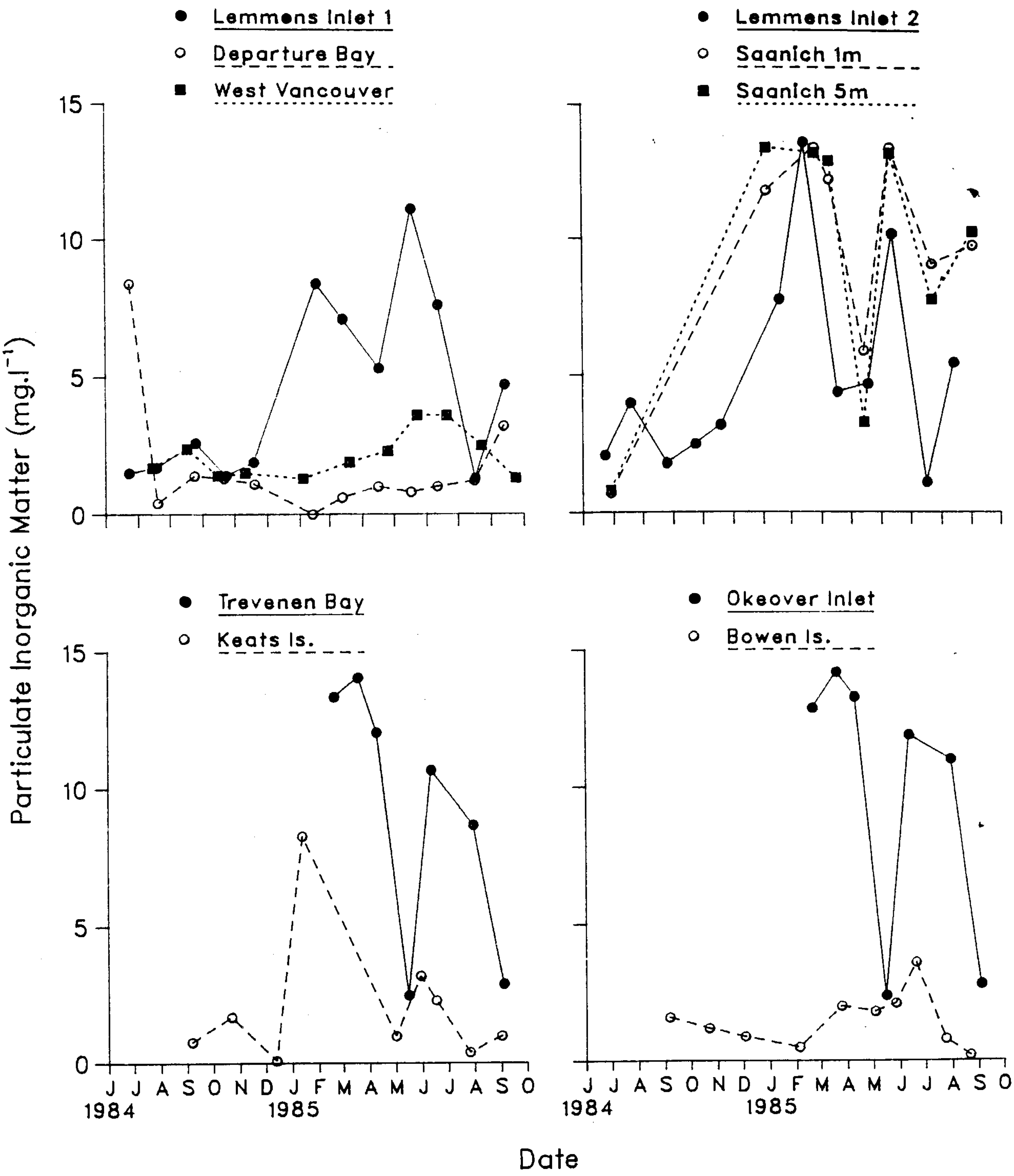

Lemmens Inlet 1
Departure Bay
West Vancouver
Lemmens Inlet 2
Saanich 1m
Saanich 5m
Trevenen Bay
Keats Is.
Okeover Inlet
Bowen Is.
Particulate Inorganic Matter (mg.l^{-1})
15
10
5
0
J J A S O N D J F M A M J J A S O
1984
1985
Date

Table A.15. Parameters of regression equations for $\log_{10}$ shell height vs $\log_{10}$ dry meat weight for Year 1 oysters. All regressions are highly significant ($p \leq 0.001$).

	Lemmens Inlet 1	Lemmens Inlet 2	Trevenen Bay	Okeover Inlet	Departure Bay	Saanich 1 m	Saanich 5 m	Bowen Island	Keats Island	West Vancouver
β_0	-5.07	-5.41	-4.22	-4.85	-5.46	-5.23	-5.34	-4.55	-4.67	-4.31
β_1	2.85	3.09	2.49	2.83	3.16	3.01	3.03	2.65	2.67	2.50
r^2	0.70	0.80	0.70	0.82	0.62	0.71	0.79	0.49	0.60	0.52
n	140	140	109	110	139	119	120	108	98	119

LITERATURE CITED

Agius, C., V. Jaccarini and D.A. Ritz. 1978. Growth trials of *Crassostrea gigas* and *Ostrea edulis* in inshore waters of Malta (Central Mediterranean). Aquaculture 15:195-218.

Aldrich, J.C. and M. Crowley. 1986. Condition and variability in *Mytilus edulis* (L.) from different habitats in Ireland. Aquaculture 52:273-286.

Amouroux, J.M. 1984. Preliminary study on the consumption of dissolved organic matter (exudates) of bacteria and phytoplankton by the marine bivalve *Venus verrucosa*. Mar. Biol. 82:109-112.

Appeldoorn, R.S. 1983. Variation in the growth rate of *Mya arenaria* and its relationship to the environment as analyzed through Principal Components Analysis and the ω parameter of the von Bertalanffy equation. Fish. Bull. 81:75-84.

Askew, C.G. 1972. The growth of oysters, *Ostrea edulis* and *Crassostrea gigas* in Emsworth Harbour. Aquaculture 1:237-259.

Bayne, B.L. and R.C. Newell. 1983. Physiological energetics of marine molluscs. In: The Mollusca: Physiology. 4(1). Ed. A.S.M. Saleuddin and K.M. Wilbur. Academic Press. New York. 523 pp.

Bayne, B.L. and J. Widdows. 1978. The physiological ecology of two populations of *Mytilus edulis* L. Oecologia 37:137-162.

Beninger, P.G. and A. Lucas. 1984. Seasonal variations in condition, reproductive activity, and gross biochemical composition of two species of adult clam reared in a common habitat: *Tapes decussatus* L.(Jeffreys) and *Tapes philippinarum* (Adams and Reeve). J. Exp. Mar. Biol. 79:19-37.

Bernard, R.F. 1983. Physiology and the mariculture of some Northeastern Pacific bivalve molluscs. Can. Special Publ. of Fish. and Aquat. Sci. 63: 24 pp.

Bourne, N. 1979. Pacific oysters, *Crassostrea gigas* Thunberg, in British Columbia and the South Pacific islands. In: Exotic species in mariculture. Ed. R. Mann. M.I.T. Press, Cambridge, MA. 363 pp.

British Columbia Min. of Agriculture and Food. 1986. Aquaculture in B.C. Victoria, B.C. 24 pp.

Buchanan, R.J. 1966. A study of the species composition and ecology of the protoplankton of a British Columbia inlet. Ph.D. thesis. University of British Columbia, Vancouver, B.C. 268 pp.

Burrell, V.G. Jr. 1985. Oyster culture. In: Crustacean and mollusk aquaculture in the United States. Ed. J.V. Huner and E.E. Brown. AVI Publishing Company. Westport, Conn. 476 pp.

Butler, P.A. 1953. Oyster growth as affected by latitudinal temperature gradients. Comm. Fish. Rev. 15:7-12.

Cake, E.W. Jr. 1983. Habitat suitability index models: Gulf of Mexico American oyster. U.S. Dept. Int. Fish Wildl. Serv. 37 pp.

Carriker, M.R. 1959. The role of physical and biological factors in the culture of *Crassostrea* and *Mercenaria* in a saltwater pond. Ecol. Monogr. 29:219-266.

Clayton, W.E.L. and T.T. Pobran. 1981. A Pacifc oyster stake culture pilot project in B.C. Fish. Dev. Rep. 30. B.C. Min. of Environment. 30 pp.

Cook, John G. and Larry L. Irwin. 1985. Validation and modification of a habitat suitability model for pronghorns. Wildl. Soc. Bull. 13:440-448.

Dame, R.F. 1972a. Comparison of various allometric relationships in intertidal and subtidal American oysters. Fish. Bull. 70:1121-1126.

Dame, R.F. 1972b. Day degree growth models for intertidal oysters. Contr. in Mar. Sc. (Texas Univ.) 19:107-112.

Dame, R.F. 1976. Energy flow in an intertidal oyster population. Estuarine and Coastal Mar. Sci. 4:243-253.

Dame, R.F., R.G. Zingmark, and E. Haskin. 1984. Oyster reefs as processors of estuarine materials. J. Exp. Mar. Biol. Ecol. 83:239-247.

Davis, J.C. 1975. Minimal dissolved oxygen requirements of aquatic life with emphasis on Canadian species: a review. J. Fish. Res. Bd. Can. 32:2295-2332.

Dickie, L.M., P.R. Boudreau, and K.R. Freeman. 1984. Influences of stock and site on growth and mortality in the blue mussel (*Mytilus edulis*). Can. J. Fish. Aquat. Sci. 41:134-140.

Dixon, W.J. ed. 1983. BMDP Statistical Software. University of California Press. Berkeley. 733 pp.

Draper, N.R. and H. Smith. 1981. Applied regression analysis. 2nd ed. John Wiley. New York. 709 pp.

Elvin, O.W. and J.J. Gonor. 1979. The thermal regime of an intertidal *Mytillus californianus* Conrad population of the central Oregon coast. J. Exp. Mar. Biol. Ecol. 39:265-279.

Engle, R.M. 1949. A comparative study of oyster condition. Science 109:593.

Epifanio, C.E., R. Srna and G. Pruder. 1975. Mariculture of shellfish in controlled environments: a prognosis. Aquaculture 5:227-241.

Farmer, A.H., M.J. Armbruster, J.W. Terrell, and R.L. Schroeder. 1982. Habitat models for land-use planning: assumptions and strategies for development. N. Amer. Wildl. and Natur. Resour. Conf. 47:47-56.

Frechette, M. and E. Bourget. 1985. Energy flow between the pelagic and benthic zones: factors controlling particulate organic matter available to an intertidal mussel bed. Can. J. Fish. Aquat. Sci. 42:1158-1165.

Galtsoff, P.S. 1964. The American oyster, *Crassostrea virginica* Gmelin. U.S. Fish Wildl. Serv. Fish. Bull. 64: 480 pp.

Gunter, G. 1938. Comments on the shape, growth and quality of the American oyster. Sci. 88:546-547.

Hall, S. 1983. A multiple regression model of oyster growth. Fish. Res. 2:167-175.

Harrison, P.J., J.D. Fulton, F.J.R. Taylor, and T.R. Parsons. 1983. Review of the biological oceanography of the Strait of Georgia: pelagic environment. Can. J. Fish. Aquat. Sci. 40:1064-1094.

Harry, H.W. 1985. Synopsis of the supraspecific classification of living oysters (Bivalvia: Gryphaeidae and Ostreidae). The Veliger. 28:121-158.

Haven, D.S. and R. Morales-Alamo. 1970. Filtration of particles from suspension by the American oyster *Crassosterea virginica*. Biol. Bull. 139:248-264.

Herlinveaux, R.H. 1962. Oceanography of Saanich Inlet in Vancouver Island, British Columbia. J. Fish. Res. Bd. Canada. 19:103-113.

Hilbish, T.J. 1986. Growth trajectories of shell and soft tissue in Bivalves: seasonal variation in *Mytilus edulis* L. J. Exp. Mar. Biol. Ecol. 96:103-113.

Holling, C.S. ed. 1978. Adaptive environmental assessment and management. John Wiley and Sons. New York. 377 pp.

Hopkins, A.E. 1936. Adaptation of the feeding mechanism of the oyster (*Ostrea gigas*) for changes in salinity. U.S. Bur. Fish. Bull. 48:345-364.

Hopkins, A.E. 1949. Determination of condition of oysters. Science 110:567-568.

Humphries, M. 1976. The production and marketing of tray cultured raft oysters in B.C. Environment Canada Fish. and Mar. Ser., Fisherman's Ser. Branch, Tech. Rep. 90: 73 pp.

Incze, L.S., R.A. Lutz, and L Watling. 1980. Relationships between effects of environmental temperature and seston on growth and mortality of *Mytilus edulis* in a temperate northern estuary. Mar. Biol. 57:147-156.

Incze, L.S., R.A. Lutz, and Ernest True. 1981. Modelling carrying capacities for bivalve molluscs in open, suspended culture systems. J. World. Maricul. Soc. 12:143-155.

Jones, G. and B. Jones. 1983. Methods for setting hatchery produced oyster larvae. B.C. Min. of Environment. Info. Rep. 4: 94 pp.

Kaspar, H.F., P.A. Gillespie, I.C. Boyer and A.L. MacKenzie. 1985. Effects of mussel aquaculture on the nitrogen cycle and benthic communities in Kenepuru Sound, Marlborough Sounds, New Zealand. Mar. Biol. 85:127-136.

King, M.G. 1977. Cultivation of the Pacific oyster, *Crassostrea gigas*, in a non-tidal hypersaline pond. Aquaculture 11:123-136.

Kiørboe, T., F. Mohlenberg, and O. Nohr. 1981. Effect of suspended bottom material on growth and energetics in *Mytilus edulis*. Mar. Biol. 61:283-288.

Kirby-Smith, W.W. and R.T. Barber. 1974. Suspension-feeding aquaculture systems: effects of phytoplankton concentration and temperature on growth of the bay scallop. Aquaculture 3:135-145.

Kucheryavenko, A.V. 1985. Estimation of oyster production potential in Novogorodskaya Bay of the Sea of Japan. Biologiya Morya. 1:59-62.

Kuwatani, Y. and T. Nishii. 1969. Effects of pH of culture water on the growth of the Japanese pearl oyster. Bull. Jap. Soc. Sci. Fish. 35:342-350.

Lancia, R.A., D.S. Miller, D.A. Adams, and D.W. Hazel. 1982. Validating habitat quality assessment: an example. N. Amer. Wildl. and Natur. Resour. Conf. 47:96-110.

Lawerence, D.R. and G.I. Scott. 1982. The determination and use of condition index of oysters. Estuarines 5:23-27.

Layher, W.G. and O.E. Maughan. 1985. Relations between habitat variables and channel catfish populations in prairie streams. Trans. Am. Fish. Soc. 114:771-781.

Loosanoff, V.L. 1958. Some aspects of behaviour of oysters at different temperatures. Biol. Bull. 114:57-70.

Loosanoff, V.L. and F.D. Tommers. 1948. Effect of suspended silt and other substances on the rate of feeding of oysters. Science 107:69-70.

Lough, R. and R. Gregory. 1975. A reevaluation of the combined effects of temperature and salinity on survival and growth of bivalve larvae using response surface techniques. Fish. Bull. 73:86-94.

Lucas, Albert, and P.G. Beninger. 1985. The use of physiological condition indices in marine bivalve aquaculture. Aquaculture 44:187-200.

MacDonald, B.A. and R.J. Thompson. 1985. Influence of temperature and food availability on the ecological energetics of the giant scallop *Placopecten magellanicus*. I. Growth rates of shell and somatic tissue. Mar. Ecol. Prog. Ser. 25:279-294.

MacKenzie, C.L., Jr. 1983. To increase oyster production in the Northeastern United States. Nat. Mar. Fish. Serv. 45:1-22.

Mallet, Andre L. and L.E. Haley. 1983. Growth rate and survival in pure population matings and crosses of the oyster *Crassostrea virginica*. Can. J. Fish. Aquat. Sci. 40:948-954.

Malouf, R.E. and W.P. Breese. 1977. Seasonal changes in the effects of temperature and water flow rate on the growth of juvenile Pacific oysters, *Crassostrea gigas* Thunberg. Aquaculture 12:1-13.

Mann, R. ed. 1979a. Exotic species in mariculture. M.I.T. Press. Cambridge, MA. 363 pp.

Mann, R. 1979b. Some biochemical and physiological aspects of growth and gametogenesis in *Crassostrea gigas* and *Ostrea edulis* grown at sustained elevated temperatures. J. Mar. Biol. Ass. U.K. 59:95-110.

Mann, R. 1978. A comparison of morphometric, biochemical and physiological indexes of condition in marine bivalve molluscs. In: Energy and environmental stress in aquatic systems. Ed. J.H. Thorpe and I.W. Gibbons. DOE Symp. Ser. 48:484-497.

Mann, R. and J.H. Ryther. 1977. Growth of six species of bivalve molluscs in a waste recycling-aquaculture system. Aquaculture 11:231-245.

Medcof, J.C. and A.W.H. Needler. 1941. The influence of temperature and salinity on the condition of oysters, *Crassostrea virginica*. J. Fish. Res. Bd. Can. 5:253-257.

Menzel, W. 1979. Clams and snails {*Mollusca: Pelecypoda*(except oysters) and *Gastropoda*}. in, Pollution ecology of estuarine invertebrates. Ed. C.W. Hart Jr. and S.L.H. Fuller. Academic Press. New York. 466 pp.

Michael, C.P. and K.K. Chew. 1976. Growth of Pacific oysters, *Crassostrea gigas* and related fouling problems under tray culture at Seabeck Bay, Washington. Proc. Natl. Shellfish. Assoc. 66:34-41.

Mitchell, P.H. 1912. The oxygen requirements of shellfish. Bull. U.S. Bureau of Fish. 32:202-222.

Neter, J.W., W. Wasserman and M.K. Kutner. 1985. Applied linear statistical models. 2nd ed. R.D. Irwin. Homeland, Ill. 547 pp.

Newell, R.I.E. 1982. An evaluation of the wet oxidation technique for use in determining the energy content of seston samples. Can. J. Fish. Aquat. Sci. 39:1383-1388.

Newell, R.I.E. and S.J. Jordan. 1983. Preferential ingestion of organic material by the American oyster, *Crassostrea virginica*. Mar. Ecol. Prog. Ser. 13:47-53.

Parsons, T.R. 1961. On the pigment composition of eleven species of marine phytoplankters. J. Fish. Res. Bd. Canada 18:1017-1024.

Parsons, T.R. and M. Takahashi. 1973. Biological oceanographic processes. Pergamon Press. Oxford. 186 pp.

Parsons, T.R., K. Stephens and R.J. LeBrasseur. 1969. Production studies in the Strait of Georgia. Part I. Primary production under the Fraser River Plume, February to May, 1967. J. Exp. Mar. Biol. 3:27-40.

Pereya, W.T. 1962. Mortality of Pacific oysters, *Crassostrea gigas* in various exposure situations in Washington. Proc. Natl. Shellfish. Assoc. 1962:53.

Pierce, S.K. 1971. Volume regulation and valve movements by marine mussels. Comp. Biochem. Physiol. 39a:103-117.

Quayle, D.B. 1971. Pacific oyster raft culture in B.C. Fish. Res. Bd. of Can. Bull. 178: 34 pp.

Quayle, D.B. 1969. Pacific oyster culture in B.C. Fish. Res. Bd. of Can. Bull. 169: 192 pp.

Quayle, D.B. 1961. Denman Island disease. Fish. Res. Bd. Can. Manus. Rep. (Biol.) 713: 9 pp.

Quayle, D.B. 1951. The seasonal growth of the Pacific oyster, *Ostrea gigas*, in Ladysmith Harbour. B.C. Prov. Dept. of Fish. Ann. Rep. 85-90.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. of the Fish. Res. Bd. of Canada. 191: 382 pp.

Rigler, F.H. and J.A. Downing. 1984. The calculation of secondary productivity. In: A manual on methods for the assessment of secondary productivity in fresh waters. Ed. J.A. Downing, and F.H. Rigler. IBP Handbook 17. Blackwell Scientific Publications. London.

Riley, J.P. and R. Chester. 1971. Introduction to marine chemistry. Academic Press, London. 465 pp.

Rodnick, K. and H.W. Li. 1983. Habitat suitability index models: little-neck clam. U.S. Dept. Int. Fish Wildl. Ser. 15 pp.

Roff, D.A. 1980. A motion for the retirement of the Von Bertalanffy Function. Can. J. Fish. Aquat. Sci. 37:127-129.

Ryder, R.A., S.R. Kerr, K.H. Loftus, and H.A. Regier. 1974. The morphoedaphic index, a fish yield estimator-review and evaluation. J. Fish. Res. Bd. Canada 31:663-688.

Schamberger, M. and W. B. Krohn. 1982. Status of the habitat of the evaluation procedures. Trans. N. Amer. Wildl. and Natur. Resour. Conf. 47:154-164.

Schlesinger, David A. and Henry A. Regier. 1982. Climatic and morphoedaphic indices of fish yields from natural lakes. Amer. Fish. Soc. 111:141-150.

Seed, R. 1973. Absolute and allometric growth in the mussel, *Mytilus edulis* L. (Mollusca Bivalvia). Proc. Malac. Soc. Lond. 40:343-357.

Sindermann, C.J. 1984. Disease in marine aquaculture. Helgolander Meeresuntersuchungen 37:505-532.

Smith, D.W. 1975. Manual for assessment of oyster growing areas. B.C. Mar. Res. Bran. Fish. Management Rep. 5. 10 pp.

Soniat, T.M., S.M. Ray and L.M. Jefferey. 1984. Components of the seston and possible available food for oysters in Galveston Bay, Texas. Contr. in Mar. Sci. (Texas Univ.) 27:127-141.

Sournia, A. 1978. Phytoplankton manual. Monogr. on Oceanogr. Methodology 6. United Nations Educational, Scientific and Cultural Organization. Paris. 337 pp.

Sparks, A.K. and K.K. Chew. 1959. Preliminary report on growth and survival of Pacific oyster in Washington waters. Proc. Natl. Shellfish. Assoc. 50:125-132.

Spencer, B.E., D. Key, P.F. Millican and M.J. Thomas. 1978. The effect of intertidal exposure on the growth and survival of hatchery-reared Pacific oysters, *Crassostrea gigas* kept in trays during their first ongrowing season. Aquaculture 13:191-203.

Stockner, J.G., D.D. Cliff and K.R.S. Shortreed. 1979. Phytoplankton ecology of the Strait of Georgia, British Columbia. J. Fish. Res. Board Can. 36:657-666.

Stockner, J.G. and D.D. Cliff. 1975. Marine phytoplankton production, distribution and species composition in Pendrell and Hotham Sound, British Columbia. Fish. and Mar. Serv. Rep. 516: 22 pp.

Strickland, J.D.H. 1960. Measuring the production of marine phytoplankton. Fish. Res. Bd. Canada Bull. 122:172.

Strickland, J.D.H. and T.R. Parsons. 1982. A practical handbook of seawater analysis. 2nd Ed. Fish. Res. Bd. of Canada Bull. 167: 310 pp.

Sumner, C.E. 1980. Growth of Pacific oysters, *Crassostrea gigas* Thunberg, cultivated in Tasmania. I. Intertidal stick culture. Aust. J. Mar. Freshwater Res. 31:129-135.

Takahashi, M. D.L. Seibert, and W.H. Thomas. 1977. Occasional blooms of phytoplankton during summer in Saanich inlet, B.C., Canada. Deep-Sea Res. 24:775-780.

Tenore, K.R. and W.M. Dunstan. 1973. Comparsion of feeding and biodeposition of three bivalves at different food levels. Mar. Biol. 21:190-195.

Thompson, R.J. and B.L. Bayne. 1974. Some relationships between growth, metabolism and food in the mussel *Mytilus edulis*. Mar. Biol. 27:317-326.

Thomson, R.E. 1981. Oceanography of the British Columbia coast. Can. Special Publ. of Fish. Aquat. Sci. 56: 291 pp.

Ulanowicz, R.E., M.l. Ali, A. Vivian, D.R. Heinle, W.A. Richkus, and J.K. Summers. 1982. Identifying climatic factors influencing commercial fish and shellfish landings in Maryland. Fish. Bull. 80:611-619.

Ulanowicz, R.E., W.C. Caplins, and E.A. Dunnington. 1980. The forecasting of oyster harvest in Central Chesapeake Bay. Estuarine and Coastal Mar. Sci. 2:101-106.

Urich, D.L., J.P. Graham, and P.E. Kelly. 1986. Statewide planning using the wildlife and fish habitat relationships system. Wildl. Soc. Bull. 14:22-30.

U.S. Fish and Wildlife Service. 1981. Standards for the development of Habitat Suitability Index models. Ecological Services Manual 103. Division of Ecological Services, USFWS, U.S. Dept. Int., Washington, D.C.

U.S. Fish and Wildlife Service. 1980. Habitat as a basis for environmental assessment. Ecological Services Manual 101. Division of Ecological Services, USFWS, U.S. Dept. Int., Washington, D.C.

Vahl, O. 1980. Seasonal variations in seston and in the growth rate of the Iceland Scallop, *Chlamys islandica* (O.F. Miller) from Balsfjord, 70'N. J. Exp. Mar. Biol. Ecol. 48:195-204.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. J. Wildl. Manage. 47:893-901.

Wallace, J.C. and T. G. Reinsnes. 1985. The significance of various environmental parameters for growth of the Iceland Scallop, *Chlamys islandica* (Pectinidae), in hanging culture. Aquaculture 44:229-242.

Walne, P.R. 1972. The influence of current speed, body size and water temperature on the filtration rate of five species of bivalves. J. Mar. Biol. Assoc. U.K. 52:345-374.

Walne, P.R. 1970. The seasonal variation of meat and glycogen content of seven populations of oysters *Ostrea edulis* L. and a review of the literature. Fish. Invest. Ser. II. 26: 34 pp.

Walne, P.R. and P.F. Millican. 1972. The condition index and organic content of small oyster spat. J. Cons. int. Explor. Mer. 38:230-233.

Westley, R.E. 1965. Some relationships between Pacific oysters, *Crassostrea gigas*, condition and the environment. Proc. Natl. Shellfish. Assoc. 55:19-33.

Whyte, J.N.C. and J.R. Englar. 1982. Seasonal variation in the chemical composition and condition indices of Pacific oysters, *Crassostrea gigas*, grown in trays or on the sea bed. Can. J. Fish. Aquat. Sci. 39:1084-1094.

Widdows, J., P. Donkin, P.N. Salkeld, J.J. Cleary, D.M. Lowe. S.V. Evans and P.E. Thompson. 1984. Relative importance of environmental factors in determining physiological differences between two populations of mussels (*Mytilus edulis*). Mar. Ecol. Prog. Ser. 17:33-47.

Widdows, J., P. Fieth, and C.M. Worrall. 1979. Relationships between seston, available food and feeding activity in the common mussel *Mytilus edulis*. Mar. Biol. 50:195-207.

Wilbur, K. M. and A.S.M. Saleuddin. 1983. Shell formation. In: The Molusca: Physiology. 4(1). Ed. A.S.M Saleuddin and K.M. Wilbur. Academic Press. New York. 523 pp.

Winter, J.E. 1978. A review on the knowledge of suspension feeding in lamellibranchiate bivalves with special reference to artifical aquaculture systems. Aquaculture 13:1-33.

Woelke, C.E. 1959a. Growth of the Pacific oyster, *Crassostrea gigas* in the waters of Washington state. Proc. Natl. Shellfish. Assoc. 50:133-143.

Woelke, C.E. 1959b. Pacific oyster, *Crassostrea gigas*, mortalities with notes on common oyster predators in Washington waters. Proc. Natl. Shellfish Assoc. 50:53-66.

Zar, J.H. 1984. Biostatistical Analysis. 2nd Ed. Prentice-Hall Canada. Toronto. 718 pp.