PLANKTON BLOOMS OF THE BRITISH COLUMBIA NORTHERN SHELF: SEASONAL DISTRIBUTIONS AND MECHANISMS INFLUENCING THEIR FORMATION

by

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ABSTRACT

The first description is presented of spatial and seasonal distributions of plankton blooms, and physical oceanographic conditions underlying their formation, on the British Columbia northern shelf. This region includes Queen Charlotte Strait and Sound, Hecate Strait, Dixon Entrance and their contiguous waters. Its biological oceanographic characteristics are virtually unknown, yet it has valuable petroleum and fishery resources.

Samples were collected between March 1978 and August 1980 using a coastal oil tanker as a ship of opportunity. Fourteen cruises were conducted, concentrated during spring and summer. Samples for salinity, nutrients, phytoplankton composition and pigments were collected from the sea water intake system (depth 3 m) while underway. Zooplankton were collected with a Miller sampler towed from the stern; temperature profiles were obtained with an XBT system.

Light penetration and vertical mixing characteristics were the principal physical properties leading to initiation of phytoplankton blooms in spring and summer. The spring (diatom) bloom was predicted by a critical - mixed depth model calculated from historical data. Summer blooms were predicted by a tidal front model, which compares tidal velocities with water depth. Bathymetry is the common feature of these two mechanisms, limiting the mixed depth in spring and maintaining tidal mixing

in shallow regions during summer.

The spring bloom progressed northward with increasing irradiance, occurring during February - March in the Strait of Georgia and during May in Dixon Entrance. However, it was predicted and observed earlier in Hecate Strait (April), where a shallow shelf limits the mixed depth, than in more southerly Queen Charlotte Sound. The bloom in Queen Charlotte Sound first developed along its southeastern coast, apparently due to runoff-related stratification. On the scale of sampling, zooplankton blooms in spring occurred in the same areas as phytoplankton.

During summer, observations confirmed low biomass (flagellates) and well-mixed conditions in shallow western Hecate Strait, and high biomass (diatoms) and stratified conditions on its eastern side. However, mean mixed layer light intensities were similar, and near-surface nutrient concentrations low, on both sides of the strait. Phytoplankton on the shallow side were probably limited by rates of nutrient resupply, while the eastern side received nutrients from upwelling or sporadic mixing by storms. This may distinguish the effect of tidal mixing in shelf seas and straits, with advection of nutrients to the mixed region of straits reduced by the shallow bottom and adjacent land boundaries.

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PREFACE

This thesis presents an analysis of data collected in the University of British Columbia, Dept. of Oceanography ship of opportunity program. These data have been made available in two data reports, and so are not included in this thesis as appendices. These reports are:

> Dilke, B.R., S. McKinnell and R.I. Perry. 1979. M.V. *Imperial Tofino* ship of opportunity program. March 1978 to March 1979. University of B.C., Dept. of Oceanography Data Rept. No. 46. 111p.

> Perry, R.I., B.R. Dilke, G.C. Louttit and S. McKinnell. 1981. M.V. *Imperial Tofino* ship of opportunity program. May 1979 to June 1980. University of B.C., Dept. of Oceanography Data Rept. No. 49. 159p.

They are available by writing

> The Librarian
> Dept. of Oceanography
> University of B.C.
> Vancouver, B.C.
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I. GENERAL INTRODUCTION AND OBJECTIVES

The coastal waters of British Columbia cover an extensive area and include fjords, passages, and a narrow continental shelf. They can be divided into three broad regions on the basis of geographic location, oceanographic characteristics, and the intensity of research effort expended in their investigation. This study is concerned with one of these regions, the northern shelf, which has resources of great economic potential yet is poorly known oceanographically. It is the first study to describe the spatial and temporal distributions of plankton blooms from winter to summer in this region, a prerequisite to more detailed productivity and fisheries investigations. Physical mechanisms initiating these blooms are also examined to understand where and how blooms develop and their potential impact upon resources of the northern coast.

The Strait of Georgia, and oceanic waters to the west of the Queen Charlotte and Vancouver Islands, make up the two other broad regions of the B.C. coast. The Strait of Georgia and its adjacent inlets can be considered as inshore estuarine-dominated due to the Fraser River and the various island barriers to circulation and exchange with the open Pacific. Wide spatial and seasonal variations of temperature are apparent (Thomson 1981). Studies on the Strait date from plankton records in 1915 (Bailey and Mackay 1916) and it has remained the most intensively studied region of the coast. A recent survey of literature

pertaining to or based on these waters lists over 300 references to biological and physical research (Harrison *et al.* in press). The relatively benign oceanographic climate and its proximity to centers of population and research are obvious reasons contributing to this extensive study.

The second region, the offshore oceanic region, includes waters west of Vancouver Island and the Queen Charlotte Islands. In general there is a narrow continental shelf, little direct freshwater input, and more constant temperature and salinity characteristics than the Strait of Georgia. The region off Vancouver Island and the mouth of Juan de Fuca Strait has recently received considerable research attention, much of it resulting from its importance in salmonid migrations. Representative studies have been made by Denman *et al.* (1981) and Freeland and Denman (1982).

The B.C. northern shelf and its adjacent waters comprise the third major region. This region includes Queen Charlotte Strait, Queen Charlotte Sound, Hecate Strait, and Dixon Entrance (Thomson 1981) and is almost ten times the area of the Strait of Georgia. It is intermediate in its oceanographic properties, being influenced directly by river runoff yet also being open to oceanic waters via Dixon Entrance and Queen Charlotte Sound, and has the most extensive continental shelf of the B.C. coast. It is also intermediate in the amount of research effort it has received, with early reports of phytoplankton composition from the United States Navy (Allen 1927), and several major physical

oceanographic surveys conducted during the 1950's and 1960's. Tabata (1980) lists some 70 primarily physical reports and papers concerning this region, while its biological oceanography has been almost entirely neglected during this period.

The northern shelf of British Columbia is potentially of great economic importance to B.C. and Canada, having extensive living and non-living marine resources. The principal non-living resource currently considered for exploitation is petroleum. The first report of hydrocarbons off mainland B.C. was a gas flare from a well drilled in 1913-1915 on the Queen Charlotte Islands (Haimila and Proctor 1982). Subsequent drilling in the adjacent offshore has occurred as recently as 1967-1971, when a moratorium on exploration drilling was imposed. Estimates made in 1980 of the natural gas and oil potential of B.C. offshore areas suggest an average expectation of 265×10^9 m^3 of gas and 38.5×10^6 m^3 of oil, with the largest area being the northern shelf (Haimila and Proctor 1982).

In September 1983, an agreement was reached between provincial and federal governments concerning formation of a joint west coast environmental review panel for assessment of offshore hydrocarbon exploration on the northern shelf. It is to report in late 1984 on conditions for possible removal of the moratorium against exploration activities. This thesis is therefore a timely addition to background knowledge concerning the biology of this region. Two other studies of the environmental and social concerns for offshore hydrocarbon

exploration and development in B.C. are McPhee (1982) and Langford (1983).

The importance of the northern shelf region for living marine resources is due both to local and migratory stocks of finfish and shellfish. Withler and Wong (1983) reviewed observations of salmon in Hecate Strait and adjacent waters and noted that they contribute significantly to B.C.'s commercial salmon landings. Hecate Strait is also an important pathway for outmigrating juveniles and maturing adults returning to their spawning streams. The juveniles are produced both locally and from streams further south, and appear to feed and grow in the strait from mid-July to November (Withler and Wong 1983).

Another important fishery resource are herring *(Clupea harengus pallasi)*, which spawn in specific locations along the coast and then migrate into open waters of the northern shelf (Taylor 1964). Langford (1983) reports that Dixon Entrance and Hecate Strait accounted for 27% of herring landings and 77% of the herring spawn-on-kelp harvest for B.C. from 1978-1980.

Groundfish fisheries are very important on the northern shelf, providing 63.1% of the annual B.C. groundfish catch during 1976-1980 (Langford 1983). Observations on sablefish *(Anoplopoma fimbria)*, currently with the highest landed value of all groundfish on Canada's Pacific coast, suggest juveniles may remain in coastal waters of the northern shelf until they mature (Mason *et al.* 1983). Pacific cod *(Gadus macrocephalus)* and halibut *(Hippoglossus stenolepis)* are also important resources,

particularily in Hecate Strait.

A recent fishery for abalone *(Haliotis kamtschatkana)* is located on both sides of Hecate Strait, mostly among kelp beds off Moresby Island and Banks Island (Breen 1980). A long-term fishery has also existed for Dungeness crab on the north coast of Graham Island in Dixon Entrance.

Considerable populations of marine mammals, sea birds, and marine plants also exist on the northern shelf, although little is known of their distributions. Langford (1983) has compiled a review of the biology of B.C. coastal waters, with several maps illustrating possible distributions of many of the foregoing marine populations.

While the resources of the northern shelf are extensive and the region serves as a probable nursery area for larval and juvenile fish (e.g. Ketchen 1956, Withler and Wong 1983), no systematic studies have been conducted to examine the distribution and regulating mechanisms of potential planktonic food items. According to the match/mismatch hypothesis (Cushing 1974), larval survival may be improved if the onset of feeding is timed to match production of their prey. The strength of the subsequent recruitment then depends on the degree of overlap. Prediction of the temporal and spatial pattern of plankton blooms on the northern shelf may aid studies of recruitment fluctuations of north coast fisheries, and provide a basis for timing the release of hatchery-reared salmonids. The pattern of blooms may also explain breeding success and population

fluctuations of planktivorous sea birds (e.g. Vermeer 1981).

Prediction of such blooms can take two approaches. One is strictly observational, where the timing and location of blooms is observed over several years, while the other is mechanistic, with predictions based on some theory of their underlying causes. The best approach is a combination of these methods, where predictions from mechanistic models are compared with observations. The northern B.C. shelf provides an opportunity for the comparison of current physical models of seasonal plankton blooms and new observations in the field. Of particular importance is the wide variation of bathymetry in the area, which may produce differences in tidal velocities across the bottom thus generating mixed and stratified water masses, with their characteristic blooms of plankton (e.g. Pingree 1978). In spring, such variations of bathymetry may also influence the pattern of the spring bloom, which can be described by the Sverdrup (1953) critical depth model.

The occurrence of adjacent mixed and stratified regions suggests that fronts may be common features of the region. Studies of circulation patterns about fronts (Pingree *et al.* 1974) indicate they are zones of convergence tending to accumulate buoyant surface materials. Thus fronts on the northern shelf are likely to be critical sites for interaction of the region's living and non-living resources. As convergent zones, they may accumulate plankton, including fish larvae, and so increase the likelihood of a match in production. However,

for the same reason they will also accumulate surface pollutants such as hydrocarbons or trace metals (e.g. Sick *et al.* 1978). Frontal zones have also been shown to be regions of increased *in situ* production resulting from these mixed and stratified waters (see Chapter 5 for a brief review). Thus, such regions on the northern shelf are likely to be important sites of enhanced biological activity.

1. OBJECTIVES

The general objectives of this study are as follows:

1. To examine the spatial and temporal distributions of plankton blooms in the open waters of the British Columbia northern shelf, including the seaward portions of the adjacent fjords and island passages. Phytoplankton and zooplankton biomass fluctuations and species composition, and changes in nutrient concentrations, are included. Distributions and timing of blooms are compared within and between regions of the northern shelf such as Queen Charlotte Sound, Hecate Strait, and Dixon Entrance, as well as with the timing of the spring bloom in the Strait of Georgia. This provides the first large scale spatial and seasonal investigation of plankton in B.C. coastal waters north of Vancouver Island.
2. To investigate potential mechanisms generating blooms and regulating the observed spatial and temporal patterns of plankton on the B.C. northern shelf. The principal mechanisms considered are the critical depth - mixed depth

model (Sverdrup 1953) for initiation of spring blooms, and the shallow sea tidal front model (Pingree 1978) for the location and development of plankton blooms during summer. Confirmation that these models apply to areas for which direct observations exist suggests they may also be used to predict bloom dynamics for the inadequately sampled areas of the northern shelf.

Each chapter describes an independent subsection of this study, with its own specific objectives and where necessary, its methodology. A guide to the contents of each chapter, and an outline to the thesis as a whole, is presented below.

2. CHAPTER SYNOPSES

Some information is available from previous studies concerning the broad outline of the physical oceanography of the northern shelf. Such information is obviously pertinent to any consideration of physical mechanisms influencing the plankton dynamics. Chapter 2 presents a brief review of these studies including the physiographic characteristics of the region as background to the results of the present study.

To increase the spatial and temporal extent of sampling over such a vast area as the northern shelf, a commercial oil tanker was used as a ship of opportunity. Chapter 3 describes this ship of opportunity (SHOP) program, outlining its origin, methods, and problems. It serves as a centralized section summarizing methods used throughout the whole of this study.

Methods specific to each chapter are discussed within that chapter.

Chapter 4 describes the spatial and seasonal patterns of plankton on the northern shelf. It begins with a review of previous studies of the region's biological oceanography, then presents a synoptic description of distributions of chlorophyll *a*, nutrients, and phytoplankton and zooplankton as determined by this study. Variability within and between regions of the northern shelf is emphasized.

The second central theme of Chapter 4 is concerned with the timing of the spring bloom, and the hypothesis that it begins first in southern waters and sweeps sequentially northwards with increasing solar radiation. The critical depth model is used to predict the bloom timing, which is compared with field observations. As an example of the spatial variability of biological characteristics that can occur at smaller scales, the spring - summer pattern of blooms in the coastal region of Queen Charlotte Strait and Queen Charlotte Sound is presented and its relationship to outmigrations of juvenile salmonids discussed.

To continue this theme of considerable spatial and temporal variability within each region of the northern shelf, Chapters 5 and 6 focus on Hecate Strait and examine its seasonal plankton distributions and organizing mechanisms. The hypothesis examined in Chapter 5 is that distributions of plankton across Hecate Strait in summer are organized by, and predictable from, variations in the intensity of vertical mixing. It is proposed

that such variations of vertical mixing result from the interaction of tidal streaming and bathymetry. In Chapter 6, mechanisms affecting plankton distributions and influencing taxonomic composition across Hecate Strait in winter and spring are examined. Such mechanisms include tidal mixing and the critical depth model, and the influence of bathymetry. In both these chapters the significance of the observed plankton distributions to fish and fisheries is discussed.

The final chapter presents a summary and general conclusions of this study. It summarizes the principal results of each chapter, and predicts temporal patterns of blooms for areas of the northern shelf not sampled by this program. It also includes a discussion of the new hypotheses and unanswered questions generated in this study that would be fruitful for further research.

II. PHYSICAL OCEANOGRAPHY OF THE NORTHERN SHELF: A BRIEF REVIEW

1. INTRODUCTION

This chapter serves as a brief review of the geography and physical oceanography of the British Columbia northern shelf region, providing necessary background for subsequent chapters concerned with its biological oceanography. A program of physical measurements in the region began in 1934 and was most intensive during the 1950's and 1960's. These data have been summarized and briefly interpreted by Dodimead (1980). Crean (1967) has described studies in Dixon Entrance, while the general oceanography of the B.C. coast including the northern shelf has been reviewed by Thomson (1981). The following is taken from Thomson (1981), except as noted.

2. PHYSIOGRAPHY

The physiography and bathymetry of the B.C. northern shelf is shown in Fig. 1. The region is characterized by a highly indented, glacially fashioned shoreline of islands, shoals and fjords which continues below sea level. The only lowland coastal plain is on northeast Graham Island, which extends into western Hecate Strait to give that region its dominant physical characteristic. With depths less than 20 m, this side of Hecate Strait is the shallowest, most regular channel of the north coast. The eastern side of Hecate Strait is much deeper, with the dominant feature being a trough running parallel to the

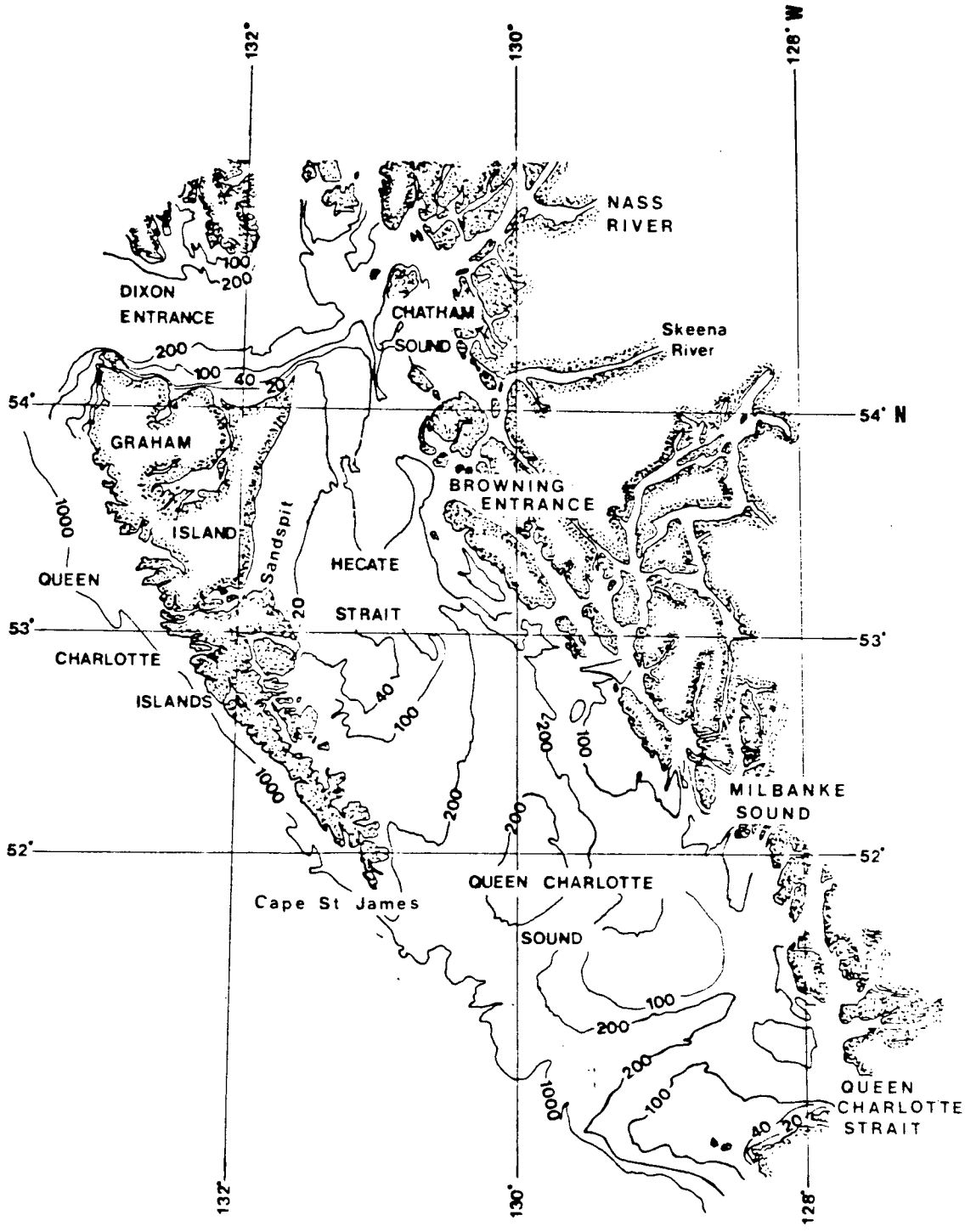

FIG. 1. Generalized map of the B.C. northern shelf study area showing locations of place names referred to in the text. Bathymetric contours are in meters.

coast from Queen Charlotte Sound to Dixon Entrance and shoaling from 300 m at the continental shelf to slightly <100 m at its northern end.

Two other troughs of 300-400 m extend from the continental shelf edge eastwards. Both are in central Queen Charlotte Sound, with the southern trough branching into Queen Charlotte Strait. Between these two troughs is a shallow bank called the Goose Island Bank, and between the southern spur and Vancouver Island is another shoal called Cook Bank. The slopes of both these banks are favoured sites for groundfish fisheries (Thomson 1981). In the north, a 400 m deep channel runs east-west forming the main basin of Dixon Entrance, with another spur into Clarence Strait within the Alaskan archipelago.

3. WINDS

As with the whole of the B.C. coast, winds in the northern shelf region are dominated by the seasonal pressure systems, the Aleutian low in winter and the North Pacific high in summer. Winds generally blow parallel to the coast channelled by the topography, with an east-west velocity gradient that is lower near the mainland shore.

In summer, light winds (5 m s^{-1}) predominate, generally from the west in Dixon Entrance and the northwest in Queen Charlotte Sound. By October, the Aleutian low dominates, with increased storm activity and stronger southeasterly winds. Gale force winds (>17 m s^{-1}) occur over 10% of the time during the

period November to February and, combined with the shallow bottom in parts of Queen Charlotte Sound and Hecate Strait, can produce very large waves and rough seas. When winter conditions are such that an inland high pressure and coastal low pressure system occur, very strong winds (>25 m s^{-1}) can blow through coastal inlets onto open water.

4. TIDES

Tides on the northern shelf are of the mixed semi-diurnal type similar to those in the Strait of Georgia. Tidal range varies with location, with shallower areas having greater amplitudes, for example 2-3 m in Hecate Strait. The flood tide generally propagates north along the west coast of Vancouver Island, then branches into Queen Charlotte Sound and up Hecate Strait. Another branch flows into Dixon Entrance and south into Hecate Strait. These northward- and southward-propagating tides meet in Hecate Strait where they can cause large tidal ranges (up to 7 m in Skidegate Inlet on the Queen Charlotte Islands).

5. CIRCULATION

Circulation patterns on the northern shelf are dominated by the semi-diurnal tidal streams but are often modified extensively by wind, runoff, bathymetry and shoreline features. In Queen Charlotte Sound, tidal streams are clockwise rotary with flood to the northeast and ebb to the southwest. In Hecate Strait, tidal streams are rectilinear due to the bathymetry,

with flood to the north and ebb to the south. In Dixon Entrance the flood current is stronger on the south side and ebb stronger on the north side due to the northward moving tide in Hecate Strait. This sets up a counterclockwise gyre in Dixon Entrance centered northwest of Rose Spit.

Non-tidal currents are predominantly caused by winds and runoff whose maximum effects are seen in different seasons. In winter a northward surface current is set up in Queen Charlotte Sound and Hecate Strait by strong southeast winds and a coastal pressure gradient created by onshore Ekman transport. It can have speeds up to 3% of the wind speed averaged over the previous several days. In summer the situation is reversed, with weak northwest winds causing offshore Ekman transport and a weak southward coastal current.

Runoff effects dominate in spring and early summer. They are most clearly seen in Chatham Sound and Dixon Entrance, fed by the significant spring discharges of the Nass and Skeena Rivers which both peak in June. The flow is northwest into Clarence Strait and west along the northern side of Dixon Entrance, creating an estuarine-type situation with brackish water moving seaward and a weak compensating return flow at depth. In other seas of the northern shelf, significant runoff is limited to the vicinity of the mainland shore.

6. TEMPERATURE AND SALINITY

Dodimead (1980) has summarized temperature and salinity data from the northern shelf. He found the seasonal variation followed the radiation and freshwater input, with an annual range of salinity from 28-32‰ and an east-west gradient with higher salinities at the western seaward edge. Temperature varied from an April minimum about 6°C to a summmer maximum about 14°C, with Dixon Entrance colder than regions to the south. Since the 1940's, six lighthouse stations in the region have collected daily temperature and salinity samples. Although these samples were from surface near-shore waters, they do illustrate the local variability on the northern shelf. Annual cycles of temperature were similar at all stations and typical of coastal waters at these latitudes. Annual ranges were less at "outside" stations (Langara Island and Cape St. James) than "inside" (Triple Island, Bonilla Island, McInnes Island, Ivory Island).

The principal differences were in the annual salinity variations, and Pickard and McLeod (1953) identified three climatological regions for the B.C. northern shelf:

- no influence of river runoff, i.e. open ocean conditions with little annual variation (Langara Island and Cape St. James);
- surface salinity dominated by runoff from snow storage, with a salinity minimum in early summer (Triple Island and Ivory Island);
- surface salinity dominated from runoff due to local

precipitation , with a minimum in winter (McInnes Island and Bonilla Island).

7. SUBSURFACE CHARACTERISTICS

Subsurface seasonal characteristics are dominated by offshore/onshore Ekman transport which deepens the halocline in winter and raises it in summer (Dodimead 1980). In summer, the surface mixed layer is relatively thin with strong gradients of temperature, salinity, density and oxygen. Oxygen concentrations reach a minimum in summer and may affect the depth migrations of demersal fish (Dodimead 1980). In winter, increased winds erode the thermocline and deepen the surface mixed layer, so that it may be isothermal to 150 m (Dodimead 1980).

III. GENERAL METHODS

1. INTRODUCTION

This study used a commercial vessel as its principal platform to examine the waters of the northern shelf. The background, logistics, sampling methodology, and problems with this ship of opportunity (SHOP) program are discussed in this chapter. All data collected by this study plus a brief review of its methods have been published in two reports (Dilke *et al.* 1979, Perry *et al.* 1981) in order to make them available to interested users as quickly as possible. They are therefore not included here as appendices, but are available from the Dept. of Oceanography, University of British Columbia, Vancouver, B.C. A comparison of ship of opportunity sampling procedures with those of standard research vessels is also included in this chapter.

Programs utilizing commercial vessels as ships of opportunity to increase spatial and temporal sampling over a given area are not new. The Continuous Plankton Recorder Survey (Glover 1967) has used merchant ships to sample the plankton of the North Atlantic and North Sea since 1930. Vessels towed an automated sampler through the water, avoiding the necessity of trained technicians to conduct the actual sampling procedure. The variables measured were therefore taxonomic composition and biomass of zooplankton, with a qualitative measure of phytoplankton abundance. Recently the towed instrument package has been modified to also record physical parameters and *in vivo*

fluorescence in an undulating vertical pattern (Aiken 1981).

One early ship of opportunity program using technicians to collect samples, and therefore to conduct chemical and productivity measurements, was run jointly by the University of Washington, Seattle, and the Canadian Fisheries Research Board in Nanaimo (Parsons and Anderson 1970, Anderson and Munson 1972). They used American Mail Lines vessels operating between Seattle and Yokohama to examine production processes in the North Pacific and test the validity of models predicting the timing of spring plankton blooms. The program continued for five years beginning in 1968. Water samples were collected from the engine room seawater system near the sea chest for chlorophyll *a*, phosphate, silicate and nitrate concentrations, phytoplankton standing stock and species enumeration, and particulate nitrogen analysis (Anderson and Munson 1972). Additional measurements included zooplankton composition and abundance, primary productivity, vertical temperature profiles and insolation. Results from these commercial vessels were backed up by an intensive investigation with a research ship (Parsons and Anderson 1970), and used to show seasonal differences of primary production and type of producer across the study area.

A long set of biological oceanographic time series observations has been produced from the Ocean Weather Station Papa (50°N, 145°W) sampling program. It began in August 1956 and continued with varying degrees of intensity until the cancellation of the Station "P" weather program in 1981. In

addition, samples were also taken along the track of the weathership (Line P) between Victoria, B.C., and Station "P". Parameters measured over different periods of time include physical data, pigments, nitrate concentrations, primary productivity, light attenuation, zooplankton composition and biomass, and echo sounding observations. This study differed from those previously described by having the ability to sample conditions at depth directly rather than via the ship's intake system, and so resembled programs of standard research vessels. The Station "P" and AML studies complement each other in terms of objectives, with Station "P" providing a temporal series within the spatial series of the AML program.

However, all these programs have concentrated on open oceanic waters while none have been concerned with routine sampling of coastal regions. Recently, other studies have been initiated using commercial ships of opportunity in coastal waters to measure both physical and biological parameters. A program similar to that described here using an ocean-going tugboat has been conducted by SeaKem Oceanography Ltd. (SeaKem Oceanography Ltd. 1979) to monitor biological conditions in the southern Strait of Georgia and off the west coast of Vancouver Island. Another study conducted by the University of British Columbia used provincial ferries running between Tsawassen and Swartz Bay to monitor the extent of the Fraser River plume (Royer and Emery 1982). On the Canadian east coast, a one year study conducted by Dalhousie University monitored the central

Gulf of Maine using ferries running between Yarmouth, N.S. and Portland, Maine (Boyd 1984). However, all these studies postdate the SHOP program described here, with the exception of the SeaKem program which was run simultaneously. The remaining sections of this chapter describe the background and methodology of the MV *Imperial Tofino* ship of opportunity program.

2. BACKGROUND

Initial planning for this program began at a workshop held at the Institute of Ocean Sciences, Pat Bay, B.C. in February 1977 entitled Pelagic Ecosystem Prediction Project (Brinkhurst 1977). It identified a need for time series of physical, chemical and biological data in the coastal zone of the northeast Pacific and suggested commercial ships of opportunity might be the only feasible method to obtain such data. Two areas were considered of principal interest: the oil transportation corridor across the subarctic Pacific from Alaska to the U.S. west coast; and the west coast of Vancouver Island and Hecate Strait-Queen Charlotte Sound. Several vessels were considered for the project, with the ultimate choice being the MV *Imperial Tofino*, operated by Imperial Oil of Canada Ltd. Funding for the project was awarded by the Natural Sciences and Engineering Research Council Strategic Grant program (Grant No. G-0068) to Dr. T. R. Parsons. Imperial Oil of Canada made various modifications to their ship to facilitate sampling, and agreed to support the technician while on board to collect samples.

3. VESSEL

Owned and operated by Imperial Oil of Canada Ltd. and registered in Vancouver, B.C., the MV *Imperial Tofino* is of all-steel construction and was built in 1973. She has a length overall of 50 m, a deadweight displacement of 1100 tonnes, and carries a crew of 11. In design it is a tanker for liquid cargoes, with the superstructure occupying the aft third of the vessel. It operates all year delivering kerosene and other fuel oils to various towns, settlements, and fishing camps along the B.C. coast.

Several modifications were made by Imperial Oil to facilitate sampling. These included access to the engine room seawater intake system to pump water directly for sampling, and the mounting of a winch and rotating davit on the stern to permit sampling for zooplankton. The hydraulic winch supplied up to 115 kg of line pull with a drum capacity of 350 m of 0.8 cm diameter hydrographic wire.

4. LOGISTICS

Choice of the *Imperial Tofino* as the ship of opportunity naturally constrained the study area to the normal operation of the vessel on its deliveries. Typical cruise tracks are shown in Fig. 2, while locations of all stations occupied are presented in Appendix I. It should be noted the usual route north to Prince Rupert followed the sheltered waters of the "Inside Passage", i.e. the Strait of Georgia, Queen Charlotte Strait,

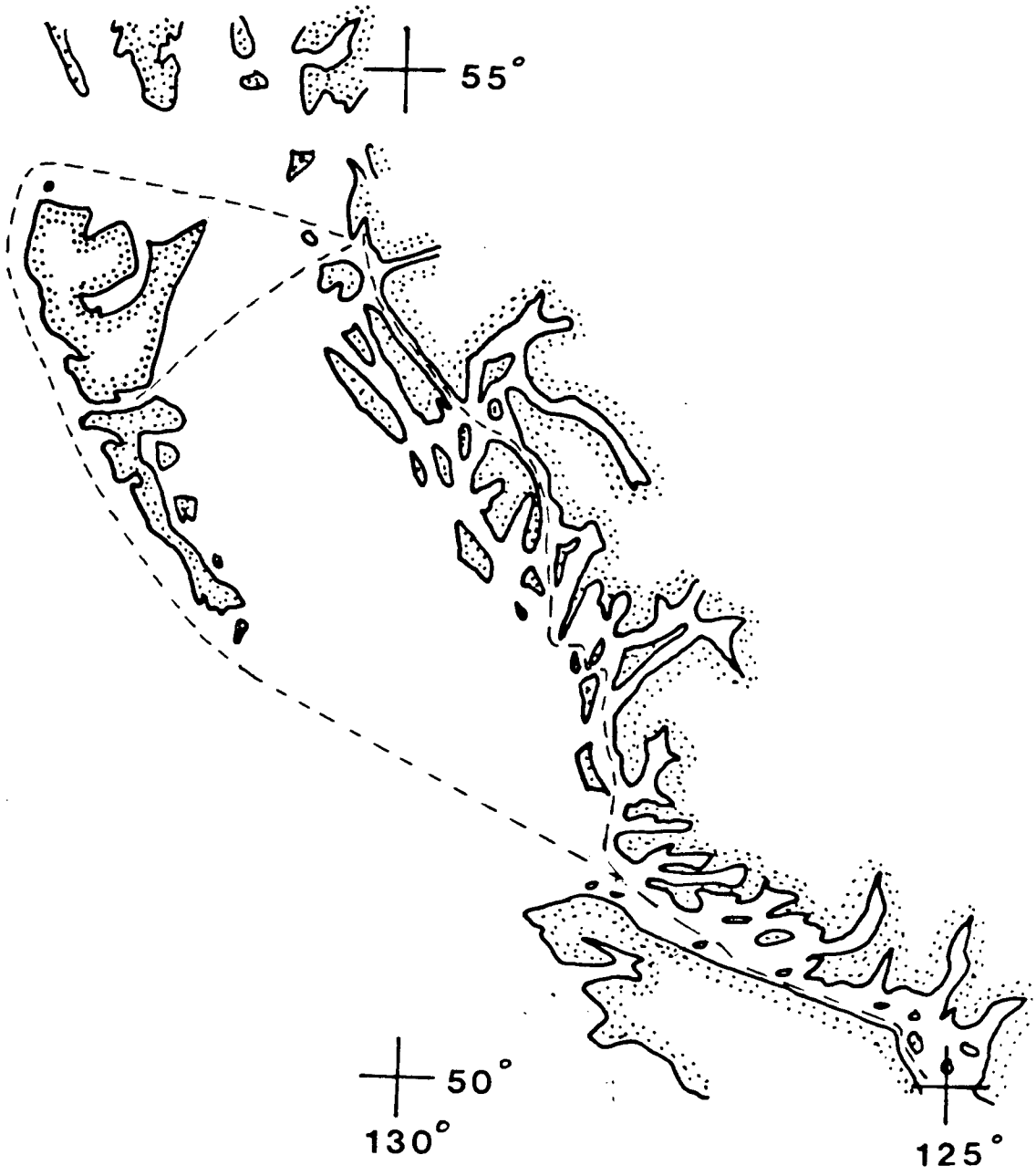

Fig. 2. Outline of the possible routes of the *Imperial Tofino* on trips to the northern shelf. Not all routes were followed on every cruise.

Fitz Hugh and Milbanke Sounds (see Fig. 9 for locations), and Princess Royal and Grenville Channels, followed by a run across Hecate Strait from Prince Rupert to Sandspit. Cruises were typically 2-3 weeks long and scheduled approximately monthly, being most intensive during spring and summer. Thus the intent was to have monthly coverage during the bloom periods over as wide an area of the northern shelf as possible.

Two technicians were hired to collect and process the samples from the commercial vessel phase of the project. Stationed at the Institute of Ocean Sciences, Pat Bay, B.C., they would determine from Imperial Oil the schedule for each northern trip of the *Tofino*, and arrange to load equipment and board at its base in Port Moody, B.C. Sampling was then conducted initially as frequently and in as many different locations as possible. However it was quickly realized this produced an enormous number of samples to analyse, especially with the monthly frequency of cruises. Consequently, upon consideration of the data from the first year of the project it was decided sampling should concentrate on the open waters of the north coast, and waters which were traversed consistently on each northern trip of the *Tofino*. These included Queen Charlotte Strait, Fitz Hugh and Milbanke Sounds, Hecate Strait and Dixon Entrance. This policy was applied to all cruises after Cruise 7 (January 1979). Table I lists the dates of all the *Tofino* SHOP cruises to the northern shelf.

TABLE I. MV *Imperial Tofino* cruise numbers, dates, and number of stations sampled for the duration of the ship of opportunity program.

CRUISE NUMBER	DATE	NUMBER OF STATIONS
01	13-20 March 1978	7
03	24 July - 3 August 1978	22
04	12-27 August 1978	37
05	11-27 September 1978	24
06	18-26 October 1978	22
07	2-7 January 1979	9
08	30 March - 8 April 1979	19
09	8-17 May 1979	21
10	9 June - 1 July 1979	23
11	13-19 July 1979	23
12	30 January - 9 February 1980	38
13	10-17 April 1980	37
14	30 May - 7 June 1980	35
15	21 August - 5 September 1980	33

5. SAMPLE COLLECTION

By definition, the primary concerns of a vessel used in a ship of opportunity program are its commercial responsibilities and scheduling; therefore, any sampling should interfere with routine operations as little as possible. In this program, sampling was done while the vessel was underway between coastal deliveries, although with the cooperation of the crew it was slowed to about 2.5 m s^{-1} (5 knots) for the duration of the sample collection. At each station the position and time was recorded in the bridge log by the Duty Officer.

Water samples for phytoplankton enumerations and pigments, salinity, and nutrients were drawn from the *Tofino's* engine room

seawater intake system. The intake is located amidship at a nominal depth of 3 m below the sea surface depending on ballast. At each station the sample volume (about 1.5 l) was pumped from the seachest by a Jabsco® impeller pump, and was integrated over the length of the zooplankton tow which occurred simultaneously. Typical sampling was 10 minutes, during which the vessel travelled about 1.5 km. The seachest is located adjacent to the intake and upstream of any engine room filters or injections. Its volume is 0.34 m^3, and with a maximum inflow of 0.091 m^3 min^{-1} the residence time of seawater is about 3-4 minutes. Over the 10 minute sample collection period there was little contamination of samples from residual water in the seachest.

Samples were then treated as described below and returned to the shore-based laboratory for analysis. Due to lack of space on board the *Tofino*, the only sample treatments that could be performed immediately were filtration and freezing, as applicable.

6. TEMPERATURE

To avoid any contamination from the engine room environment, temperature was measured in surface casts made from the deck of the vessel instead of through the seachest system. A modified bucket sampler was cast from the ship then brought on board and the temperature recorded. This sampler was designed by Mr. Bruce Dilke, and consisted of a 50 cm length of 5 cm I.D. PVC pipe, closed at the bottom, with two 3 cm wide slits along

the side, attached to a length of rope. Mounted inside this tube, with its bulb extending into the closed bottom end of the pipe, was a thermometer accurate to 0.1°C. Two styrofoam rings attached about the outside top and bottom of the sampler prevented damage against the side of the ship.

An expendable bathythermograph (XBT) system was used at each station and occasionally between stations on cruises after Cruise 7 to obtain profiles of temperature against depth. This system consisted of a Sippican chart recorder, hand-held probe launcher, and type T6 probes (depth range to 460 m, Sippican Corp. 1971). XBT surface temperatures were calibrated against surface bucket thermometer readings for accuracy.

7. SALINITY

From the seachest, 240 mL of sample was collected in 250 mL glass bottles with polyethylene-sealing screw caps. Conductivity was determined ashore with an Autosal salinometer (Guildline Instruments, model 8400), and salinity calculated from the conductivity measurements.

8. NUTRIENTS

Nutrients were determined from water samples collected from the seachest, with 125 mL filtered immediately through Gelman type A/E glass fiber filters to remove particulate matter and the filtrate stored frozen in plastic bottles. On shore, analyses for nitrate plus nitrite (NO_3+NO_2), phosphate (PO_4) and

silicate (SiO_4) were carried out using a Technicon® Auto Analyser as described in Strickland and Parsons (1972) using standard colourimetric procedures. Lower limits of detection were NO_3+NO_2: 0.10 μM; PO_4: 0.05 μM; SiO_4: 0.10 μM.

9. PHYTOPLANKTON

Samples for both enumeration and pigment analysis were collected from the ship's seachest. For enumeration, 240 mL was collected and preserved with 10 drops of Lugol's solution in a 250 mL screw-cap bottle. On shore, enumeration followed Utermöhl's (1958) method, with 10 mL or 100 mL of sample being settled depending on the cell density. Cell numbers were identified with an inverted microscope at 250X for larger cells and 1000X for small cells. To facilitate the counting of large numbers of samples, cells were identified to species where possible (for large, distinctly identifiable cells), or to genus and size category when more detailed identification would be considerably more time consuming.

Analyses for chlorophyll *a* and phaeopigments followed the *in vitro* fluorometric method outlined in Strickland and Parsons (1972). Seawater from the seachest was collected, and 200 mL filtered through Whatman GF/C glass fiber filters (or equivalent) with a trace of $MgCO_3$ added. Filters were then frozen and returned to the laboratory onshore, where they were ground with a tissue grinder in 90% acetone, the residue removed by filtration and the fluorescence of the filtrate determined by

a Turner model 111 fluorometer. Phaeopigments were determined with the addition of two drops of 10% HCL to the filtrate and remeasurement of the fluorescence (Strickland and Parsons 1972).

On Cruise 14 (June 1980) and Cruise 15 (August 1980) near-surface *in vivo* chlorophyll fluorescence was measured on transects across Hecate Strait. Seawater was pumped continuously from the seachest through a bubble trap to a Turner model 111 fluorometer fitted with a flow-through door, with the ouput recorded on a strip-chart recorder (Lorenzen 1966). On Cruise 15, temperature was also measured and recorded continuously with a small thermistor set into the flow to the fluorometer. Water samples were collected at intervals to measure chlorophyll *a* concentrations, although an insufficient number of samples were collected on Cruise 15 to permit conversion of fluorescence to chlorophyll. The flow rate to the fluorometer was about 2 L min^{-1}. There is some uncertainty as to the effect of flow rate on measured *in vivo* fluorescence, with some authors reporting no relationship at flow rates up to 2 L min^{-1} (Setser 1980, quoted in Sweet and Guinasso 1984) while others have found a direct relation at flows between 0.5 and 1.5 L min^{-1} (Sweet and Guinasso 1984). The latter investigators also note the effect is likely to vary considerably with different phytoplankton communities. This problem of fluorescence response to varying flow rates was reduced in the present study by using a constant flow rate.

Mackas and Owen (1982) have examined continuous horizontal sampling systems and found that a system involving a seachest can cause substantial blurring of the input signal. This means that features with spatial scales less than about 0.5 km, depending on the actual inlet configuration, cannot be resolved. Such blurring would not be a problem for the discrete stations of this study, where water samples were integrated over the length of the simultaneous zooplankton tow, but may be a consideration for the continuous transects.

10. ZOOPLANKTON

On Cruise 1 (the "shakedown" cruise), zooplankton were collected from the seachest system following the water sample, and concentrated through a series of nets. For all subsequent cruises however, a winch and rotating davit were installed at the stern to tow a high speed plankton sampler (Miller 1961). The sampler consisted of a 1 m long PVC pipe of 8 cm internal diameter, with 3 PVC fins attached to the back of the pipe for stability and a net of 350 μm mesh attached to the rear. A calibrated flow meter was installed within the first 20 cm of the pipe to measure the volume of water filtered. Tows were generally done at 2.5 m s^{-1} (5 knots) for 10 minutes, with the depth of the sampler adjusted to approximate that of the ship's seawater intake (3 m). Upon completion, the net was washed with seawater, the organisms poured into 200 mL plastic or glass jars, and preserved in a 7% solution of sodium borate - buffered

formalin. Enumeration with stereomicroscopes was done on shore, with identification of organisms following the same procedure as for phytoplankton (i.e. to species, or genus if detailed identification would prove excessively time consuming). However, zooplankton were not sampled from every station on each cruise because of crew objections over the noisy operation of the hydraulic winch.

11. PROBLEMS

Every ship of opportunity program will encounter difficulties, some inherent in the nature of such a program and others specific to the vessel and regions sampled. One major difficulty with this program is illustrated by Fig. 2. The *Tofino* has rather flexible and widespread destinations, and the actual route travelled on any trip to the north coast would depend on the locations of its deliveries. On one trip the *Tofino* might travel across the open waters of Queen Charlotte Sound, while on others it would follow the "Inside Passage". At its best, slight variations of route meant not all stations could be repetitively sampled on consecutive monthly cruises, while at its worst whole areas such as Dixon Entrance or Queen Charlotte Sound might be missed. With sampling frequency approximately monthly there is a close coupling of temporal scales of sampling and the events under investigation, such that events could be missed with these variations in route. This problem was reduced somewhat after Cruise 7 (January 1979) by

the change in sampling procedure, which sampled more intensively those areas of interest covered on almost every cruise.

A second specific problem is also illustrated by Fig. 2. The preferred route north was amongst the islands and fjords of the Inside Passage. These are obviously restricted coastal waters, with highly variable conditions influenced by local or isolated events. This has been shown by Dodimead (1980) in his review of lighthouse temperature and salinity data collected at the seaward ends of these passages (reviewed in Chapter 2). Thus, the rather limited scales of coverage offered by the *Tofino* were not appropriate for monitoring the much shorter spatial and temporal events along the Inside Passage. The modified sampling procedure after Cruise 7 reduced the coverage of these inside waters.

The frequency of cruises during spring and summer (monthly) was barely adequate for studying such processes as bloom development, yet at times the number of samples and data produced created large backlogs. The most time-consuming aspects were the taxonomic identifications and enumerations; development and implementation of automated procedures for their collection would be most useful. Attempts at automated recording of biomass are being pursued (Mackas and Boyd 1979, Seakem Oceanography Ltd. 1979).

A fourth difficulty, common to all SHOP-type programs, is that most information gained deals with surface or near surface conditions. Features important to studies of bloom initiation

and productivity often occur at depth, such as the depth of the halocline and deep chlorophyll maximum layers, which may not be adequately sampled by surface ship of opportunity technologies. In the case of the American Mail Lines program, this difficulty was reduced by concurrent intensive studies from a research vessel, which was able to sample the subsurface properties (Parsons and Anderson 1970). A similar comparison was done in the present study, and is discussed in the next section.

12. COMPARISON OF SURFACE AND DEPTH SAMPLING

In any routine large-scale survey of oceanic areas, the measurement of surface properties will be continuous and less time-consuming than vertical profiles at many discrete stations. However, the problem of whether or not such near surface measurements adequately represent conditions at depth must be considered, especially in areas where there may be substantial vertical stratification.

Lorenzen (1970) examined this question, and estimated statistical relationships between surface chlorophyll *a* concentrations and the depth of the euphotic zone, total euphotic zone chlorophyll *a* and total primary productivity for three low latitude areas of the Atlantic and Pacific Oceans. He found all relationships were statistically significant and suggested surface chlorophyll was a useful index of depth-integrated chlorophyll and primary production. Recently, considerable interest has focussed on this question due to its

relevence to satellite studies of horizontal chlorophyll distributions. The question is the same: how representative are remotely-sensed near surface chlorophyll concentrations of depth-integrated concentrations? Such satellite measurements do in fact include some depth information depending on the attenuation coefficient, although this often represents only 5% or less of the total phytoplankton biomass in the water column (Platt and Herman 1983). Despite such limitations, remotely-sensed near-surface chlorophyll measurements have been shown to be useful indices of the mean water column chlorophyll concentration and even primary productivity over wide regions of the ocean (Smith 1981, Smith *et al.* 1982, Platt and Herman 1983).

However, these studies have been criticized by Hayward and Venrick (1982) on the basis that they aggregated data from a wide variety of areas, and therefore reflect global scale organization (such as upwelling centers *vs.* oligotrophic gyres) rather than local variations. Their study examined the relation of surface chlorophyll to depth-integrated chlorophyll and primary productivity in the California Current and the central North Pacific. In the California Current, surface chlorophyll was significantly correlated with both integrated chlorophyll and primary productivity, although there was considerable scatter in the relationship from spatial and temporal variations. In the central North Pacific, surface chlorophyll did not correlate with integrated chlorophyll or primary

productivity due to the low surface concentrations and a deep maximum. They suggested surface chlorophyll would be a useful indicator of depth-integrated concentrations in areas with strong horizontal gradients and wide ranges of concentrations, but less useful in homogeneous areas with marked vertical gradients. The region of the B.C. northern shelf is likely to have horizontal gradients resembling those of the California Current, suggesting surface chlorophyll should be a useful index of mean vertical concentrations.

To test this, chemical properties sampled by ship of opportunity and standard research vessel methodologies were compared for regions of the northern B.C. shelf with MV *Pandora II* (Dept. of Oceanography, University of B.C. Cruise 80-7, 28 April to 3 May 1980). Samples were collected from the laboratory seawater supply (originally drawn from the seachest intake) as *Pandora* steamed across each station, to simulate the sampling procedure followed by the *Imperial Tofino*. *Pandora* then returned on station and sampled properties at depth using standard hydrocasts to 2,3,5,10 and 20 m, with bucket casts providing surface water. The SHOP-method samples and those from the hydrocasts were then analysed in the same manner.

Samples collected using the ship of opportunity technique were compared with those from the hydrocasts in two ways. The seachest intake of *Pandora* is at a depth of 4 m; therefore, these SHOP samples were compared with the mean of the 3 and 5 m hydrocast samples as a direct estimation of the ability of the

underway sampling technique to represent conditions at its depth of intake. The SHOP samples were also compared with surface to 20 m integrated values to test their use as an index of upper layer water column properties. Regression equations for these two analyses for chlorophyll *a* and NO_3+NO_2 are presented in Table II. These equations indicate very good agreement between underway samples and those from the hydrocasts, suggesting the technique used by the *Tofino* represents near surface properties quite well, and can act as an index for 0-20 m integrated concentrations. It should be noted these comparisons included both stratified and mixed water columns as indicated by Figs. 14 and 15, although in the case of the stratified stations (Stations 7 and 22) the high chlorophyll region occurred in near surface waters rather than as a deep maximum.

Two weeks prior to the *Pandora* cruise the *Imperial Tofino* had also intensively sampled the coastal southeast Queen Charlotte Sound area, and it is interesting to compare the two results when discussing the validity of the SHOP methodology. Only general patterns will be considered here, while a more detailed comparison of this area is presented in Chapter 4. The northbound leg of *Tofino* Cruise 13 found low chlorophyll and high nutrient concentrations typical of winter in the Queen Charlotte Sound - Fitz Hugh Sound area, while on its southbound leg 5 days later higher chlorophyll and lower nutrient concentrations were recorded (data in Perry *et al.* 1981). The pattern sampled by the *Pandora* in this area was the same as

TABLE II. Regression equations comparing near surface (SHOP, 4 m) and depth sampled chlorophlyll *a* and NO_3+NO_2 concentrations collected during *Pandora II* cruise 80-7 (28 April - 3 May 1980) to the B.C. northern shelf.

CHLOROPHYLL

i) Y = SHOP chl. (mg m^{-3}) X = 3-5 m mean chl. (mg m^{-3})
$Y = 0.22 + 0.73 X$ $r^2=0.99$ n=11

ii) Y = SHOP chl. (mg m^{-3}) X = 0-20 m integrated chl. (mg m^{-2})
$Y = -0.13 + 0.05 X$ $r^2=0.91$ n=11

NO_3+NO_2

i) Y=SHOP NO_3+NO_2 (mmol m^{-3}) X=3-5 m mean NO_3+NO_2 (mmol m^{-3})
$Y = 0.92 + 0.94 X$ $r^2=0.98$ n=10

ii) Y = SHOP NO_3+NO_2 (mmol m^{-3}) X = 0-20 m integrated NO_3+NO_2 (mmol m^{-2})
$Y = -3.14 + 0.06 X$ $r^2=0.88$ n=9

Tofino's southbound leg, with the highest near-surface chlorophyll concentrations at the mouth of Fitz Hugh Sound. However, absolute concentrations measured with the SHOP-sampling procedure by *Pandora* were greater than those from *Tofino*, which is consistent with a bloom beginning to develop during the *Tofino* cruise and continuing during the *Pandora* cruise two weeks later.

The necessity of collecting zooplankton from high speed near-surface tows, and how representative these might be of concentrations and compositions at depth, was also examined. At selected stations on *Pandora* cruise 80-7 a Miller sampler

(described above) was towed behind the ship in the same manner as the *Tofino* sampling procedure. Once the ship had returned to the station and the hydrocasts were completed, a vertical zooplankton tow was made from near bottom to surface using a SCOR net with 202 μm mesh. Results, with organisms identified to taxonomic group only, are presented in Table III and suggest considerable variability between the two types of tows. In general it appears the near-surface horizontal tows sample different distributions than the vertical tows. This results in higher abundance estimates and lower diversity than vertical tows, depending on the area. Such differences are not surprising considering the depth stratification of zooplankton and the preference of many larger species for deep water. Thus, while the near-surface tows may not be representative of the detailed zooplankton composition and abundance throughout the water column, they may indicate the general structure of the community, for example the relative importance of copepods, decapod larvae, and barnacle nauplii.

TABLE III. Comparison of zooplankton taxonomic groups sampled by *Pandora II* using Miller (MLR) and vertical (VERT) net tows. Note vertical tows used a SCOR net with 202 μm mesh, horizontal tows used a Miller sampler with 351 μm mesh. Taxonomic abundances expressed as number m^{-3} of water filtered.

Station	3	3	18	18	16	16	19	19
Lat (°N)	49.7		53.2		54.2		50.8	
Long (°W)	124.7		128.8		130.7		127.8	
Type of Tow	VERT	MLR	VERT	MLR	VERT	MLR	VERT	MLR
Max Depth (m)	300	3	150	3	100	3	150	3
Copepods (<2mm)	134.5	1417.1	26.6	35.4	690.1	63.4	124.3	128
Copepods (>2mm)	102.0	402.3	2.9	-	36.2	0.7	94.6	2.3
Decapod larvae	26.9	7140.6	0.9	15.4	8.3	-	13.0	11.
Decapods	7.4	228.6	0.1	1.7	-	-	1.9	
Crab larvae	26.0	-	-	-	58.4	2.2	-	
Chaetognaths	1.9	27.4	1.0	-	2.8	-	18.6	2.3
Pteropods	3.7	-	-	-	55.7	1.4	-	
Barnacle nauplii	-	-	-	-	39.0	25.9	-	

IV. BIOLOGICAL OCEANOGRAPHY OF THE NORTHERN SHELF: SEASONAL PATTERNS

A. INTRODUCTION

The biological oceanography of the British Columbia northern shelf has been poorly studied. Exploratory fisheries investigations and population studies using commercial catch statistics (e.g. Ketchen 1964, Archibald *et al.* 1983) have been conducted, yet no information is available concerning the temporal distributions of plankton in the open waters and mechanisms influencing their production. This chapter presents synoptic descriptions of the spatial and temporal distributions of the plankton as determined from the *Imperial Tofino* ship of opportunity program. The ability of the Sverdrup (1953) critical depth - mixed depth model to predict the phytoplankton growing season is examined by comparison with the observed distributions.

This chapter has two main purposes. The first is to present a summary of biological data collected from the ship of opportunity program as the first general description for the northern shelf. The focus is on the general spatial and temporal patterns of chlorophyll *a*, nutrients, phytoplankton and zooplankton taxonomic composition and abundance, although variability within regions will also be stressed. As an example of this within-region variability, spatial and temporal

characteristics of the plankton of southeastern Queen Charlotte Sound and their potential importance to survival of migrating salmon fry will be discussed.

The second purpose of this chapter is to examine the hypothesis that initiation of the spring phytoplankton bloom occurs first in southern waters of the B.C. coast such as the Strait of Georgia, then sweeps sequentially northward with the seasonal increase of solar radiation. Such a pattern should be apparent from the phytoplankton growing seasons predicted separately for each region of the coast by the critical depth model and in the timing of the onset of the bloom as observed by the field program. This progressive northern pattern was implied by Parsons (1965) from a critical depth model calculated for southern and northern coastal waters; however, no phytoplankton data were presented to substantiate the prediction. In a more detailed study of the eastern subarctic Pacific, Parsons *et al.* (1966) again calculated critical depths and proposed a northwesterly advance of the spring bloom about the coastal rim of the Gulf of Alaska. This pattern was supported by the distribution of copepods during April, suggesting much of the primary production was quickly transferred to secondary production via grazing.

Similar timing of the spring bloom (April) was found for Norwegian coastal waters by Braarud and Nygaard (1978), although there was a lag of three weeks between 62° and 69°N.

1. PREVIOUS STUDIES

No biological measurements were recorded on the physical oceanographic cruises to the B.C. northern coast during the 1950's and 1960's. One of the earliest cruises to measure parameters of importance to phytoplankton production was in June 1958 (Strickland 1958a). It measured nutrient and light attenuation properties in Hecate Strait and the Gulf of Alaska, but no biomass measurements were reported. Silicate, nitrate, and nitrite concentrations were below detection in the relatively shallow water of western Hecate Strait, and it was concluded plant growth was nearly zero or increasing very slowly following the collapse of the spring bloom.

Antia *et al.* (1962) report on data collected in Hecate Strait during July 1962. They found nitrate concentrations <2 μM at depths less than 25 m, and about 11 μM at 50 m. Chlorophyll *a* concentrations in southwestern Hecate Strait were about 4 $\mu g\ L^{-1}$ between 5-30 m, while in central Hecate Strait they were <1 $\mu g\ L^{-1}$ between the surface and 30 m.

The Sverdrup (1953) critical depth model was used by Parsons (1965) to predict the phytoplankton growing season for three regions of the B.C. coast. This model is a theoretical comparison of the depth of the surface mixed layer and the depth at which phytoplankton production and respiration for the water column are equal; it will be discussed in more detail in the next section. Parsons (1965) defined the growing season for phytoplankton in Queen Charlotte Sound and Hecate Strait as

April to October (on the basis of critical and mixed depths calculated for adjacent oceanic waters), while for the Strait of Georgia it began in March-April, and not until May at Station "P" in the subarctic Pacific.

No phytoplankton biomass data were available for Parsons (1965) to validate his prediction for the Queen Charlotte Sound-Hecate Strait region. Instead he used nutrient data to infer the pattern of phytoplankton growth. Nitrate concentrations were high in winter (20 μM), variable (5-15 μM) in spring, possibly indicating local biological depletion, and <5 μM during summer. No spatial analyses of these data were attempted.

In the mid 1970's, the fjords and seaways adjacent to Hecate Strait were sampled as part of the Kitimat oil pipeline and terminal proposal (Kitimat Pipe Line Ltd. 1976). Douglas Channel and the inlets leading to Kitimat were of principal interest, but samples were also collected from Browning Entrance adjacent to northern Hecate Strait. In September 1976, phytoplankton biomass in Browning Entrance was slightly greater than 2 mg Chl *a* m^{-3} in the upper 5 m of the water column, with a maximum in primary productivity of 3.47 mg C m^{-3} h^{-1} at 5 m depth. Subsequent studies of the hydrography of this system (Macdonald 1983) suggest there can be considerable exchange of water with Hecate Strait, but few biological measurements were taken.

Zooplankton on the northern shelf have been studied in slightly greater detail than phytoplankton, chiefly as a result

of their direct importance to salmonids. Types of zooplankton occurring in the region and their relative importance to fish can be determined from analysis of stomach contents. LeBrasseur (1966) reports on a study of the stomach contents of commercially caught salmonids from the northeast Pacific, including the northern shelf in a "coastal" domain. Amphipods, copepods, euphausiids and the pteropod *Limacina* spp. occurred most frequently in pink, sockeye and coho salmon within this domain. He suggested prey availability was more important to feeding than preferences for specific prey items.

Manzer (1969) examined stomach contents of juvenile salmon collected during summer 1955 from Chatham Sound and adjacent waters. Most common in the stomachs of juvenile pinks, chum, and sockeye were copepods and larvaceans, followed by barnacle and decapod larvae. Amphipods and euphausiids were also present, but more abundant in the stomach contents of coho salmon.

In connection with this study of juvenile salmon, plankton samples were collected in Dixon Entrance and Chatham Sound in the summer of 1955 (LeBrasseur 1956). Large biomass volumes were recorded from western and southern Dixon Entrance, small volumes from northern and eastern Dixon Entrance. These differences were also reflected by the composition, with crustaceans (mostly copepods) in the large volume region, and various organisms in the small volume waters (i.e. annelids, cladocerans, jelly-fishes). It was concluded these variations reflected different water masses, with the southern waters of oceanic

origin and the northern waters of brackish coastal origin. This pattern agrees with the estuarine outflow of Skeena River water toward the oceanic Pacific described in Chapter 2.

Another study of zooplankton in the Skeena River estuary was conducted in response to the proposed deep-water port development near Prince Rupert (Hoos 1975). In August and October 1971, zooplankton were dominated by copepodites, with larvaceans and copepods such as *Pseudocalanus* and *Acartia* also present. Further sampling in summer 1972 indicated calanoid copepods were most abundant, with a large proportion being nauplii and copepodites.

A few studies have examined specific groups of zooplankton in various parts of the region. They find distributions can generally be related to physical properties and water mass exchange. Lea (1955) examined chaetognath distributions along the B.C. coast in summer 1953 and identified four species, of which only two occurred with any frequency. *Sagitta elegans* was most common, its presence representing mixed coastal waters, while *Eukrohnia hamata* was also frequently identified from waters of the northern shelf open to oceanic influence. These two species often occurred in near-surface waters of the northern shelf, but not where temperatures were relatively high. In Dixon Entrance and Hecate Strait no chaetognaths occurred at stations where bottom temperatures were >9°C.

Cameron (1957) studied the distribution of copepods about the Queen Charlotte Islands also during summer 1953. She

identified 32 species of copepods in Dixon Entrance and Hecate Strait, and grouped them into surface, subsurface, and deep-water forms. She concluded that currents were primarily responsible for their distribution, and that reproduction took place in areas with well defined temperature and salinity characteristics. *Paracalanus parvus* was associated with temperatures >10°C north of Massett Inlet. *Acartia clausii* was common (>50 L^{-1}) in Massett Inlet and northwest of Graham Island, while *Centropages mcmurrichi* (now *Centropages abdominalis;* Harrison *et al.* 1983) was common in Hecate Strait.

Gardner (1980, 1982a, 1982b) has described the occurrence of several groups of zooplankton on the northern shelf and adjacent waters from a spring and a fall cruise in 1977. He found distributions of three species of copepods and two species of chaetognaths supported previously defined hydrographic regions along the coast (Gardner 1982a). Actual patterns of distribution depended on physical transport processes and variations of species tolerance. The chaetognaths *Sagitta elegans* and *Eukrohnia hamata* were relatively uniform throughout the whole region at densities of 0.5-1.0 m^{-3}. *Eucalanus bungii bungii* and *Calanus plumchrus* (now *Neocalanus plumchrus*, Harrison *et al.* 1983) were less common in open waters than in inlets of the north coast and both were more common in areas with deep maximum depths, which is consistent with their life cycle as described for the Strait of Georgia by Fulton (1973). *Calanus cristatus* (now *Neocalanus cristatus;* Harrison *et al.* 1983) was

less common in the study area, occurring at stations with direct access to open water in April, but was relatively rare by November. The presence, in samples collected from Queen Charlotte Sound and Hecate Strait, of several normally subtropical zooplankton species led Gardner (1982b) to conclude the region may experience occasional deep intrusions of Pacific equatorial water.

Only two studies have considered the temporal distribution of zooplankton on the northern shelf. Parsons (1965) reports that a series of tows taken over four months in spring and summer produced maximum quantities of zooplankton in May and minimum quantities in March.

Fulton *et al.* (1982) report on zooplankton collected along the B.C. coast on monthly cruises from January to April 1980 in connection with an ichthyoplankton survey program. The whole water column was sampled, with tows taken obliquely from near bottom to surface. During winter (January and February), zooplankton were abundant only along the outer continental shelf and the deep trough of Dixon Entrance. Most common was *Neocalanus plumchrus*, although chaetognaths were common at a station in southern Hecate Strait. In March, zooplankton biomass had increased throughout the northern shelf, except for stations on the shallow banks of western Hecate Strait. A gradient of decreasing biomass was apparent moving eastward from the continental shelf. The dominant organisms were *N. plumchrus* stage 4 and 5, although large concentrations of barnacle nauplii

and *Sagitta elegans* were noted at various stations. By April, biomass in the shallow waters of Hecate Strait and Queen Charlotte Sound had decreased, with clogging of the nets by phytoplankton noted at several stations. Highest biomass still occurred over the edge of the continental shelf. It was apparent *N. plumchrus* overwintered in waters deeper than 500 m, with the timing of recruitment and appearance in surface waters similar to that described for the Strait of Georgia (Fulton 1973).

B. METHODS

In addition to the general methods described in Chapter 3, the Sverdrup (1953) critical depth model was used to estimate the phytoplankton growing season for each region of the northern shelf. This section describes this model, its assumptions and calculations.

1. CRITICAL DEPTH MODEL

The effects of mixing and water column transparency on primary production in the sea were noted by Marshall and Orr (1930). In an analysis of the spring bloom in a Scottish Loch, they concluded that stability of the water column played an important role in the diatom increase. Gran and Braarud (1935) noted optimal conditions of primary production occurred when photosynthesis exceeded respiration, and the greater the population within the euphotic zone, the greater was its

increase. This concept was extended by Riley (1942) who found the relationship between plankton and stability (calculated as the density difference between the surface and 50 m) on Georges Bank to be zero in March, positive in April and negative in May. He concluded that, for constant euphotic zone depth, rates of photosynthesis, and respiration, the increase of phytoplankton was inversely related to the depth of vertical mixing.

Sverdrup (1953) formulated these ideas into an analytical expression for the critical depth, which was defined as the depth at which primary production equaled phytoplankton respiration summed over the water column. A net increase in production will occur if the depth of mixing is less than this depth, maintaining the majority of the population within the net productive layer. The equation proposed by Sverdrup (1953) was

$$Z_{cr} = \frac{0.2\ I_o}{k\ \ I_c}\ (1-e^{-k\ Z_{cr}})$$

where Z_{cr} is the critical depth (m), k the attenuation coefficient for the water column, I_c the compensation light intensity (the intensity at which production and respiration are equal for a single cell), and I_o the incoming solar radiation corrected for surface reflection (the factor 0.2 was added to correct for the radiation absorbed in the first meter of water). Parsons *et al.* (1984) recommend dropping the exponential term (in general it is little different than 1) and using 0.5 in

place of 0.2 as the correction factor to include the effect of the entire photosynthetically active radiation spectrum.

Several assumptions are involved in this model and are discussed by Sverdrup (1953);

- there exists a well mixed surface layer,
- plankton are distributed evenly within this layer,
- production is not nutrient limited,
- the attenuation coefficient is constant within this layer,
- the production of organic matter is proportional to the amount of radiation, and
- the compensation light intensity is known for the population under study.

These assumptions are in general most likely to be met during spring, and this model has been most successful at predicting the timing of the spring phytoplankton bloom (Semina 1960; Parsons *et al.* 1966; Kaiser and Schultz 1978; Sinclair *et al.* 1981). According to Legendre and Demers (1984) it has become the classic textbook explanation for its outbreak.

2. CALCULATION OF CRITICAL DEPTHS

Critical depths were calculated separately for four regions of the B.C. coast, defined as the Strait of Georgia (Lat. >49°N), Queen Charlotte Strait and Sound (50°10'N <Lat. ≤52°N), Hecate Strait (52°N <Lat. ≤54°10'N) and Dixon Entrance (Lat.>54°10'N). A total of 350 Secchi depth records collected from 1954 to 1965 on the northern shelf, and 222 Secchi

measurements between 1958 and 1968 in Georgia Strait were used to calculate attenuation coefficients. [1]

Monthly mean critical depths were estimated using the Sverdrup (1953) equation as modified by Parsons *et al.* (1984); example calculations are in Appendix II. Incident solar radiation was taken as the normal daily solar radiation for each month recorded at Sandspit (for Hecate Strait and Dixon Entrance), Cape St. James (Queen Charlotte Sound), and Nanaimo (the Strait of Georgia). These data are available in the Monthly Radiation Summary (Atmospheric Environment Service, Environment Canada, Ottawa), and were converted to J cm^{-2} d^{-1}, then corrected for surface reflection due to monthly sun angle using values presented in Parsons *et al.* (1966) for the subarctic Pacific. Attenuation coefficients for photosynthetically active radiation were calculated from Secchi depth (Z_s) data using

$$k = \frac{1.45}{Z_s}$$

(Walker 1980). The compensation light intensity (I_c) was taken as 58 J cm^{-2} d^{-1} from work by Hobson (1981) on phytoplankton production in Saanich Inlet, B.C. This value is at the high end

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[1] These data are available in Fish. Res. Board Can., MS Rep. Ser. (Oceanographic and Limnological) Nos. 17, 29, 30, 36, 43, 47, 52, 58, 83, 91, 111, 113, 129, 138, 211, 915, 968.

of the range of compensation intensities determined by Falkowski and Owens (1978) for *Skeletonema costatum*, a common diatom in the region during spring and summer (Harrison *et al.* 1983; this study), but well within the full range of intensities given for the six species of marine phytoplankton examined by Falkowski and Owens (1978). Critical depths were calcuated for each Secchi depth measurement, and monthly means and 95% confidence limits calculated using Student's t distribution to correct for variable sample sizes as described by Sokal and Rohlf (1981)

$$95\% \text{ Confidence Interval} = t_{0.5,(n-1)} \frac{s}{\sqrt{n}}$$

where s is the standard deviation and n the sample size for that area and month. Note that variation in monthly critical depth estimates is based on the variability of attenuation coefficients.

The other important feature of the critical depth model is the depth of the surface mixed layer. Variations in the thickness of this layer have several components: a diel cycle due to daytime heating and nighttime cooling, a climatological cycle based on the passage of atmospheric disturbances, and a seasonal cycle connected with the annual pattern of solar radiation. Woods and Onken (1982) have modelled the effect of diel variations in mixed layer depth on phytoplankton distributions. When the response of individual cells scattered

throughout the euphotic layer are taken into account, some proportion of cells will be entrained into the deepened mixed layer every night. During daytime heating however, the mixed layer shoals, leaving some of the cells to settle deeper into the water column. Repeated simulations demonstrated that this results in a deep chlorophyll maximum just below the maximum depth of nighttime mixing. This layer, of course, can then be mixed back into the surface layer with the passage of storms on the climatological scale. When this model was run with conditions typical of different seasons, it did reproduce the general characteristics of the shoaling seasonal thermocline originally used by Sverdrup (1953).

I have therefore disregarded any potential effects of diel or climatological variations in mixed layer depth, primarily due to lack of appropriate data for the northern shelf, and have calculated this layer as monthly (=seasonal) composites for the Strait of Georgia and the three regions of the northern shelf defined previously. Density versus depth data measured on the physical oceanographic cruises to the northern shelf from 1954 to 1971 (available from the Marine Environmental Data Service, Dept. of Fisheries and Oceans, Ottawa; dates and cruise identifications listed in Appendix III) and for the Strait of Georgia from a series of monthly cruises from December 1967 to December 1968 (Crean and Ages 1971), were used in the calculations. For the Strait of Georgia (Lat. >49°N), 537 stations were used (approximately 43 per month), 485 for Queen

Charlotte Sound, 369 for Hecate Strait, and 562 for Dixon Entrance.

At each station, the depth interval at which the gradient ($d\sigma_t$ /dZ) was a maximum was determined. If this maximum was greater than 0.01 σ_t units m^{-1}, the mean of that depth interval was defined as the depth of the surface mixed layer. If the maximum was less than this value, then either the maximum depth of the water or the depth of the 33.7‰ isohaline (for the northern shelf; the 30.5‰ isohaline for the Strait of Georgia), whichever was shallower, was defined as the mixed depth. The 33.7‰ isohaline has been defined as the depth of the permanent halocline on the northern shelf (Dodimead and Pickard 1967), and it was assumed this would represent the maximum potential mixed depth in the region. Waldichuk (1957) has noted waters of the Strait of Georgia below the depth of the 30.5‰ isohaline tend to be homogeneous year round.

The use of 0.01 σ_t units m^{-1} to define the pycnocline is based on a study of surface layer characteristics in the north Pacific Ocean (Giovando and Robinson 1965). They defined a thermocline as a negative temperature gradient greater than 0.07°C m^{-1}. Assuming a constant salinity, such a gradient is equivalent to a density gradient of 0.01 σ_t units m^{-1}; the more usual situation where salinity increases with depth produces a stronger density gradient. As with the critical depths, mixed layer depths are presented as 95% confidence intervals of monthly means for data pooled over all years using the above

equation from Sokal and Rohlf (1981).

Much of the taxonomic data collected in this study are in terms of abundance. In order to reduce the effect of small-sized but numerous taxa when abundance estimates are used (e.g. flagellates versus diatoms), a phytoplankton biomass index was calculated by weighting abundances with a relative size coefficient (Mackas and Sefton 1982). An example of the identified taxonomic groups, their relative size coefficients, and mean abundances for cruises across Hecate Strait are given in Table IX (Chapter 6). Replacement of the relative size coefficients with estimated carbon per cell values for Saanich Inlet populations (unpublished data of the Controlled Ecosystems Pollution Experiment, also Carruthers 1981) produced no major changes in the relative ordering of biomass estimates.

The relative state of the phytoplankton bloom during spring 1979 and 1980 between the major regions of the coast can be estimated using the qualitative technique of Braarud and Nygaard (1978). It involves defining *a priori* multi-parameter categories representing the relative state of the spring bloom, then assigning stations within each area to the appropriate category. The difficulty, however, is defining limits to these parameters representing bloom and non-bloom conditions that are applicable to all regions of the study. Based on characteristics of the well-defined spring bloom in western Hecate Strait in April 1980 (Fig. 6, and Chapter 6), the following categories were used:

I - pre-bloom : chl *a* $<1 \mu g\ L^{-1}$;

$<10^6$ phytoplankton cells L^{-1}; NO_3+NO_2 >8 μM

II - early bloom : chl *a* >5 μg L^{-1}; $>10^6$ cells L^{-1}; NO_3+NO_2 ≃8-10 μM

III - late bloom : chl *a* >2 μg L^{-1}; $>10^6$ cells L^{-1}; NO_3+NO_2 <8 μM

IV - post-bloom : chl *a* <2 μg L^{-1}; $<10^6$ cells L^{-1}; NO^3+NO^2 <8 μM.

It has been assumed that spring blooms have identical characteristics throughout all regions of the northern shelf, which can be defined by the above categories.

C. RESULTS

1. CRITICAL DEPTH MODEL

The general annual pattern of calculated critical depths is similar between the three regions of the northern shelf, but different from that in the Strait of Georgia (Fig. 3). On the northern shelf, critical depths increase during spring, reaching their deepest range in May, then shoal to their minimum range in December. However, annual mean critical depths differed between regions during the period 1954 to 1971, being shallower in Dixon Entrance (51 m; n=124, standard deviation(s)=35 m) than in either Hecate Strait (72 m; n=86, s=36 m) or Queen Charlotte Sound (67 m; n=132, s=34 m). The spring freshet from the Skeena River reaches its maximum during June, and may add silt or organic material to Dixon Entrance during the summer months,

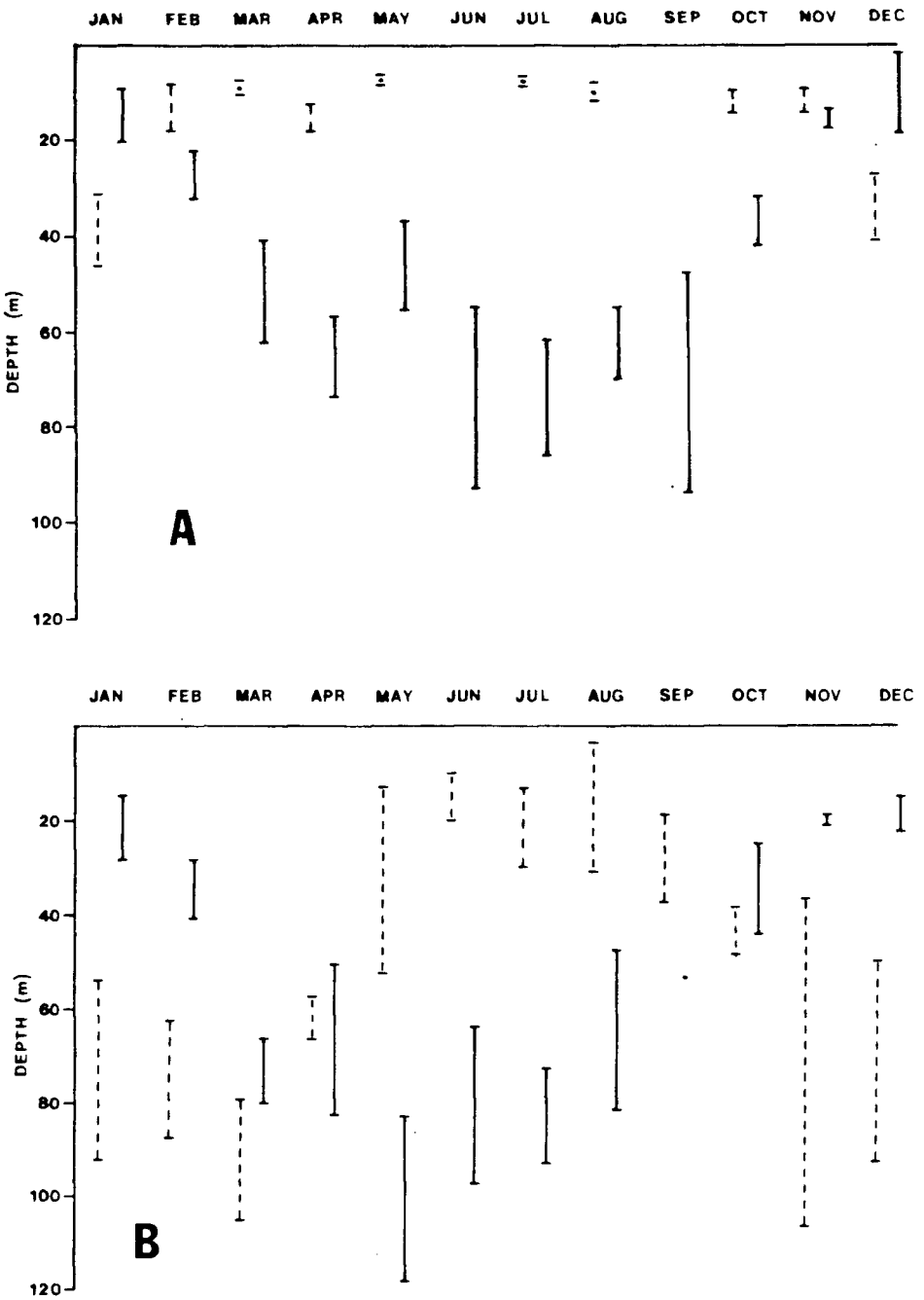
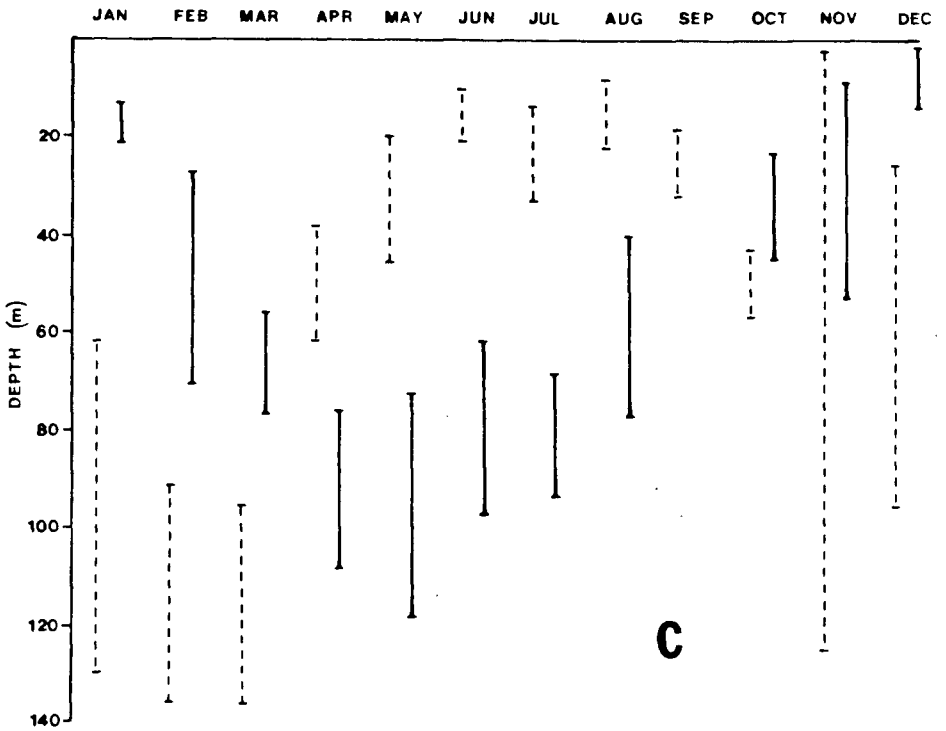


FIGURE 3. Critical depth (solid line) and mixed depth (dashed line) 95% confidence intervals of the monthly means from 1954 to 1971 in the Strait of Georgia (Lat >49°N; A), Queen Charlotte Sound (B), Hecate Strait (C), and Dixon Entrance (D). See text for explanation of calculations.



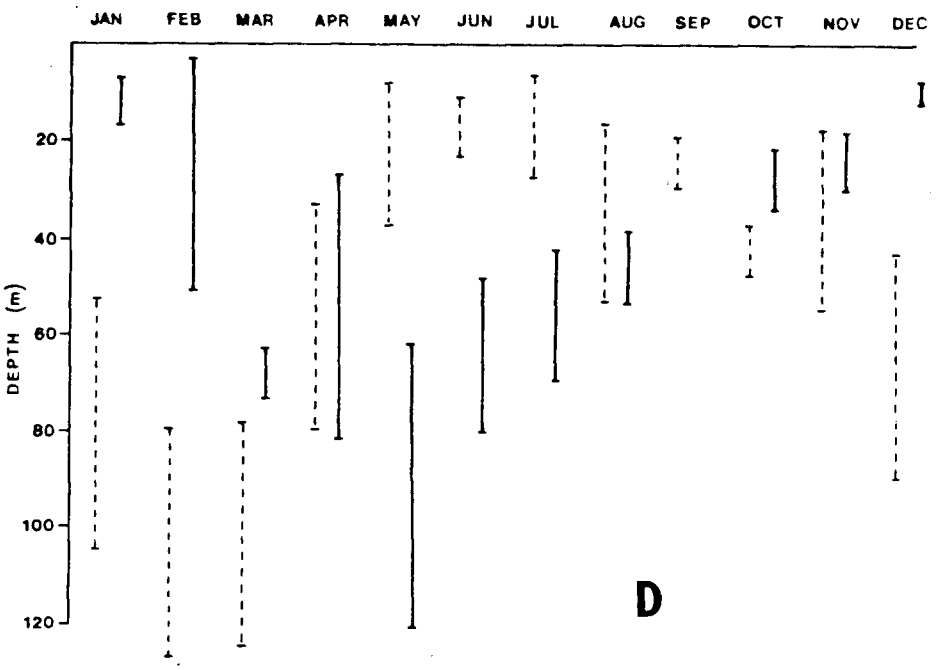


FIGURE 3 (Continued).

decreasing the critical depth. Fig. 3 indicates that critical depths in Dixon Entrance during summer are indeed shallower than Hecate Strait or Queen Charlotte Sound.

In the central and northern sections of the Strait of Georgia, critical depths also progressively deepen during spring, reaching a maximum in June, then shoal to a minimum in December. The annual mean depth is 52 m (n=168, s=30 m), which is similar to that in Dixon Entrance.

The general annual pattern of mixed layer depths is also consistent on the northern shelf, but different from that of the Strait of Georgia (Fig. 3). On the north coast, mixed depths are deepest in late winter (usually March) reflecting the influence of winter storms and cooling, decrease sharply in April, and are shallowest during summer. In a study of the heat budget of Dixon Entrance, Tabata (1958) noted March was a period of no net transfer to or from the water, where sea surface temperatures were at their annual minimum. In the Strait of Georgia, mixed depths are considerably shallower due to stabilization by freshwater runoff. Deepest ranges occurred during December and January, while the rest of the year had relatively little variation.

There is a reduction in the length of the phytoplankton growing season, defined as those months when the critical depth is deeper than the mixed layer depth, with increasing latitude along the B.C. coast. However, the progression does not occur sequentially from the Strait of Georgia to Dixon Entrance. In

the Strait of Georgia, a net increase is predicted from February to October (Fig. 3A), compared with Parsons (1979) who predicted March to October, and the comment by Harrison *et al.* (1983) that production may be light limited from October to February. The difference in the predicted start of the bloom between that estimated by Parsons (1979) and that shown in Fig. 3A may be due to calm weather conditions during spring 1968 when the data on which this figure was based were collected. However, in a seasonal study of the maximum photosynthetic rate of phytoplankton in Saanich Inlet, Hobson (1981) concluded critical depths were always greater than mixed depths, principally due to stabilization from freshwater runoff and precipitation. He suggested the diatom outburst required a threshold irradiance which occurred in March or April. It is apparent that areas with different hydrographic conditions may produce critical:mixed depth ratios that differ from the mean pattern.

In Queen Charlotte Sound (Fig. 3B), the predicted growing season is May to September, although it may begin in April given conditions of calm clear weather. In Hecate Strait, the phytoplankton growing season is predicted to occur from April to September (Fig. 3C), and for Dixon Entrance it is from May to August (Fig. 3D). Parsons (1965) predicted favourable conditions for growth in the Queen Charlotte Sound - Hecate Strait region from April or May to September, the same as the more detailed analysis of the present study. Such comparisons involve mean conditions however, and there is likely to be considerable

variability of the start of the spring bloom within each region.

2. PHYSICAL PROPERTIES

A brief description of the temperature and salinity data collected on the ship of opportunity cruises will serve as background for the biological data. The basic annual pattern was similar between 1979 and 1980, and typical of other temperate coastal waters. During winter, surface temperature - salinity plots of northern shelf data (e.g. Cruise 12, February 1980, Fig. 4A) indicate relatively homogeneous conditions, yet each region is distinguishable. However, by summer (e.g. Cruise 11, July 1979, Fig. 4B) surface temperatures and salinity were much more variable. Stream flow data (Water Resources Branch 1977) show spring discharges begin in April and peak in June, with no difference in monthly timing between rivers emptying into Queen Charlotte Strait in the south and Dixon Entrance in the north.

The magnitude and timing of the annual cycle of temperature was similar between the three regions of the northern shelf, but different from the Strait of Georgia where the seasonal increase occurred earlier. Data from Hecate Strait (as representative of the northern shelf) and the Strait of Georgia pooled from August 1978 to July 1979 were compared with a t-test (using the SPSS statistical package, Nie *et al.* 1975). Mean temperature and salinity were significantly different between the two regions at the 95% probability level. A more detailed analysis between local areas on the northern shelf using T/S diagrams suggested

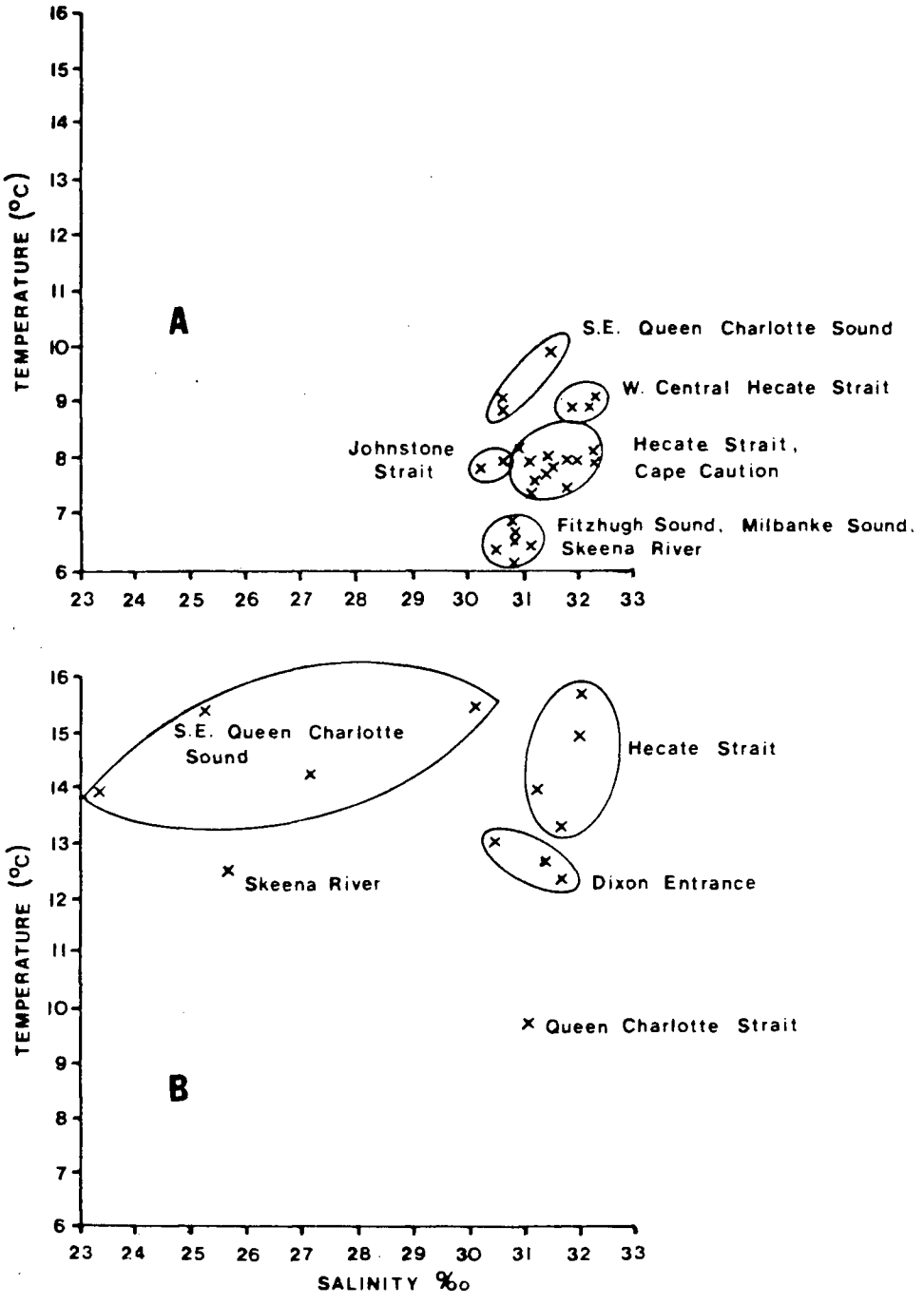


FIGURE 4. Near surface (3 m) temperature/salinity plots for Cruise 12 (February 1980; A) and Cruise 11 (July 1979; B), with stations grouped into geographic areas.

there can be considerable differences in temperature and salinity seasonal patterns. For example, Fitz Hugh Sound had a strong influence of low salinity water in late spring and summer, while Milbanke Sound had less than a 2‰ variation of salinity all year, even though both areas are adjacent to southeastern Queen Charlotte Sound. Such spatial heterogeneity is indicative of the local effects of runoff, advection and mixing demonstrated by Dodimead (1980; reviewed in Chapter 2) using north coast lighthouse data.

3. CHLOROPHYLL

The seasonal pattern of chlorophyll on the northern shelf is typical of temperate coastal waters, i.e. a phytoplankton bloom in spring, relatively low concentrations in summer with a secondary bloom during the fall. However, as was demonstrated above for physical properties, there can be considerable local scale variability. Fig. 5 indicates chlorophyll temporal variability for a south - north gradient from Queen Charlotte Sound to Dixon Entrance, although most of the stations in this latter region were located in the southeast corner. The spatial variability of chlorophyll within each region is demonstrated by the large standard deviations. Fig. 5 does, however, suggest regional differences in timing of the spring bloom, from April in coastal Queen Charlotte Sound and Hecate Strait to June in Dixon Entrance.

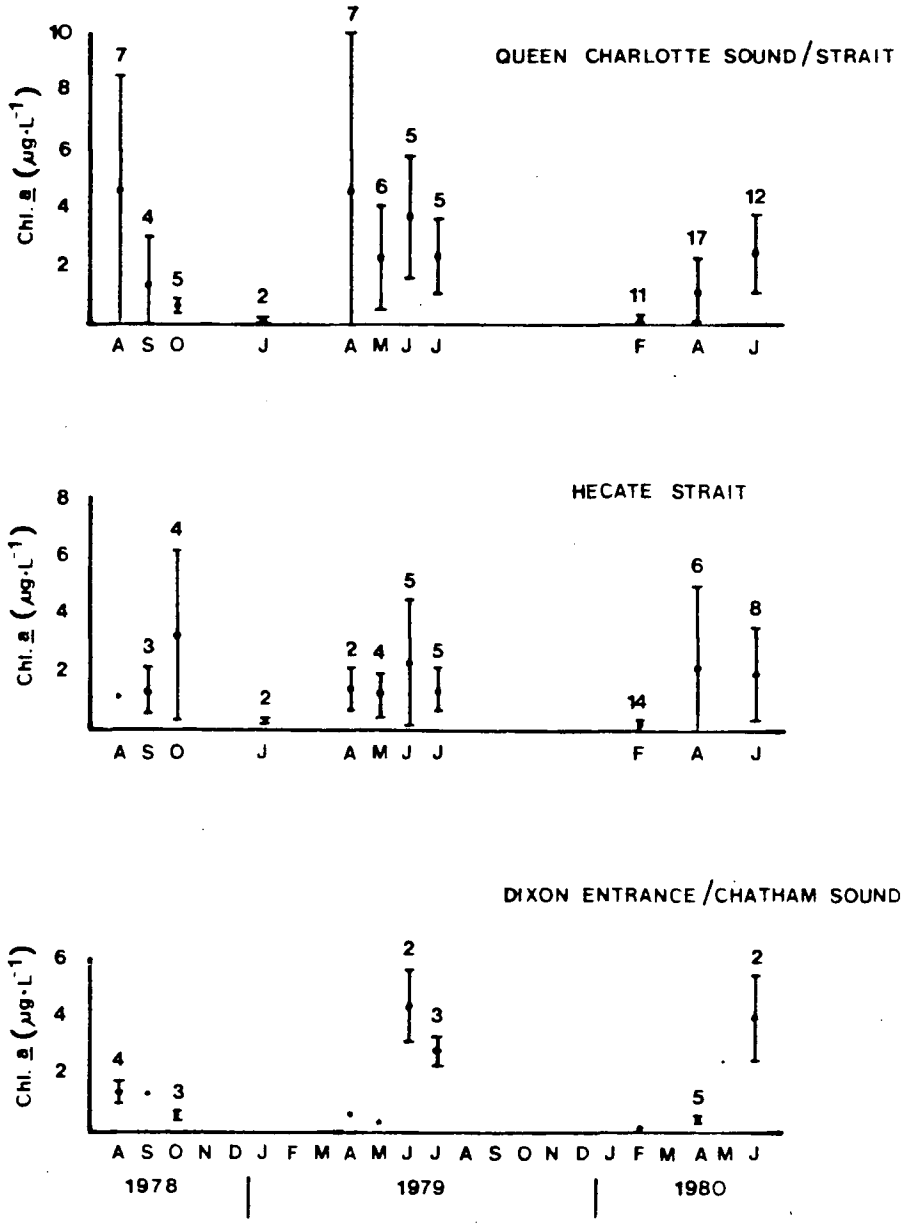


FIGURE 5. Temporal distribution of 3 m chlorophyll as sampled by *Imperial Tofino* in Queen Charlotte Sound and Strait, Hecate Strait, and Dixon Entrance. Values are presented as chl *a* monthly means ± 1 standard deviation. Numbers represent number of stations sampled that month in each area. Dots without numbers indicate a single sample.

TABLE IV. Monthly mean chlorophyll *a* concentrations and variances on the B.C. northern shelf as measured on *Imperial Tofino* cruises; number of stations (n); standard deviation (s); coefficient of variation (CV).

DATE	n	MEAN CHL $\mu g\ L^{-1}$	CV(%)	s
Aug 78	17	2.77	110.7	3.06
Sep 78	15	1.21	82.5	0.99
Oct 78	22	1.11	137.6	1.53
Jan 79	7	0.17	69.9	0.12
Apr 79	11	3.28	141.4	4.64
May 79	18	2.13	83.7	1.78
Jun 79	15	3.02	65.0	1.96
Jul 79	18	2.11	56.0	1.18
Feb 80	30	0.17	43.0	0.07
Apr 80	35	1.29	115.0	1.48
Jun 80	28	2.50	64.3	1.61

Chlorophyll *a* concentrations measured on the northern shelf ranged from a low of 0.05 $\mu g\ L^{-1}$ in winter (February 1980) to a high in spring of 15 $\mu g\ L^{-1}$ (April 1980). The monthly variability of chlorophyll *a* in the region is shown in Table IV. Lowest mean values and coefficients of variation (standard deviation to mean ratio expressed as a percentage) occurred in winter suggesting concentrations of chlorophyll were relatively homogeneous throughout the region. The highest mean value in 1979 occurred in spring (April), while in 1980 it was in June. Highest coefficients of variation occurred in April of both years and in October 1978, each being periods when blooms would be expected in localized areas producing considerable spatial

heterogeneity. The high mean chlorophyll values of June 1979 and 1980 with lower coefficients of variation suggest most areas had experienced the spring increase of phytoplankton by this time.

An indication of the spatial distribution of chlorophyll over the northern shelf is given by Figs. 6 and 7. In April 1980 (Fig. 6A) highest chlorophyll concentrations were observed over the shallow banks of western Hecate Strait, with surrounding concentrations less than 1 $\mu g\ L^{-1}$. Concentrations were also high (1-6 $\mu g\ L^{-1}$) in coastal areas of southeastern Queen Charlotte Sound, specifically Fitz Hugh Sound, while over the shelf break of central Queen Charlotte Sound concentrations were again <1 $\mu g\ L^{-1}$. In June 1980 (Fig. 7A) concentrations in western Hecate Strait had decreased to <1 $\mu g\ L^{-1}$ but increased to 2-5 $\mu g\ L^{-1}$ in eastern Hecate Strait. Coastal areas of Queen Charlotte Sound were still >1.5 $\mu g\ L^{-1}$ chlorophyll.

Such a seasonal and regional chlorophyll pattern for the northern shelf can be compared with that for the Strait of Georgia as described in the literature. Parsons *et al.* (1970) reviewed results from a four year study conducted during the late 1960's. Mean chlorophyll concentrations (0-20 m averages) from ten stations scattered throughout the strait were highest in June and lowest during November, while the highest coefficients of variation (75%) occurred during March and June. However, as with the northern shelf, Parsons *et al.* (1970) noted considerable spatial variation of chlorophyll, particularily in the vicinity of the Fraser River plume. In a later study

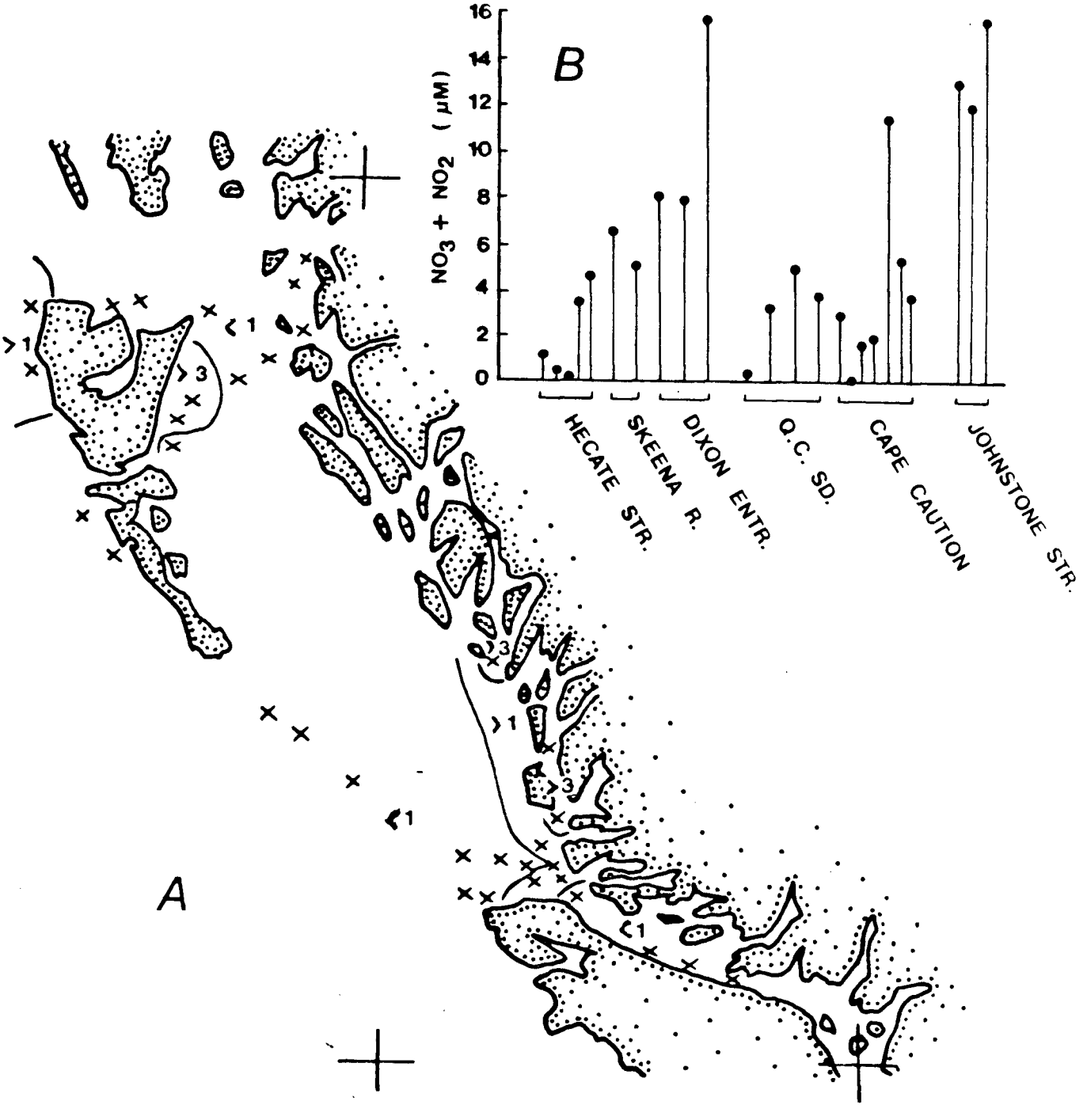


FIGURE 6. A. Chlorophyll *a* in μg L^{-1} (numbers on map) spatial distribution on 10-17 April 1980 (Cruise 13). Crosses represent station locations. B. Histograms of NO_3+NO_2 concentrations (μM) measured at the same locations as chlorophyll, and grouped into geographic areas.

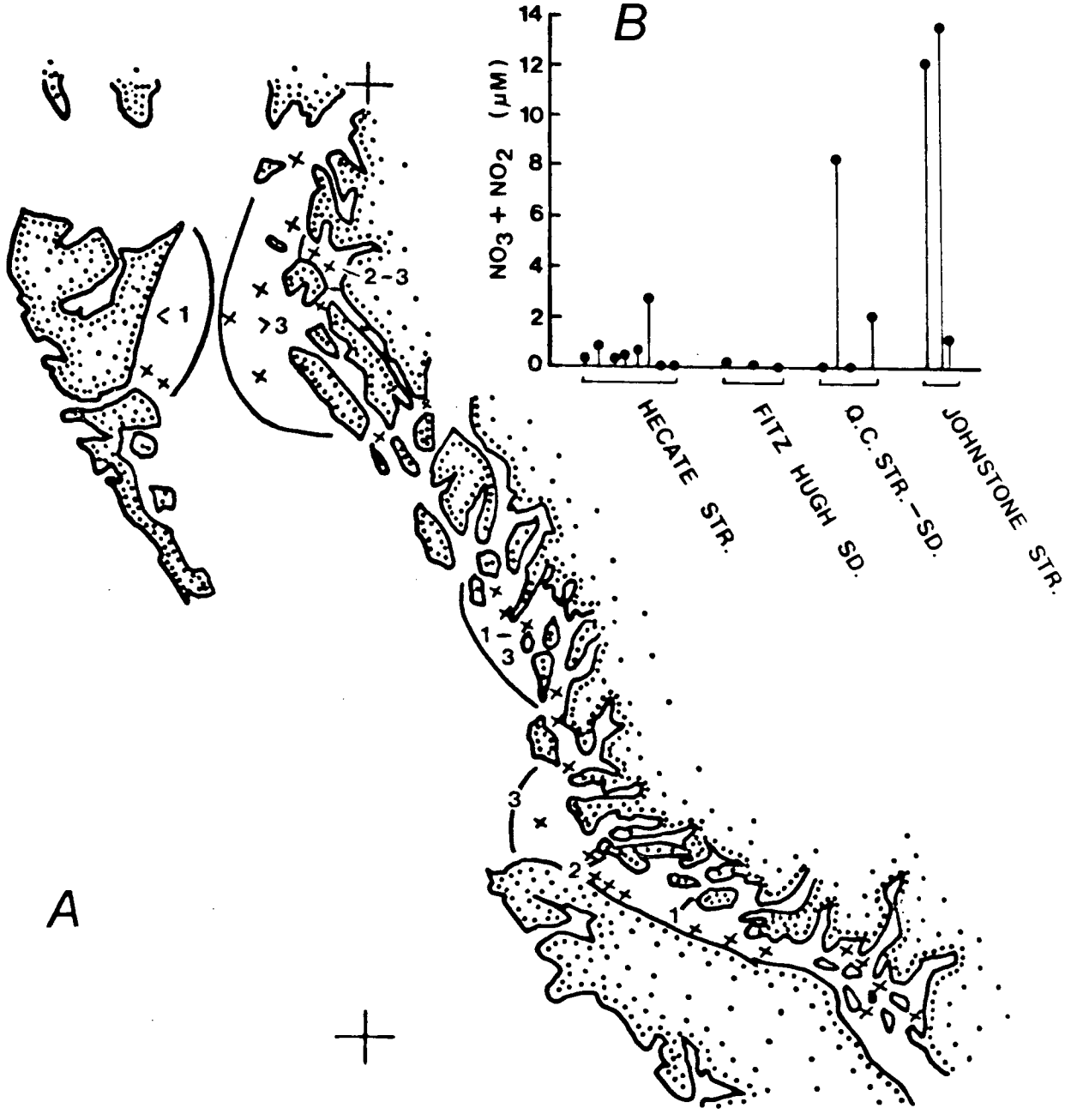


FIGURE 7. A. Chlorophyll *a* (μg L^{-1}) spatial distribution on 1-7 June 1980 (Cruise 14). Crosses represent station locations. B. Histograms of NO_3+NO_2 concentrations (μM) measured at the same locations as chlorophyll, and grouped into geographic areas.

(Parsons *et al.* 1981), considerable variability of surface chlorophyll concentration was also noted in the northern part of the Strait of Georgia in connection with tidal mixing among the constricted island passages.

4. NUTRIENTS

Samples for nitrate plus nitrite, silicate, and phosphate were routinely taken on the *Tofino* ship of opportunity cruises. Non-parametric Spearman rank correlation coefficients calculated for these nutrients for the period August 1978 to July 1979 indicated all were positively correlated ($p<0.05$) in each region of the northern shelf. Non-parametric correlations were used because the Kolmogorov-Smirnov goodness-of-fit test indicated these variables were not normally distributed. Calculations were done using the SPSS statistical programs (Nie *et al.* 1975). As a result of this correlation, I will present data for nitrate plus nitrite as representative of the general seasonal pattern of nutrients on the northern shelf.

Nitrate plus nitrite concentrations ranged from 25 μM in winter to negligible values in summer, with large variability during spring. In general, this was the reverse seasonal trend to chlorophyll *a*, and for the period August 1978 to July 1979 chlorophyll and nutrients were inversely correlated ($p<0.05$, Spearman correlation coefficient). Nitrate plus nitrite spatial distributions are illustrated in Figs. 6B and 7B for comparison with that of chlorophyll *a*. Certain areas such as Johnstone

Strait - eastern Queen Charlotte Strait show high nitrate plus nitrite concentrations (>10 μM) in all samples, reflecting the strong tidal mixing which characterizes this region (Thomson 1981).

5. PHYTOPLANKTON

During winter, small flagellates were the numerically dominant taxonomic group throughout the northern shelf. In spring, diatoms dominated many stations, with the bloom predominately composed of the genera *Chaetoceros*, *Thalassiosira* and the species *Skeletonema costatum*. This is comparable with the composition of the spring bloom in the Strait of Georgia, where the principal groups are *Thalassiosira* spp. and *S. costatum*, with blooms of *Chaetoceros* often occurring in late spring (Harrison *et al.* 1983). Small unidentified flagellates were again numerically dominant at most stations on the northern shelf during summer, although there was much more variety than in the winter with dinoflagellates (e.g. *Ceratium* spp.) and residual spring bloom diatoms abundant at some stations.

However, when considered in terms of the two major groups, diatoms and flagellates, it is clear that estimates of dominance on the basis of numerical abundance alone can be misleading. This problem has been partially remedied with the use of a biomass index estimated for each taxonomic group, as described in the methods section of this chapter. A similar conversion of abundance to approximate biomass (Harrison *et al.* 1983) shows

that nanoflagellates were numerically important during spring and summer, yet they comprised only 10% of the observed phytoplankton carbon in Saanich Inlet.

A seasonal pattern of the changing dominance of this biomass index between these two groups can be presented from summer 1978 to spring 1980 (Fig. 8). The pattern clearly represents the peak of diatom biomass over the whole of the northern shelf by late spring, similar to the pattern of seasonal chlorophyll (Table IV) which showed high concentrations and low variance during June. During July 1978, diatoms dominated the estimated biomass index in all areas sampled except shallow western Hecate Strait, where they comprised <25% of the total biomass index. From August to October 1978 the frequency of stations at which diatoms dominated the biomass decreased until it was <50% at all stations sampled during January 1979. Considerable variability of the major contributor to phytoplankton biomass was again apparent by April 1979, suggesting variability in the outburst of the spring bloom, while by early summer diatom biomass was again >50% at all stations except in western Hecate Strait. The pattern was similar during spring 1980.

To emphasize the spatial variability of dominance by diatoms during spring, data from April 1980 show they comprised >50% of the total number of phytoplankton (and therefore >50% of the biomass index) at stations in western Hecate Strait, the Cape Caution - Fitz Hugh Sound area in southeastern Queen

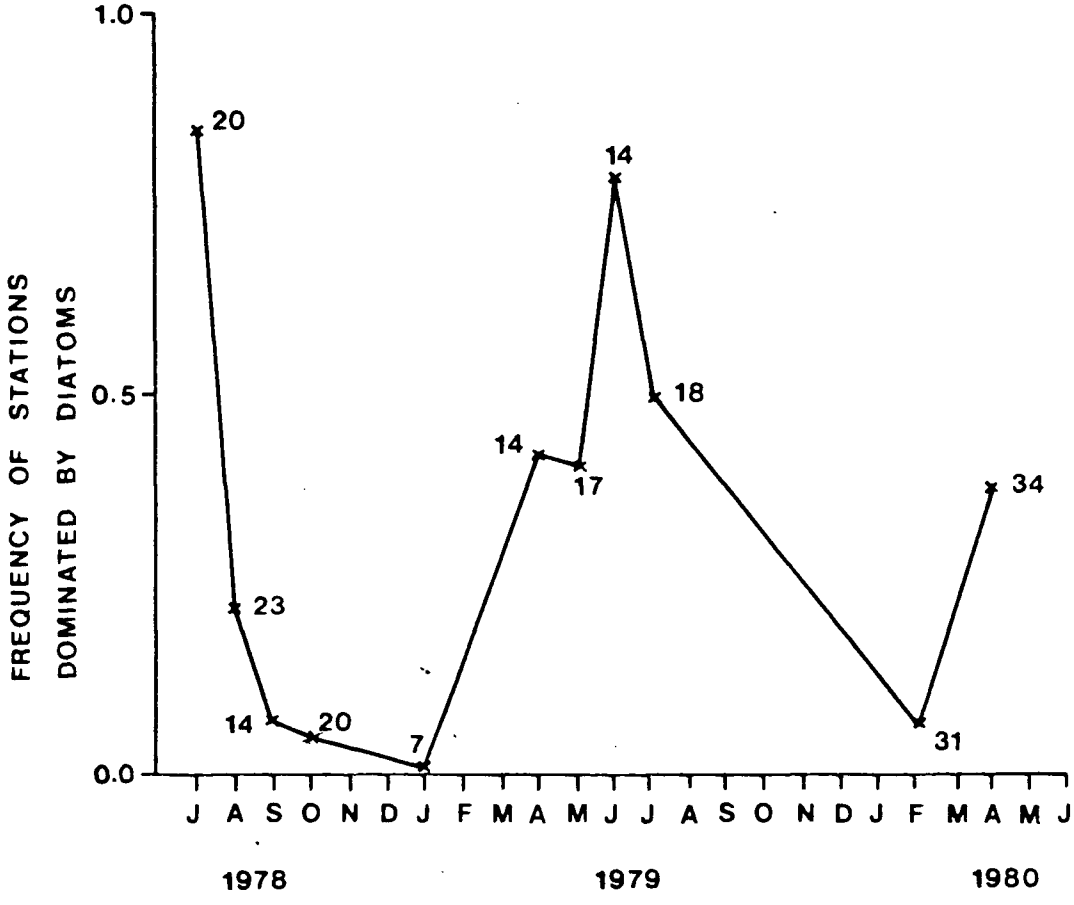


FIGURE 8. Frequency of stations sampled by *Imperial Tofino* in Queen Charlotte Sound, Hecate Strait, and Dixon Entrance where the calculated diatom biomass index (see text) is greater than the flagellate biomass index. Numbers beside x's represent the total number of stations sampled during that cruise.

Charlotte Sound, and Johnstone Strait. This station in Johnstone Strait was somewhat surprising, although the high diatom abundance may not be due to *in situ* production because of the intense tidal mixing. Instead, it may represent populations advected westward from the northern Strait of Georgia. Data in Perry *et al.* (1981) indicate chlorophyll concentrations during April 1980 in waters adjacent to Stuart Island at the mouth of Bute Inlet (northern Strait of Georgia) were >4 $\mu g\ L^{-1}$. The lowest numbers of total phytoplankton, and lack of appreciable numbers of diatoms, occurred at stations in Queen Charlotte Sound over the continental shelf break and in central Dixon Entrance.

Correlations between chlorophyll *a* concentrations and phytoplankton composition for stations sampled during February and April 1980 (Cruises 12 and 13) were calculated to determine contributions to the spring increase of chlorophyll. No significant ($p>0.05$) correlations occurred for chlorophyll *a* (as $\mu g\ L^{-1}$) against either $\log_{10}$ of total numbers of phytoplankton or $\log_{10}$ of the number of diatoms L^{-1} from data of Cruise 12 (February). However, for Cruise 13 (April) a significant correlation ($r=0.63$, $p<0.05$) occurred between chlorophyll and $\log_{10}$ number of diatoms L^{-1} (accounting for 40% of the variance). Not surprisingly then, a significant but weaker correlation ($r=0.52$) occurred between chlorophyll and the $\log_{10}$ of total numbers of phytoplankton (27% of the variance explained). Evidently the spring increase of chlorophyll was due

to the increase in diatom abundance.

6. ZOOPLANKTON

Analysis of zooplankton collected on these ship of opportunity cruises is complicated by two factors: zooplankton were not sampled from every station on each cruise, reducing further the spatial coverage; and samples were collected during both day and night, perhaps biasing night samples with vertically migrating taxa. However, general trends can be determined, while detailed analyses have been conducted primarily on night samples.

Zooplankton abundance was lowest in winter, ranging from 2 to 38 m^{-3} in January 1979 and 2 to 89 m^{-3} in February 1980. Although station locations were not identical in both years, highest numbers were sampled from southeastern Queen Charlotte Sound: the Cook Bank area just north of Vancouver Island in 1979 and the mouth of Fitz Hugh Sound in 1980. Copepods were the dominant group, with *Metridia pacifica* and *Pseudocalanus minutus* the most common. *Pseudocalanus* is also very common in the Strait of Georgia during winter, particularily in shallow near-shore waters where it grazes on small flagellates (Harrison *et al.* 1983). In spring the range of zooplankton densities was much greater than during winter, corresponding with the greater variability of chlorophyll and phytoplankton concentrations at this time. During April 1979 the range was 80-1800 m^{-3}, with copepods comprising >50% of total zooplankton numbers at all

stations except off Skidegate Inlet in western Hecate Strait, where barnacle nauplii made over 90% of total zooplankton numbers. In April 1980, highest concentrations of copepods were sampled from western Hecate Strait (180 copepods m^{-3}) and the coastal passages of southeastern Queen Charlotte Sound, while other areas had <40 copepods m^{-3}. *P. minutus* was again most common numerically during spring, while *Calanus pacificus* was common about Graham Island in northern Hecate Strait and Dixon Entrance.

The zooplankton other than copepods were fewer in number than copepods, but followed a similar distribution pattern, being most abundant during spring in western Hecate Strait and Fitz Hugh Sound (where >90% were barnacle nauplii in April 1980). Most common groups of non-copepod zooplankton were barnacle nauplii (often a major component off Rose Spit and in Fitz Hugh Sound), euphausiids and brachyuran crab zoea (in western Hecate Strait, Dixon Entrance, and Milbanke Sound), and the pteropod *Limacina* (about the Queen Charlotte Islands). Larval stages of decapods and barnacles are often reported from plankton surveys in the Strait of Georgia, but their importance has not been studied (Levings *et al.* 1983). However, such large pulses of meroplankton are likely to have significant impacts on phytoplankton biomass at certain times.

During spring 1979 and 1980, higher zooplankton abundances appeared to coincide with higher phytoplankton concentrations, especially in western Hecate Strait and southeastern Queen

Charlotte Sound. Correlations calculated for cruises during winter and spring 1980 (Cruises 12 and 13) between zooplankton and phytoplankton, between diatoms and zooplankton, and between diatoms and copepods (all log-transformed numerical abundances) produced only one significant ($p<0.05$) correlation: diatoms against total zooplankton for spring (Cruise 13, $r=0.62$ for 40% of the variance explained).

7. ANALYSIS OF BLOOM TIMING

An estimate of the relative timing of the spring phytoplankton bloom (which is predominately due to diatoms) between the Strait of Georgia, Queen Charlotte Sound, Hecate Strait, and Dixon Entrance using the method of Braarud and Nygaard (1978) is presented in Table V. During winter (January 1979, February 1980) all stations in all regions were clearly in the low productivity pre-bloom category with high nutrient concentrations.

By April 1979 and 1980, considerable variability in the relative state of the spring bloom was evident, as already noted in the previous discussions of chlorophyll, nutrient, and plankton characteristics (e.g. Table IV). All locations in the Strait of Georgia during April 1979 indicated bloom or post-bloom conditions, while the only station sampled in 1980 was located among the island passages at the northern end of the strait, an area known for its vigorous tidal mixing (Parsons *et al.* 1981). This station had low chlorophyll and high nutrient

TABLE V. Qualitative spring bloom analysis following the technique of Braarud and Nygaard (1978) applied to B.C. coastal waters. Roman numerals refer to the bloom categories: I - pre-bloom; II - early bloom; III - late bloom; IV - post-bloom. Arabic numerals refer to the number of stations on each IMPERIAL TOFINO cruise which fell into each bloom category.

	1979				1980	
	JANUARY	APRIL	MAY	JUNE	FEBRUARY	APRIL
	1st week	1st week	2nd-3rd week	4th week	1st week	2nd week
	Cr. 7	Cr. 8	Cr. 9	Cr. 10	Cr. 12	Cr. 13
GEORGIA STRAIT	I 2	II III IV 2 2 1	II IV 1 2	III IV 4 3	I 7	I 1
QUEEN CHARLOTTE SOUND	I 2	I II III 1 1 3	III IV 1 4	III IV 3 1	I 11	I III IV 2 3 7
HECATE STRAIT	I 2	I IV 1 1	III IV 2 1	III IV 2 2	I 12	II III IV 1 2 2
DIXON ENTRANCE		I 2	I 2	III IV 2 1	I 2	I IV 3 2

concentrations typical of winter or vertically well-mixed locations. Queen Charlotte Sound and Hecate Strait generally indicated bloom conditions, with some variability depending on the location of stations. Although locations were not identical between years the bloom appeared to be more advanced throughout both these regions by the second week of April in 1980 than the first week of April in 1979. The data as presented are insufficient to distinguish the timing of blooms between Queen Charlotte Sound and Hecate Strait. Also during April, stations in Dixon Entrance remained in the pre-bloom category typical of winter, except for two stations in Chatham Sound in 1980. These stations may not have been well represented by the definitions of the bloom categories given in the methods section, as both chlorophyll and phytoplankton concentrations were low yet nitrate was only 5 μM.

By May, all locations sampled in the Strait of Georgia, Queen Charlotte Sound and Hecate Strait were typical of the bloom and post-bloom categories, while the two stations in Dixon Entrance were still in pre-bloom conditions. Stations in Dixon Entrance did not show bloom characteristics until June 1979. Therefore, based on the rather coarse monthly sampling series of January, April, May, June 1979 and February, April 1980, the spring diatom bloom occurred by April in the northern Strait of Georgia, Queen Charlotte Sound and Hecate Strait, with an indication of it being slightly more advanced in the Strait of Georgia in 1979. Dixon Entrance did not generally show

characteristics of a bloom until later in the spring (June in 1979).

8. SOUTHEASTERN QUEEN CHARLOTTE SOUND

The qualitative analysis of bloom timing emphasizes large scale patterns between the four regions of the coast rather than variability within regions. However, as much of the foregoing discussion of ship of opportunity data makes clear, there can be considerable variability with location in a given area, a problem compounded by the small number of stations. To examine the coarse scale within-region variability, characteristics of two areas will be considered in some detail. This section discusses the southeastern corner of Queen Charlotte Sound, while the following two chapters focus on seasonal mechanisms in Hecate Strait.

One area of the northern shelf consistently sampled by the *Tofino* was southeastern Queen Charlotte Sound (Fig. 9), including Johnstone Strait, Queen Charlotte Strait, Pine Island and Cape Caution, Fitz Hugh Sound, and Milbanke Sound. It is coastal and likely to be strongly influenced by local runoff and mixing conditions as demonstrated for similar areas by the north coast lighthouse data (Dodimead 1980, and Chapter 2). Discussion of this transect will emphasize regional differences between Queen Charlotte Strait, Fitz Hugh Sound and Milbanke Sound rather than the small scale variations that result from local conditions.

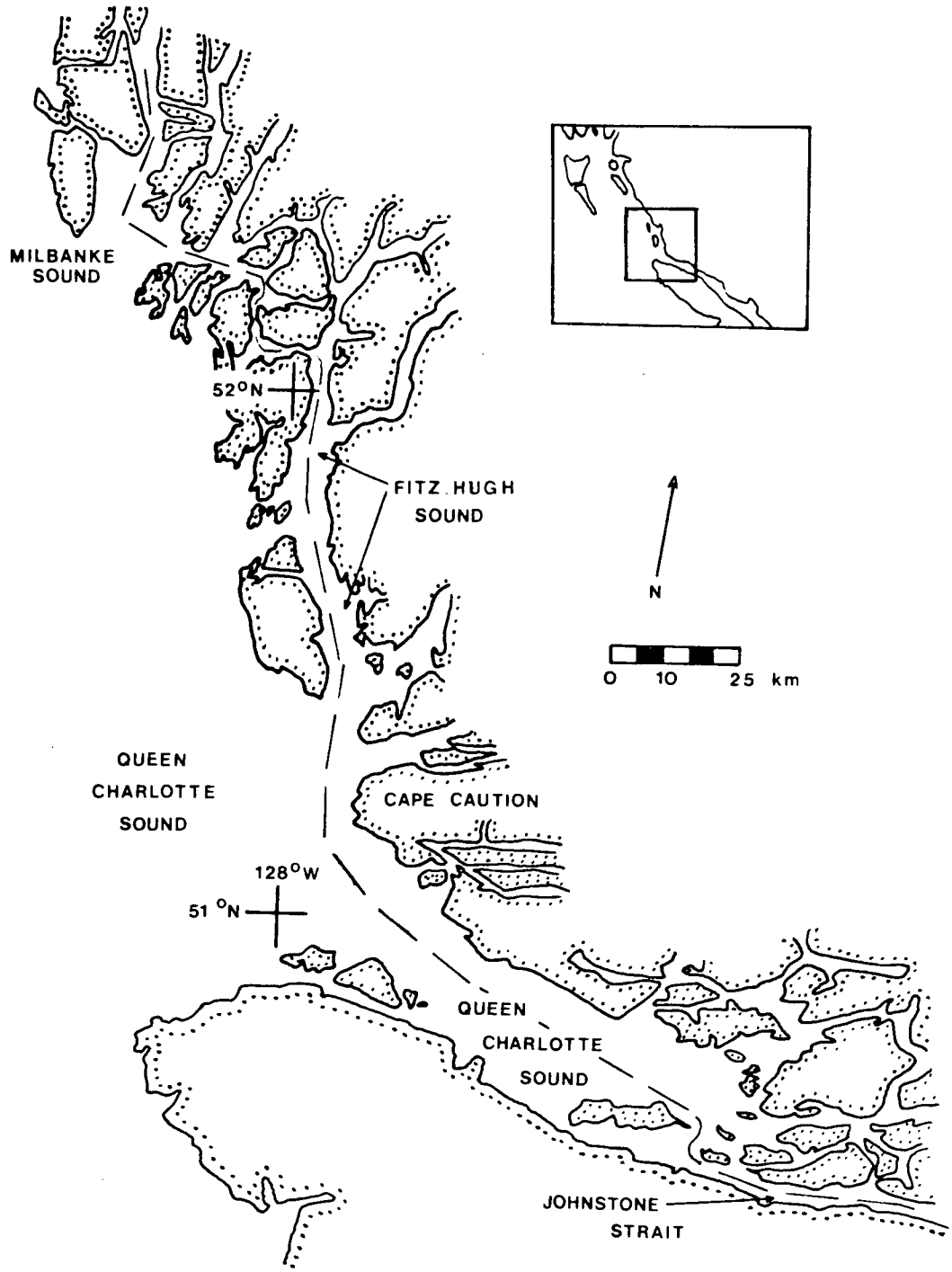


FIGURE 9. Location map showing the route of *Imperial Tofino* (dashed line) through southeastern Queen Charlotte Sound and place names referred to in the text.

Conditions during winter 1979 were typical of those throughout the northern shelf, with low diatom and zooplankton abundances, chlorophyll *a* concentrations <1 $\mu g\ L^{-1}$, and abundant nutrients with nitrate plus nitrite generally >20 μM. By spring (April 1979, Fig. 10) diatom, copepod and chlorophyll *a* concentrations were much greater in Fitz Hugh Sound and Milbanke Sound than Queen Charlotte Strait. This difference is most clearly marked between stations at the mouth of Fitz Hugh Sound and the mouth of Queen Charlotte Strait. Salinity was also minimum at the mouth of Fitz Hugh Sound, probably related to increased runoff into Rivers Inlet adjacent to Fitz Hugh Sound which begins in April (Water Resources Branch 1977).

In May 1979 (Fig. 11), concentrations of chlorophyll, diatoms and copepods were highest at the mouth of Fitz Hugh Sound and in Queen Charlotte Sound adjacent to Cape Caution. XBT profiles suggest relatively shallow stratification in this area, which may be runoff related (note lower salinity at Station 18) and act to decrease the depth of surface mixing. Conditions in Queen Charlotte Strait were still similar to April (Fig. 10), with low biomass, high nutrients, and vertically well-mixed conditions as indicated by the XBT profiles.

Queen Charlotte Strait showed some indication of a phytoplankton bloom in June 1979 with chlorophyll concentrations about 7 $\mu g\ L^{-1}$ and copepod concentrations about 1000 m^{-3}, although nitrate plus nitrite was still high (11 μM). The spatial extent of this bloom is not known as only the one

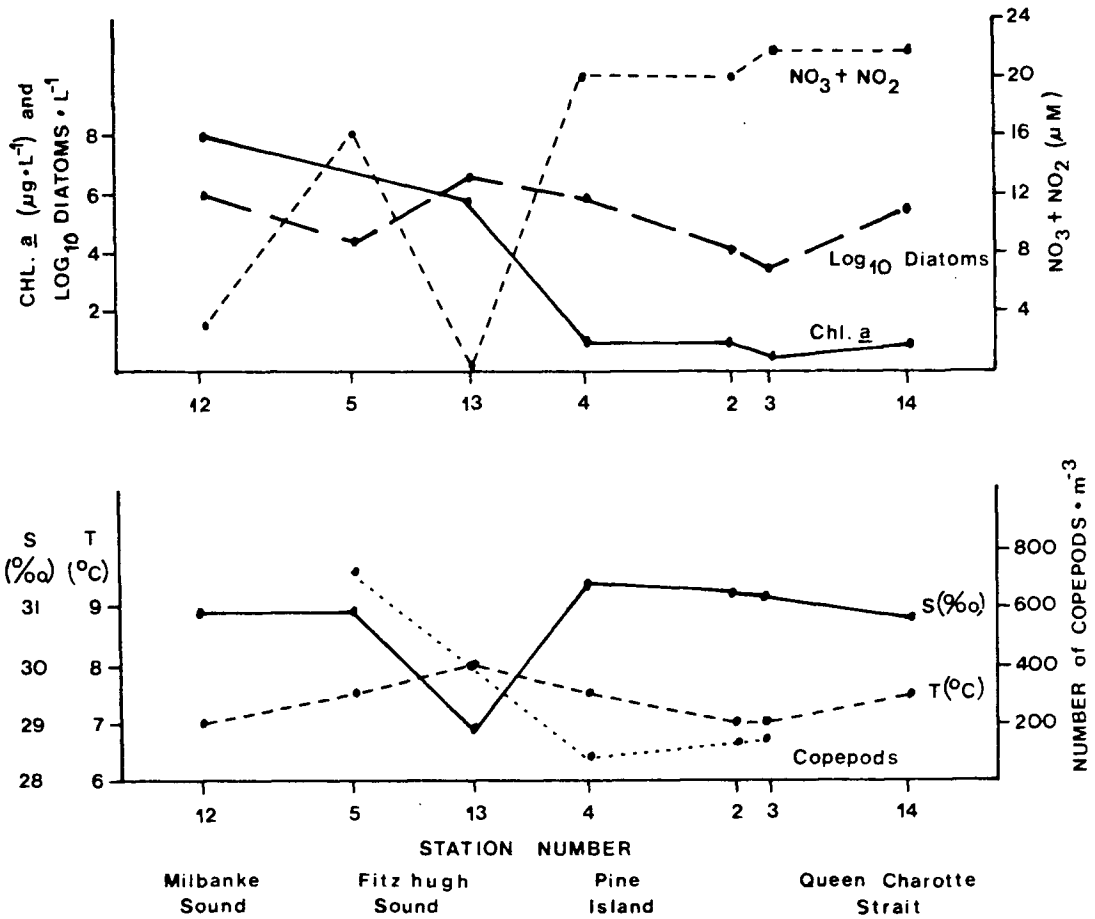


FIGURE 10. *Imperial Tofino* transect through coastal Queen Charlotte Sound, 1-8 April 1979 (Cruise 8). Data are from discrete stations at 3 m depth, not continuous transects; for precise station locations see Appendix I.

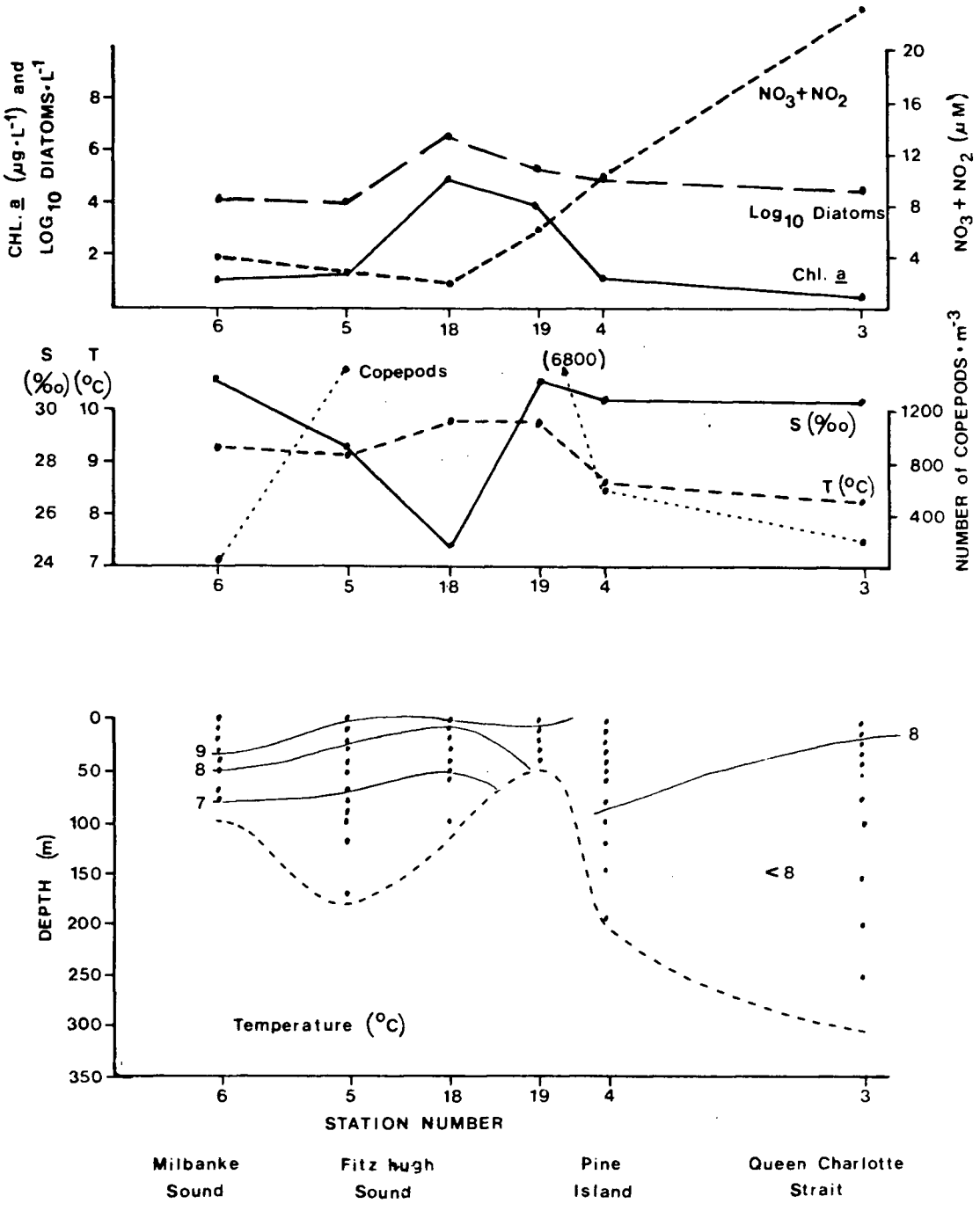


FIGURE 11. *Imperial Tofino* transect through coastal Queen Charlotte Sound, 9-16 May 1979 (Cruise 9). Data are from discrete stations at 3 m depth; for precise locations see Appendix I. Bottom panel shows the vertical temperature structure and approximate bathymetry from XBT profiles (dots).

station was sampled in Queen Charlotte Strait (Cruise 10, Station 7). However, by July 1979 (Fig. 12) this area again indicated low biomass, high nutrients and relatively well-mixed conditions, while the highest biomass occurred in Queen Charlotte Sound between Fitz Hugh Sound and Queen Charlotte Strait. The low salinity, high temperature surface water had spread throughout the area to the mouth of Queen Charlotte Strait, resulting in well-established vertical stratification. Two stations, in Queen Charlotte Sound and Milbanke Sound, had 3000-4000 copepods m^{-3}, with *Centropages abdominalis*, *Acartia* spp. and *Pseudocalanus* spp. most common, along with large concentrations of barnacle nauplii in Milbanke Sound (70 m^{-3}). Data from cruises through this area in spring 1980 show a similar pattern of low biomass "winter" conditions in Queen Charlotte Strait and higher biomass "spring" conditions in Fitz Hugh and Milbanke Sounds.

The spatial heterogeneity throughout this region and the apparent spread of the bloom from Fitz Hugh Sound into Queen Charlotte Sound is demonstrated by data collected from the MV *Pandora II* (DOUBC Cruise 80-7) from 28 April to 3 May 1980. Fig. 13 maps the near-surface (4 m) chlorophyll *a* distribution as measured by continuous fluorescence on transects across the region. Chlorophyll was calculated from fluorescence using a regression equation of extracted chlorophyll versus its fluorescence line height (FLH)

$$\log_{10} \text{chl. } a(\mu g\ L^{-1}) = -1.13 + 0.23 * \text{FLH},$$

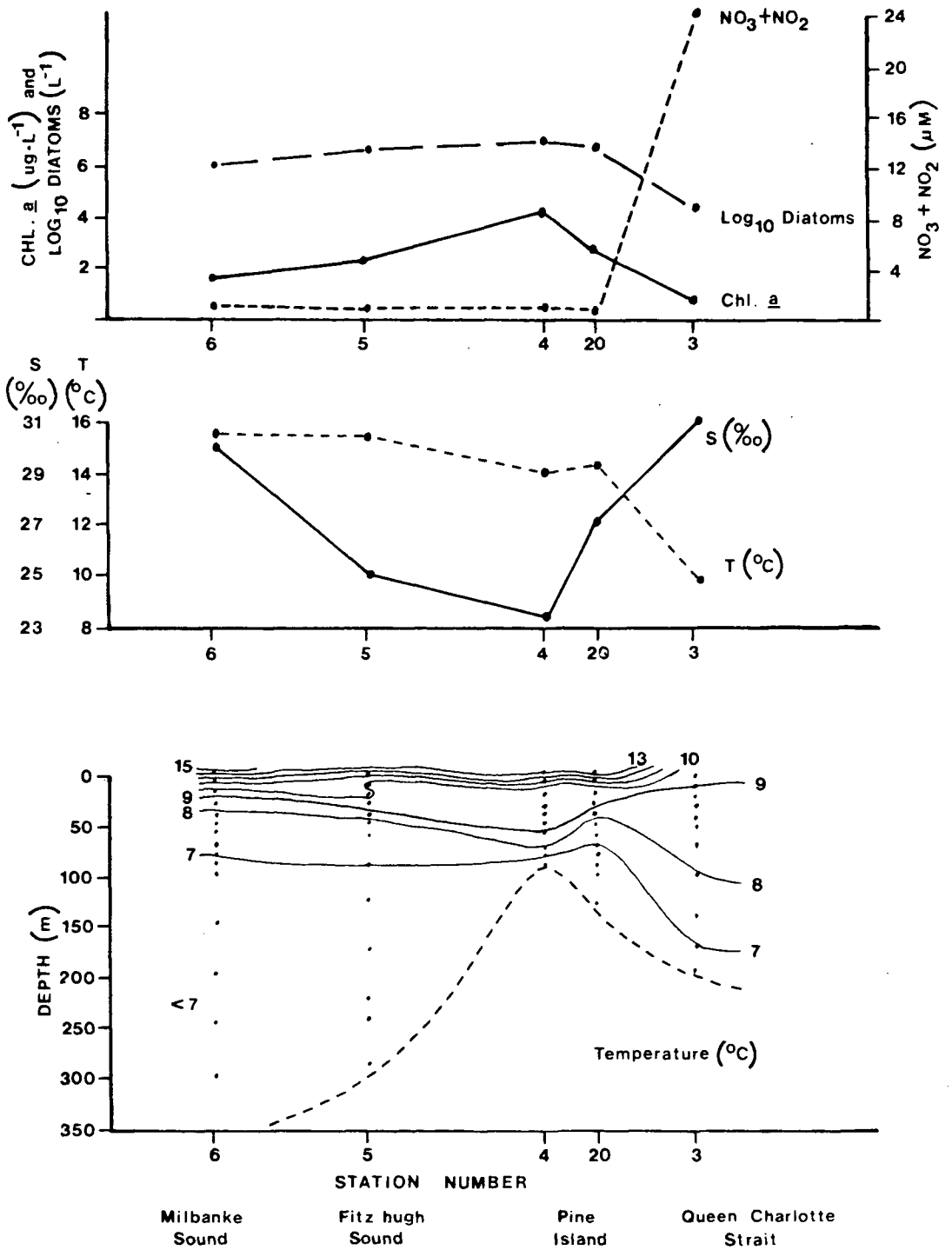


FIGURE 12. *Imperial Tofino* transect through coastal Queen Charlotte Sound, 16-27 July 1979 (Cruise 11). For station locations see Appendix I. Bottom panel shows the vertical temperature structure and approximate bathymetry from XBT profiles (dots).

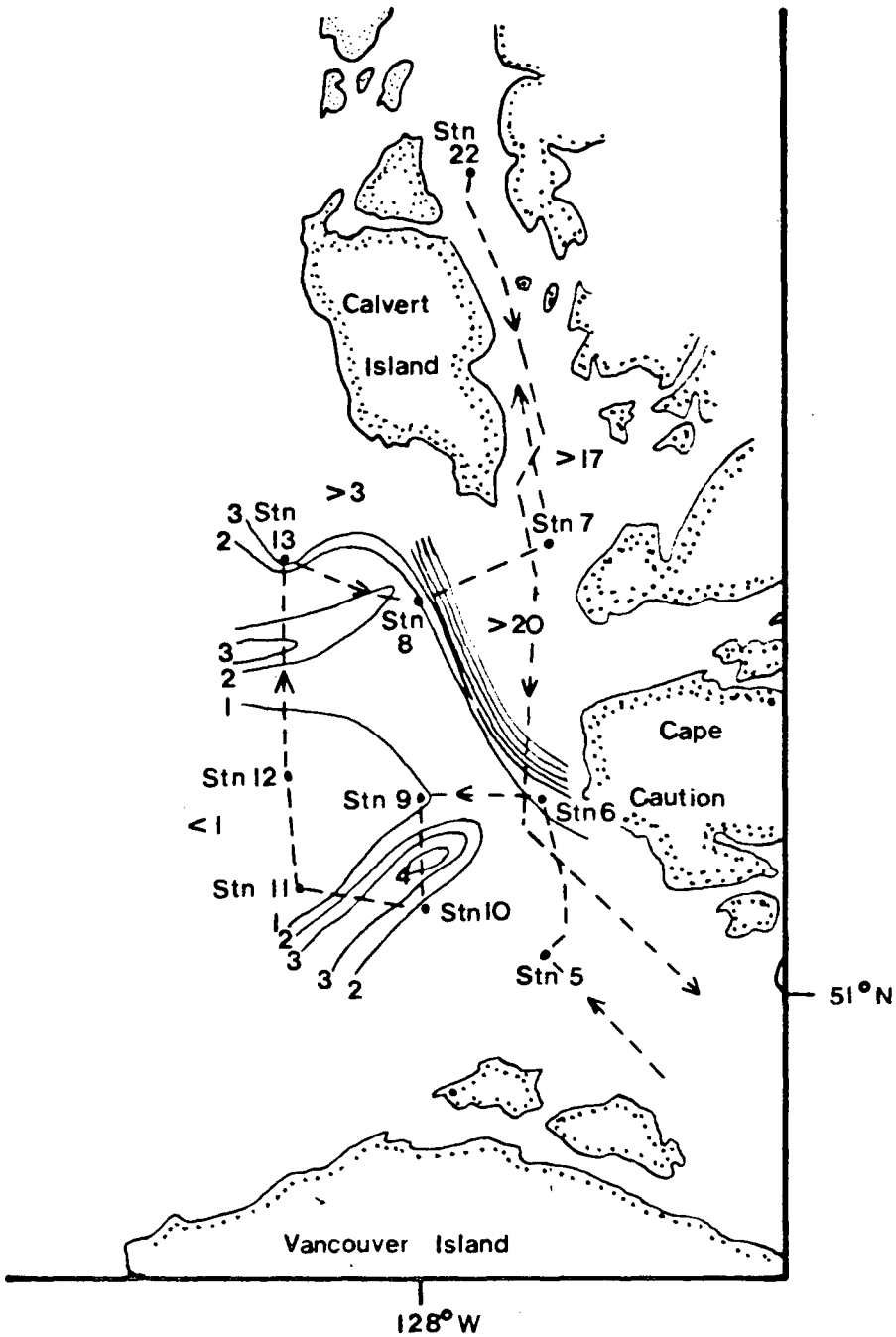


FIGURE 13. Near surface (4 m) chlorophyll ($\mu g\ L^{-1}$) distribution as measured on 29 April 1980 by *Pandora II* (DOUBC cruise 80-7) in southeastern Queen Charlotte Sound. Values have been converted from continuous *in vivo* fluorescence data as measured along the cruise track (dashed line), and contoured by hand.

with r^2=0.96 for n=9 samples. The extent of the bloom and its leading edge in Queen Charlotte Sound are clearly indicated. No qualitative observations of the appearance of this front are available as it was crossed at night.

Vertical profiles of chlorophyll, temperature and salinity at stations on either side of this front are presented in Fig. 14. Chlorophyll *a* was low and uniform with depth at Stations 13 and 8 outside the bloom (see Fig. 13), with little variation of temperature or salinity. At Stations 7 and 22 inside Fitz Hugh Sound however, there was considerable vertical structure of chlorophyll. Near the front (Station 7), chlorophyll was very high within the upper 0-5 m, with decreased salinity and higher temperatures near the surface suggesting some vertical stratification. Further inside Fitz Hugh Sound at Station 22, near-surface chlorophyll concentrations were lower with a subsurface chlorophyll maximum. The pattern of nutrients at these four stations was the inverse to that for chlorophyll. Temperature profiles from XBT casts also indicated a shallow stratified layer inside Fitz Hugh Sound.

A subsequent cruise to this area onboard CNAV *Endeavour* (DOUBC Cruise 81-10, 6-9 April 1981) found conditions typical of winter, with low chlorophyll and high nutrients. This is consistent with the pattern of initiation of the bloom in this area suggested by *Tofino* Cruise 13, where winter conditions prevailed on the northbound leg on 11 April 1980, while on the southbound leg 5 days later the bloom had appeared. This bloom

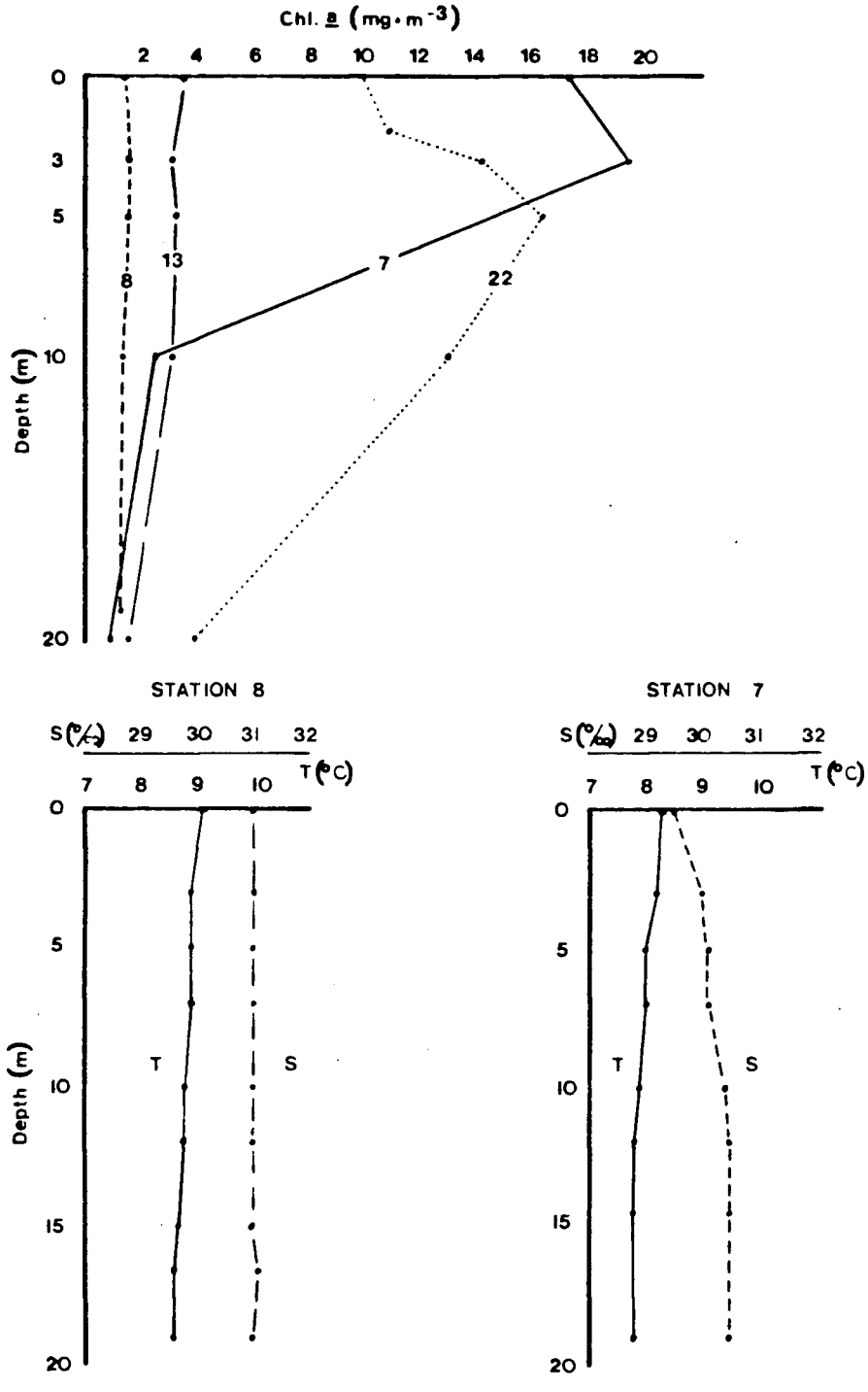


FIGURE 14. Vertical profiles of chlorophyll *a* (top, Stations 7,8,13,22) and temperature and salinity (bottom, Stations 7 and 8) measured by *Pandora II* on 29 April 1980 in southeastern Queen Charlotte Sound. See Fig. 13 for station locations; note Stations 8 and 13 are outside the bloom, Stations 7 and 22 inside.

was subsequently analysed in more detail by the *Pandora II* cruise.

D. DISCUSSION

As this study is the first to examine phytoplankton distributions on the northern shelf of B.C. in a systematic manner, no previous data are available for comparison. However, zooplankton data are available from previous studies, and can be compared with the ship of opportunity results. Analysis of stomach contents of salmonids (e.g. Manzer 1969) indicate copepods, larvaceans, barnacle and decapod larvae, amphipods and euphausiids are potential prey. All these have been identified from north coastal waters by the SHOP program, often with considerable spatial and temporal heterogeneity. For example, decapod larvae and crab zoea were extremely abundant in western Hecate Strait and barnacle larvae were abundant in eastern Hecate Strait in June 1979 and 1980 (data in Perry *et al.* 1981 and Chapters 5 and 6 of this thesis). LeBrasseur's (1966) conclusion that prey availability may be more important to feeding than prey preference suggests such large concentrations may be very important for survival of juvenile fish.

The more common copepod species identified by Cameron (1957) about the Queen Charlotte Islands included *Paracalanus parvus*, *Acartia clausii*, *Centropages abdominalis*, and *Tortanus discaudatus*. She took vertical tows, but in general found all

the above except *T. discaudatus* distributed within the upper 14 m. These zooplankters should therefore have been representatively sampled by the Miller sampler towed from the *Tofino*. In Cameron's (1957) study, relatively rare forms in Hecate Strait included *P. parvus*, *A. clausii*, and *T. discaudatus*, while *C. abdominalis* was relatively common. In the SHOP collections from June 1979 and 1980, *C. abdominalis* was common at most stations sampled throughout the northern shelf, and especially abundant in Hecate Strait and Fitz Hugh Sound. *Acartia* spp. were also common at all stations, although *A. longiremis* was more typical than *A. clausii*. *P. parvus* was not particularily common, although the morphologically similar species *Pseudocalanus minutus* was the most abundant copepod throughout the northern shelf. Corkett and McLaren (1978) identified *Pseudocalanus* as a very important food source for larval fishes, and its abundance during spring and summer may play a critical role in their survival.

The most complete spatial sampling for zooplankton has been done by Fulton *et al.* (1982), although it covered only the period January to April 1980. These samples are not strictly comparable with the ship of opportunity collections, being oblique tows from bottom to surface with stations located in open water rather than among the coastal passages as are many of the SHOP stations. As a result, while Fulton *et al.* (1982) did find some stations dominated by barnacle nauplii as on the *Tofino* cruises, the dominant organism throughout the northern

shelf was *Neocalanus plumchrus*. In the *Tofino* samples, *N. plumchrus* was abundant only from deep water stations located in Fitz Hugh Sound during June 1980; Gardner (1982a) also noted abundant populations of early stage *N. plumchrus* at the head of Fitz Hugh Sound in April 1977.

1. SPRING BLOOM TIMING

The critical depth - mixed depth pattern of Fig. 3 demonstrates a northward progression of conditions appropriate for a spring diatom bloom along the B.C. coast, but it is not entirely sequential between adjacent areas. The Strait of Georgia certainly supports the longest growing season with the earliest spring bloom, while conditions in Dixon Entrance suggest the latest bloom and the shortest season. However, Queen Charlotte Sound and Hecate Strait appear to have very similar growing seasons with similar timing of the spring bloom despite a distance of 300 km between their extreme boundaries. Normal daily solar radiation summarized by month for three locations along the coast (Table VI) indicate typically higher values during spring and summer in the Strait of Georgia (Nanaimo), but relatively similar intensities for both Queen Charlotte Sound (Cape St. James) and Hecate Strait (Sandspit). However, it must be noted irradiance and the critical depth - mixed depth analyses are based on general features measured over several years, with station locations predominately in open waters. Such an analysis is not capable of distinguishing small scale

TABLE VI. Normal daily solar radiation values for each month (measured as MJ m^{-2} d^{-1}) for three stations on the B.C. coast representative of the Strait of Georgia (Nanaimo), Queen Charlotte Sound (Cape St. James), and Hecate Strait (Sandspit). Data are from the Monthly Radiation Summary, Atmospheric Environment Service, Ottawa; normals are calculated for the period 1967-1980 (Sandspit and Cape St. James) and 1959-1980 (Nanaimo).

MONTH	NANAIMO	CAPE ST. JAMES	SANDSPIT	HOURS OF LIGHT
January	2.904	2.636	2.415	10
February	6.050	5.174	4.896	12
March	10.488	9.009	8.984	14
April	16.439	13.934	13.578	15
May	21.120	19.087	18.159	16
June	22.188	19.676	17.773	18
July	23.718	19.092	17.174	18
August	19.587	16.610	15.049	16
September	13.994	12.174	13.576	14
October	7.725	6.629	5.874	12
November	3.149	3.243	4.102	10
December	2.333	3.779	1.804	8

variations within each region, which can be quite important in determining the precise pattern of bloom initiation.

The variability of conditions within each region of the coast is well demonstrated by the *Tofino* ship of opportunity data. Both chlorophyll concentrations and the estimated phytoplankton biomass index showed their greatest variability throughout the northern shelf during April, suggesting the bloom had begun at some stations. The spatial distribution of chlorophyll and nutrients during spring (Fig. 6A) shows this variability clearly, with high concentrations of chlorophyll in coastal regions of southeastern Queen Charlotte Sound and

shallow western Hecate Strait. Lowest concentrations of chlorophyll were in Dixon Entrance, eastern Hecate Strait, and over the continental shelf edge in western Queen Charlotte Sound. Diatom biomass followed the pattern for chlorophyll, suggesting the spring phytoplankton increase was predominately a diatom bloom.

High zooplankton abundances coincided with high diatom concentrations during spring, especially in the areas of western Hecate Strait and southwestern Queen Charlotte Sound, at least on the time scales of sampling. Copepods, barnacle and decapod larvae were major constituents of these blooms, suggesting that invertebrates in these areas with meroplanktonic larvae were reproducing at the same time as the holoplanktonic fauna and the phytoplankton.

The general pattern of the biological observations along the B.C. coast, which tends to integrate this within-region variability, is summarized by the qualitative bloom analysis technique and reported in Table V. It suggests the spring bloom began early in the Strait of Georgia, probably by March in 1979. The timing for Queen Charlotte Sound and Hecate Strait could not be distinguished, with the bloom in both areas appearing to develop at the beginning of April. In Dixon Entrance, the bloom was not apparent until late May or early June in 1979.

These observations of the progression of the spring bloom along the coast in general match those predicted by the critical depth - mixed depth analysis. However, the predicted timing of

the outburst did not agree with the observations from the Strait of Georgia and Queen Charlotte Sound. In Queen Charlotte Sound, the bloom was observed to occur earlier than predicted by the critical depth model. The simplest explanation concerns the locations of stations used for prediction and observation. Critical depth model predictions were based on open oceanic waters, while *Tofino* observations were predominately in coastal areas. As demonstrated by the *Pandora II* cruise results for Queen Charlotte Sound in April 1980, diatom blooms may occur earlier in waters near shore than offshore, especially in the Fitz Hugh Sound area.

In the northern Strait of Georgia, the bloom was observed to occur later than predicted by the critical depth model. However, this region also suffers from a poor distribution of stations in the SHOP program, so that the bloom may have occurred in either February (as predicted) or March. The predictions of this thesis also agree with the predictions of Parsons (1965) for the Queen Charlotte Sound and Hecate Strait regions, even though he used mixed depth data for adjacent oceanic waters, and with Parsons *et al.* (1966), who predicted a bloom for oceanic waters of the eastern subarctic Pacific by April. The timing predicted in this thesis for a bloom in Dixon Entrance during May rather than April may in part be due to the lack of adequate measurements of the attenuation coefficient, resulting in a biased estimate of the critical depth (note only 5 measurements were available for Dixon Entrance in April). The

timing does, however, agree with studies on the spring plankton bloom in the waters of southeastern Alaska. Near Prince of Wales Island, just north of Dixon Entrance, it usually began in late April or May, and was dominated by *Chaetoceros* spp. and *Skeletonema* spp. (Alaska Dept. of Fish and Game 1979, quoted in Petro-Canada 1983). Highest mean biomass of zooplankton in this area (in 1972) occurred in May and June, but dropped sharply during July (Mattson and Wing 1978). Copepods dominated the biomass, followed by chaetognaths, euphausiids, amphipods, amd barnacle nauplii, which is similar to the composition sampled from Dixon Entrance and Hecate Strait.

2. COASTAL QUEEN CHARLOTTE SOUND

The southwestern corner of Queen Charlotte Sound, including Fitz Hugh Sound and Milbanke Sound, has been shown by the ship of opportunity observations to have an early spring bloom, along with western Hecate Strait (e.g. Fig. 6A). More detailed transects indicated this bloom can be well developed by April, and compared this region with Queen Charlotte Strait, which showed considerable patchiness.

The precise cause of this bloom in Fitz Hugh Sound is unknown, although a potential mechanism (untested in this thesis) is freshwater runoff. The seasonal increase of solar radiation progressing from south to north (Table VI) may begin to melt the snowpack of southern coastal areas first. Rivers flowing into the Fitz Hugh and Milbanke Sound systems have a

larger percentage increase in their flow volumes from March to April than do rivers further north, and in fact the Dean River (flowing into Dean Channel and the head of Fitz Hugh Sound) reaches its peak mean flow during May (Water Resources Branch 1977). This freshwater should increase stability within the inlet system, and potentially increase the flow towards the open sea as a result of the hyraulic pressure gradient. That stratification does increase is shown by the XBT profiles of Figs. 11 and 12, while the extent of the flow of lower salinity water into open Queen Charlotte Sound is clearly shown by Dodimead (1980, p. 130 and 131). Nutrient-rich subsurface water would likely be entrained into this seaward-flowing surface layer, creating a relatively high light, high nutrient environment ideal for phytoplankton growth.

The early marine phase of the life cycle may be critical to feeding success and mortality rates of outmigrating juvenile salmonids, therefore affecting the size of the returning population (Healey 1980). Several studies have examined the seaward migrations of pink salmon *(Oncorhynchus gorbuscha)* through the Fitz Hugh Sound and Milbanke Sound system to the open sea, and it is interesting to compare their results with the ship of opportunity findings for that area. Parker (1965) studied the 1961 pink fry brood year and found the rate of natural mortality was considerably higher during the inital short period in coastal waters compared with the remaining period of sea life.

Healey (1967) described the seaward migration of these fry, which took about one month to swim from the Bella Coola River down Burke Channel to the open sea (Queen Charlotte Sound). In his study, large numbers of fry reached the upper waters of Fitz Hugh Sound by the end of May and beginning of June. Plankton characteristics during May 1979 (Fig. 11) showed very high copepod concentrations in this area. Pink salmon fry grow quickly and require a large food supply (Healey 1967), which may be provided by calanoid copepods during this migration. In a study of pink fry feeding in an inlet of the Alaskan coast, Bailey *et al.* (1976) noted all fish collected in daylight contained food, of which copepods (both calanoids and cyclopoids) were dominant. Barnacle nauplii were also common in both the inlet and the stomach contents, as has been suggested for the Fitz Hugh Sound region by the ship of opportunity data. In the Skeena River area, Manzer and Shepard (1962) suggested the greatest number of pink salmon fry migrate to the ocean about mid-May and spend time growing in inshore waters. This timing is also similar to that predicted for the spring bloom in Dixon Entrance by the critical depth model and observed on the *Tofino* cruises.

E. SUMMARY

Despite the importance of the northern shelf region for fishery and petroleum resources of the British Columbia coast,

its biological oceanography has been very poorly studied. A review of the literature indicates a few studies have examined zooplankton at selected sites in the region, but phytoplankton have been almost neglected. This chapter has two main purposes: to present the first general survey of plankton on the northern shelf by summarizing observations made from the *Imperial Tofino* from 1978 to 1980; and to examine the pattern of initiation of the spring diatom bloom on the B.C. northern coast.

The summary of the observations focussed on temporal variability between cruises, and spatial variability between and within the regions of the northern shelf. Chlorophyll concentrations were lowest during winter, highest in summer, and most variable during spring, suggesting differences in timing of the spring bloom. Spatially, highest chlorophyll concentrations during spring (April 1980) occurred in western Hecate Strait and southeastern Queen Charlotte Sound. Nutrient distributions were found to be the inverse of chlorophyll.

Phytoplankton biomass has been summarized in terms of diatoms and flagellates, using both abundance and an estimated biomass index. The temporal pattern was similar to chlorophyll, with the dominant component being flagellates during winter, and diatoms during late spring and early summer. During spring, diatoms were the major components of the biomass index at stations in western Hecate Strait and southeastern Queen Charlotte Sound. Correlations of diatom abundance and chlorophyll concentrations were significant during April 1980

suggesting that the spring increase of chlorophyll was due to a diatom bloom. Zooplankton also followed this basic seasonal pattern, appearing to coincide (on the scale of sampling) with higher phytoplankton concentrations. Copepods were most abundant generally, with barnacle nauplii and decapod larvae abundant at specific locations.

Critical depth - mixed depth calculations suggest conditions are appropriate for a phytoplankton spring bloom by April-May in Queen Charlotte Sound, April in Hecate Strait, and May in Dixon Entrance. Observations of the spring blooms in 1979 and 1980 agreed with the predicted timing for Hecate Strait and Dixon Entrance, but suggested it occurred earlier than predicted (April) in Queen Charlotte Sound. This latter may be due in part to the station locations, as the observations were predominantly in coastal southeastern Queen Charlotte Sound, while the critical depth calculations were from the open waters of Queen Charlotte Sound. The general pattern of the spring bloom therefore followed a northward progression from the Strait of Georgia to Dixon Entrance, although Queen Charlotte Sound and Hecate Strait could not be distinguished in this analysis. Chapter 6 suggests part of Hecate Strait experiences an early spring bloom due to its shallow bottom depth.

As an example of the small-scale variability that occurs within a region, detailed plankton distributions and events leading to a spring bloom were examined on several *Imperial Tofino* transects through southeastern Queen Charlotte Sound.

Implications of this bloom for the survival of outmigrating juvenile salmonids are discussed using studies in this region from the literature.

V. SUMMER PLANKTON DISTRIBUTIONS IN HECATE STRAIT

A. INTRODUCTION

This chapter is concerned with the spatial variability of plankton and other biological parameters within one area of the northern shelf. Where the previous chapter emphasized temporal and spatial variability between areas, this chapter focuses on the variability across northern Hecate Strait during summer. As noted in Chapter 2, Hecate Strait is an area with east-west contrasts of physiographic and oceanographic features. Bathymetry is most distinct, with very shallow banks on the western side adjacent to the Queen Charlotte Islands and a deep trough on the east parallel to the mainland shore (Chapter 2, and Fig. 15). Current patterns also differ, with flow predominately north-south along the eastern side, and a suggestion of a gyre over the shallow western banks (Bell 1963).

Recently, considerable interest has focussed (reviewed below) on the ability of the tide to mix shallow water columns, and the contrasting biological effects such mixing can have when it occurs adjacent to a deeper, more stratified body of water. With its east-west bathymetric gradient, Hecate Strait is a good area to examine the influence of tidal mixing on plankton distributions and other biological parameters. The hypothesis examined in this chapter is that bathymetric differences across Hecate Strait, combined with tidal streaming, generate

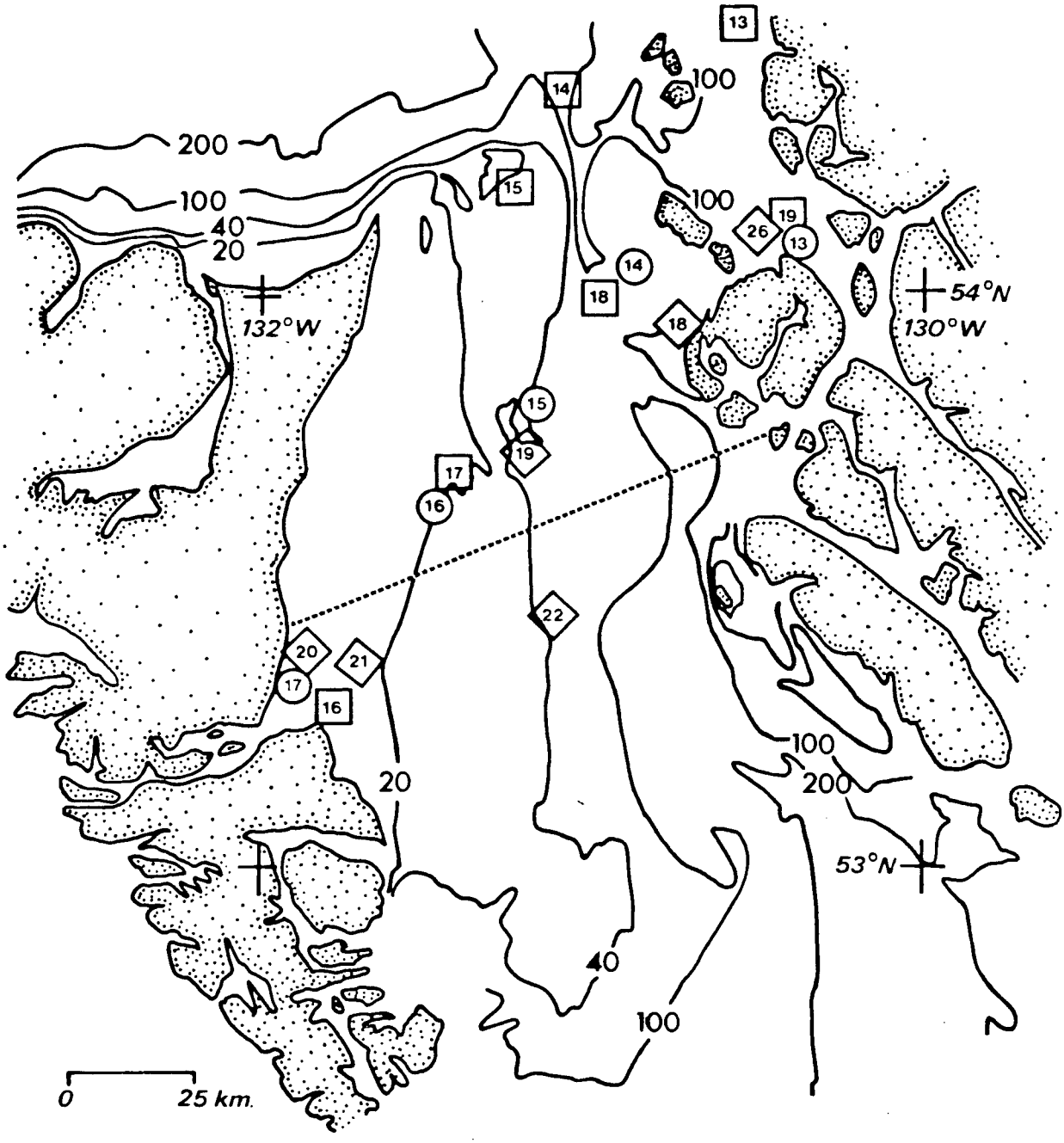


FIGURE 15. Bathymetric map of Hecate Strait (depths in meters) showing locations of stations on Cruise 10 (squares), 11 (circles), and 14 (diamonds). Dashed line indicates route of continuous transect during Cruise 15.

vertically well-mixed conditions in western Hecate Strait and relatively more stratified conditions in eastern Hecate Strait. Such variations of vertical mixing then influence the biological characteristics, with low biomass in well-mixed waters and high biomass at the boundary or front between the characteristic mixing zones. The null hypothesis, then, suggests no difference in biomass or biological properties between deep and shallow areas of the strait due to tidal mixing. Conditions are examined during summer to emphasize the mixed and stratified regimes. The majority of this chapter has already been published (Perry *et al.* 1983).

1. LITERATURE REVIEW

This section briefly reviews the basic theory of shallow sea tidal fronts and their influence upon biological production and distributions. For greater detail, collections of specific studies of coastal fronts can be found in Bowman and Esaias (1977) and Swallow *et al.* (1981).

The shallow sea tidal front model was initially developed and applied to waters about the British Isles, especially the relatively shallow Celtic Sea where freshwater runoff effects are minimal. The model was proposed by Simpson and Hunter (1974) and later elaborated by Simpson *et al.* (1978) and Pingree (1978). It identifies well-mixed and stratified water masses in a given area separated by a relatively sharp discontinuity or front. The Celtic Sea will serve as an example. Increasing solar

radiation from spring to summer warms the surface waters, decreasing its density and increasing its buoyancy. As wind strength declines, a stage will be reached where the water column can be modelled as a two-layer system, with a surface wind-mixed layer of depth h and density ρ_1, overlying a near-bottom tidally mixed layer of denser water (ρ_3), separated by a pycnocline (or often a thermocline). However, in an adjacent area which is sufficiently shallow, the action of surface winds and bottom tidal currents will eventually overlap, disrupting the pycnocline and causing mixing from surface to bottom with a mean density ρ_2. If such mixed and stratified regions occur in proximity, they must be separated by a discontinuity, or front, which can be visualized as an upturning of the pycnocline (or thermocline). The situation as described is diagrammed in Fig. 16.

Disregarding the surface wind stress and assuming the surface heat flux, which increases the buoyancy, is constant over the area being considered, combinations of tidal velocity and water depth producing mixed and stratified regimes can be identified using a stratification parameter (S; Pingree 1978):

$$S = \mathrm{Log}_{10} \frac{h}{C_d \quad |\bar{U}|^3}$$

where h is the water depth, C_d a bottom drag coefficient and $|\bar{U}|$ the magnitude of the tidal stream velocity averaged over one tidal cycle. Using C_d = 0.0025, the critical value of S (using

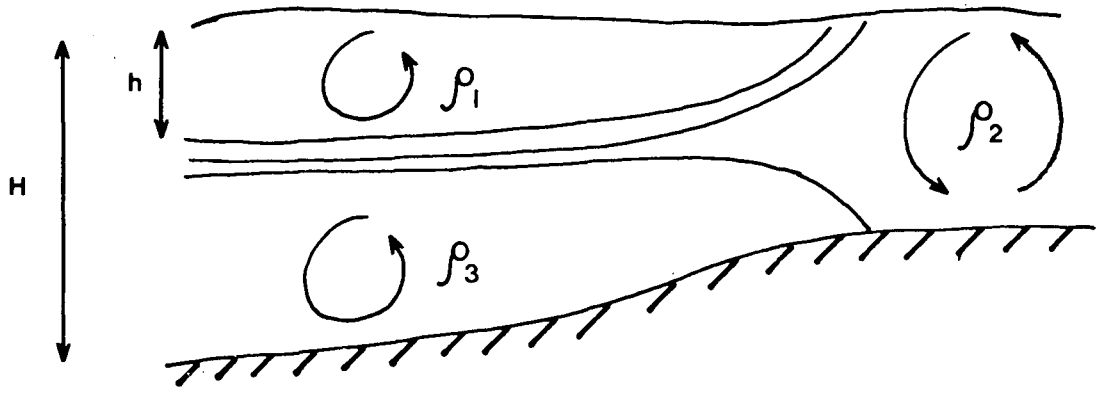


FIGURE 16. Diagram illustating the basic structure of a shallow sea tidal front ($\rho_1 < \rho_2 < \rho_3$). H is the total water depth, h the depth of the surface wind mixed layer; for further details, see text.

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cgs units) which indicates the presence of a front is 1.5, with values <1.0 representing well mixed regions and S>2.0 well stratified regions. Field studies have confirmed the predicted locations of these fronts (Pingree *et al.* 1978), although they may alter position somewhat with the neap-spring tidal cycle.

Such frontal regions also have characteristic distributions of plankton and nutrients during summer. Phytoplankton biomass and production will be low on the mixed side of the front because of low mean light levels (due to the greater depth of mixing), and also low on the stratified side (at least within

the upper layers) due to nutrient exhaustion (Pingree 1978). High phytoplankton biomass and production in the transition zone between these two regions results from a flux of nutrients across the front and a favourable light regime induced by a shallow thermocline.

Plankton composition also differs between the three characteristic regions. Pingree *et al.* (1978) and Holligan *et al.* (1984) report diatoms characterize the tidally mixed waters, small flagellates are most common in well stratified waters (and may form a sub-surface chlorophyll maximum), while the frontal region is often composed of monospecific blooms of dinoflagellates. Zooplankton were noted by Holligan *et al.* (1984) to have their largest biomass in stratified waters, although it is not clear to what extent this was due to avoidance of the dinoflagellate bloom in the frontal region. These authors further suggest the characteristic mixing zones may give rise to different food webs, with the largest proportion of carbon residing in the phytoplankton in mixed waters, but in the zooplankton, supplemented by bacteria and protozoa, in stratified waters. Floodgate *et al.* (1981) noted maximum copepod abundance at the front itself and suggested zooplankton may initially be advected to the front by the associated convergent circulation patterns, where they would then grow at an accelerated rate by feeding on the higher biomass. The width of the frontal transition zone can vary, being sharp and well-defined about the British Isles (Pingree *et*

al. 1978) but rather extensive among the islands of the southern Strait of Georgia, B.C., depending on such factors as local runoff and light extinction properties (Parsons *et al*. 1983).

Several studies have applied this shallow sea frontal model to areas other than the British Isles, including areas with considerable freshwater influence. Garrett *et al*. (1978) developed essentially the same model for the Bay of Fundy and Gulf of Maine, while Griffiths *et al*. (1981) applied the Simpson and Hunter (1974) model to Hudson Bay. Successful application of the model and its importance to plankton production in major estuaries was reported by Bowman and Esaias (1981) and Bowman *et al*. (1981) for Long Island Sound, and by Parsons *et al*. (1981) for the Strait of Georgia, where principal zones of mixing were located among the island passages at the northern and southern ends. The tidal mixing model has also been applied successfully to the shelf seas about New Zealand (Bowman *et al*. 1983).

The importance of coastal fronts to higher trophic levels, especially as areas of concentrated food sources, has also been investigated. An extensive study of physical-biological interactions in the Bering Sea (Iverson *et al*. 1979) found a series of three fronts (one a shelf break front) dividing the shelf into three zones. The mixed inner shelf supported large stocks of benthic fauna and demersal fish while the deeper, outer shelf region supported primarily pelagic fish stocks. Large aggregations of sea birds along these fronts have also been noted (Schneider 1982). Feeding by marine mammals at tidal

convergences in eastern Canada has also been cited by Gaskin (1976). Observations that fronts may influence circulation patterns led Iles and Sinclair (1982) to suggest that they may hydrodynamically "enclose" bodies of water and reduce dispersal of herring larvae in the Gulf of St. Lawrence, thus maintaining the integrity of individual spawning stocks.

B. METHODS

Data for this study were obtained by the *Imperial Tofino* on routine ship of opportunity cruises. The area of northern Hecate Strait between Prince Rupert and Sandspit was covered consistently on almost every cruise, providing reasonable temporal and spatial coverage. In addition, it is an area of open water and not highly influenced by local events such as runoff. Methods for this study are those described in Chapter 3. Due to the covariation of nutrient concentrations, results are reported for nitrate and nitrite only.

Mixed and stratified regions were determined for Hecate Strait and Dixon Entrance using the Simpson-Hunter stratification parameter S (defined above). Tidal current velocities were obtained from a two-dimensional, depth averaged numerical tidal model calculated to predict oil spill movements for the Kitimat Pipeline Project (Kinney *et al.* 1976). The model includes Hecate Strait and Dixon Entrance between 52°N and 55°N, and 128°W and 133°W using a grid network with 9.3 km (5 nautical

mile) spacing. Interpolations of tide table data were required across the open sides of the model in Queen Charlotte Sound, Dixon Entrance, and Clarence Strait at the southern end of the Alaskan archipelago. The tidal component calculated in the model is the M_2 tide with a period of 12.42 hours.

The stratification parameter was calculated using h as the mean water depth for each of the tide model's 9.3 km grid squares (averaged from Canadian Hydrographic chart no. 3002). The bottom drag coefficient was assumed to be 0.0025, and the mean tidal speed ($\bar{U}$) was averaged over the tidal cycle for each grid position regardless of direction. To verify the existence of well-mixed and stratified zones predicted by this equation independently of tidal current and depth measurements, the bulk stratification of the surface layer was calculated for Hecate Strait and Dixon Entrance. Bulk surface stratification was defined as the difference of σ_t between the surface and 50 m or the bottom (whichever was less), expressed as $\Delta\sigma_t$ m^{-1}. These data were obtained from the Marine Environmental Data Service of Fisheries and Oceans Canada, and consisted of vertical profiles of temperature and salinity collected in Dixon Entrance and Hecate Strait during summer from 1954 to 1971. They are part of the same data set used in Chapter 4 for calculation of the surface mixed layer depth.

C. RESULTS

1. TIDAL MODEL

Tidal ellipses for Hecate Strait and Dixon Entrance computed by the tide model are redrawn from Kinney *et al.* (1976) in Fig. 17. These ellipses represent the movement of a parcel of water over one tidal cycle in the absence of a residual current. The linearly directed tidal currents in eastern Hecate Strait and the circularly directed currents in the west are clearly indicated. Largest ellipses (computed currents up to 0.75 m s^{-1}) occur off the northeast coast of Graham Island. It must be emphasized that these are estimated averages computed for a 9.3 km grid spacing. Thomson (1981) has noted there can be considerable distortion of tidal streams near broken shorelines in the area, which would be too small for inclusion in this model. Any sharp, localized discontinuity of bathymetry would similarly not be represented.

Comparison of these tidal ellipses with the bathymetry (Fig. 15) shows the greatest tidal current velocities occur over the shallowest banks of Hecate Strait. Calculation of the stratification parameter for Hecate Strait and Dixon Entrance also indicates this to be a region of intense mixing, surrounded by a transition zone (S between 1 and 2) of varying width, whereas the remainder of the strait is potentially stratified during summer (Fig. 18). Sharpest horizontal gradients of vertical mixing characteristics should occur between Dixon

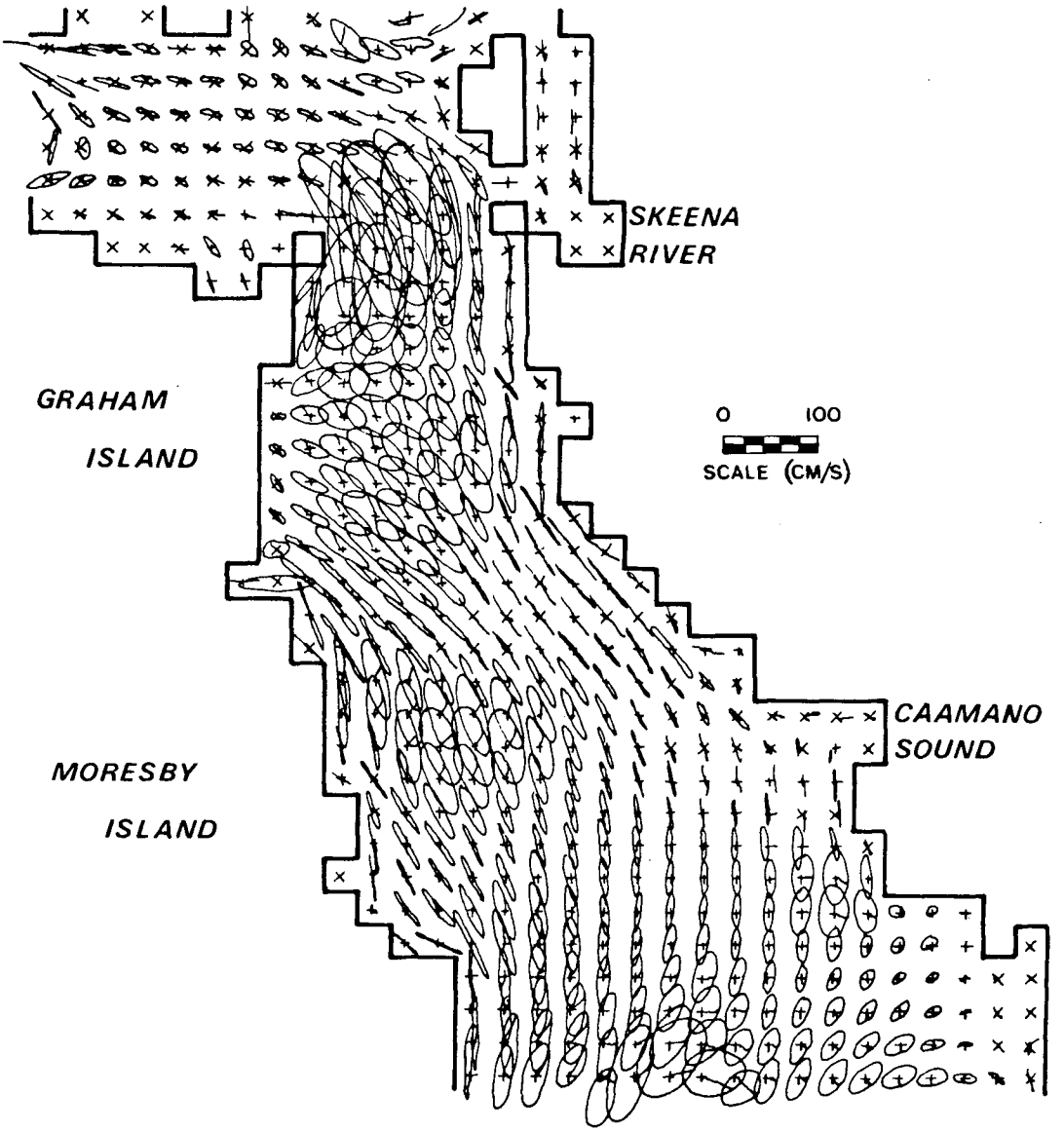

FIGURE 17. Tidal current ellipses computed from the oil spill drift prediction model for Hecate Strait and Dixon Entrance. Redrawn with permission after Kinney *et al.* (1976).

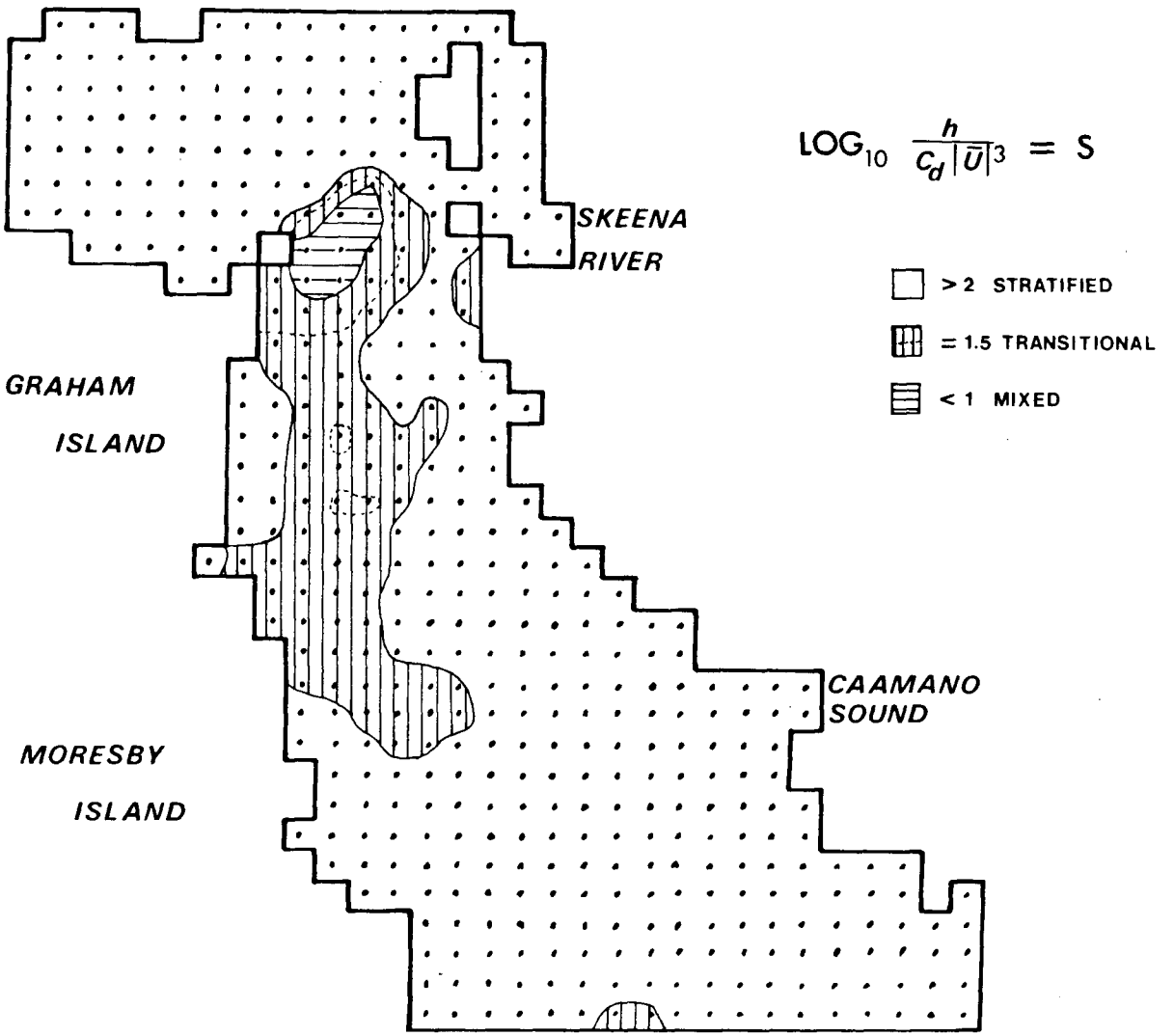

FIGURE 18. Calculations of the Simpson - Hunter stratification parameter, with h the depth of the water, $\bar{U}$ the tidal current velocity averaged over one tidal cycle (both cgs units), and a drag coefficient (Cd) of 0.0025. Values for stratified, transitional, and mixed zones are from Pingree (1978). Dots represent data locations; dashed line represents the S=1.5 contour.

Entrance and Hecate Strait, and between Graham Island and Chatham Sound, coinciding closely with marked changes of bathymetry. This latter gradient should also be strengthened by the seaward estuarine flow induced by the Skeena River. These are the locations where fronts are expected, being the boundary between well-mixed and stratified water masses.

For comparison with the Simpson-Hunter stratification parameter, bulk surface stratification values are grouped into the same 9.3 km squares used for the tidal calculations (Fig. 19). Although the sampling density is much less than that used for the tidal stratification, there is a reasonable comparison with mixed and stratified regions. Bulk stratification values over shallow western Hecate Strait are less than 0.01 σ_t units m^{-1} indicating well mixed conditions, whereas eastern Hecate Strait is more stratified with values greater than 0.03 σ_t units m^{-1}. As with the tidal model, the sharpest gradient of surface stratification occurs in northern Hecate Strait. The influence of the Skeena River is also clear, with the surface stratification of eastern Dixon Entrance well over 10 σ_t units m^{-1} and the contour lines indicating the general northward and westward flow. Correlations of the two measures of stratification for the grid squares in which they coincide are moderately large and significant ($p<0.05$) except for July, and are shown in Table VII.

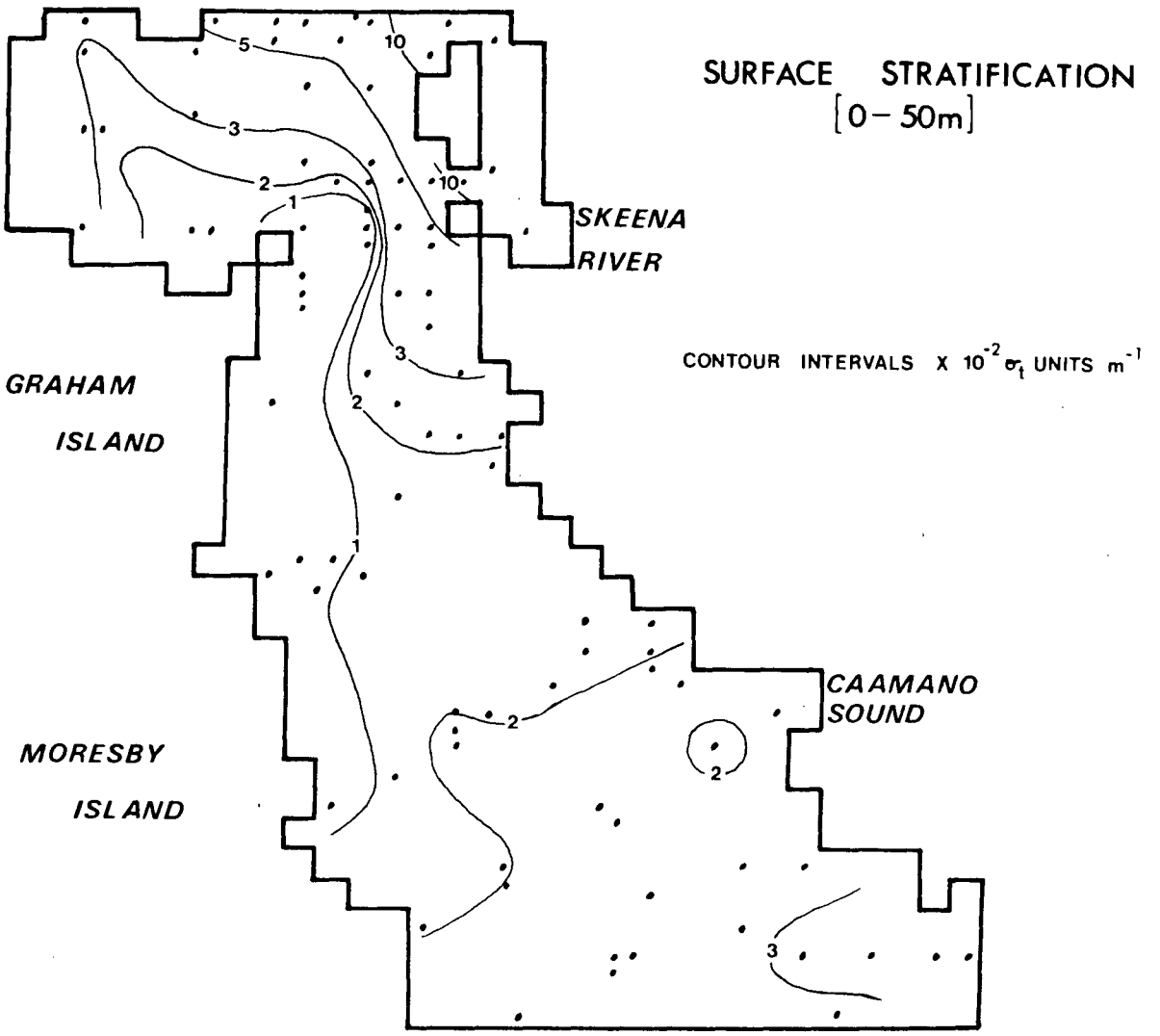

FIGURE 19. Bulk stratification, the σt difference from the surface to the bottom or 50 m (whichever is less) normalized per meter, for Hecate Strait and Dixon Entrance. Data presented are a composite of June, July and August calculated from temperature and salinity measurements from 1954 to 1971. Dots represent station locations.

TABLE VII. Correlation of bulk surface stratification ($\Delta\sigma t$ from surface to 50 m or the bottom) with the tidal stratification parameter (S) for grid squares in which they coincide. Significance represents the probability of the correlation coefficient being equal to zero.

	JUNE TO AUGUST INCLUSIVE	JUNE	JULY	AUGUST
Correlation Coeff.	0.37	0.40	0.30	0.49
Significance	0.00	0.00	0.08	0.00
Number of Observations	168	86	42	40

2. BIOLOGICAL DISTRIBUTIONS

Stations occupied by the *Tofino* on transects across Chatham Sound and northern Hecate Strait are shown in Fig. 15. A similar transect was repeated on all three cruises with occasional stations in Dixon Entrance and off Banks Island in eastern Hecate Strait. Data from the transects are presented in Figs. 20 to 23, with station numbers aligned so that distances are comparable between all cruises.

Cruise 10 (June 1979) has been divided into two transects, a northern transect from Chatham Sound and Sandspit (Fig. 20), and a central transect from Sandspit back to Prince Rupert at the mouth of the Skeena River (Fig. 21). On the nothern transect (Fig. 20), concentrations of chlorophyll, diatoms, nitrate, and copepods were lowest in the well-mixed, shallow western strait (Fig. 20C), and higher in the stratified eastern strait. The sharpest change occurred between Stations 17 and 15, where

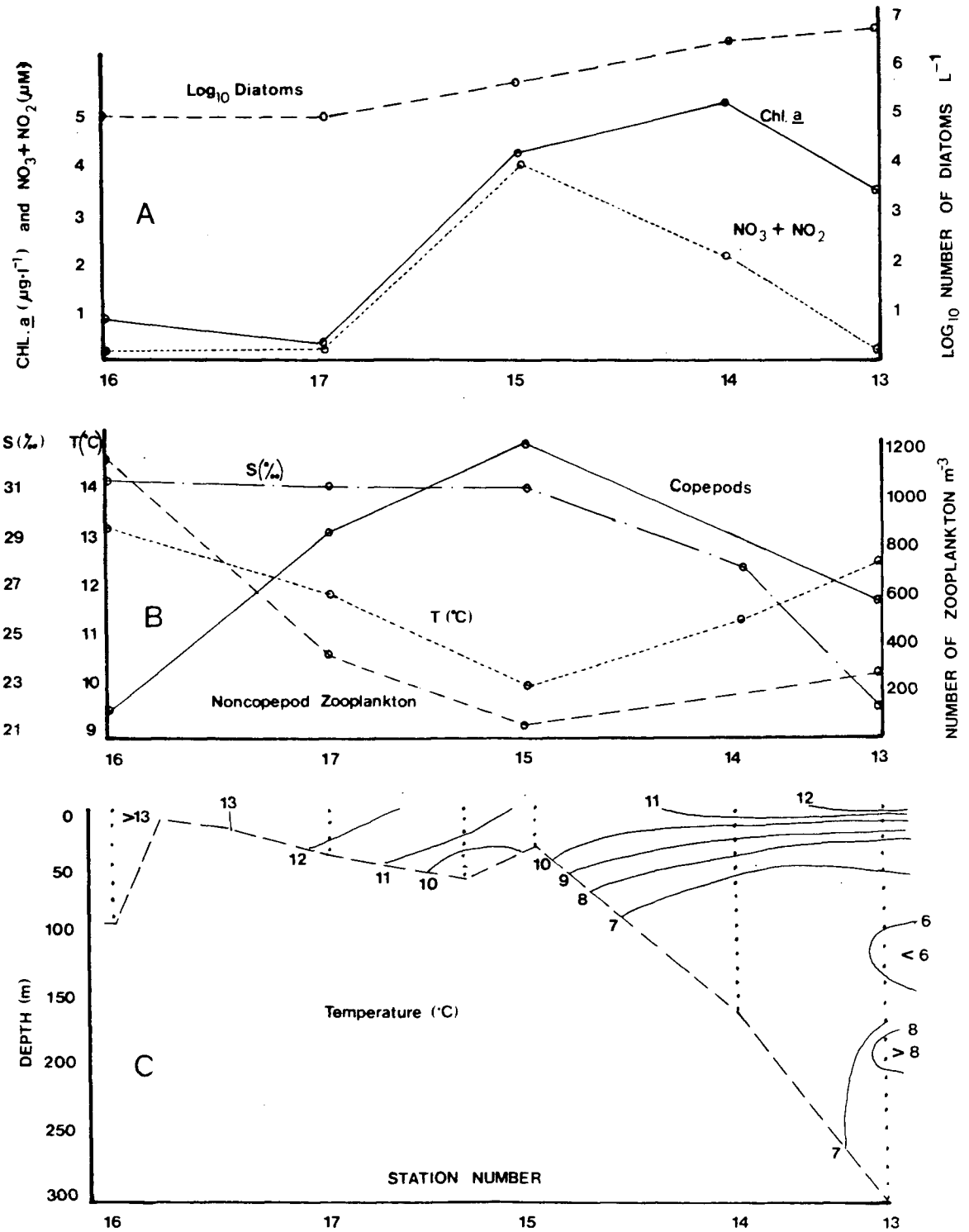

FIGURE 20. Data from Cruise 10, northern transect from Chatham Sound to Sandspit, June 27, 1979. A. Near surface (3 m) chlorophyll *a* ($\mu g\ L^{-1}$), NO_3+NO_2 ($\mu mol\ L^{-1}$), diatoms (log_{10} Number L^{-1}). B. Near surface copepods, other zooplankton (non-copepod zooplankton), salinity and temperature. C. Vertical dots represent XBT temperature profiles; bathymetry is approximated from these profiles.

vertical stratification was first encountered and surface temperature was lowest. The decrease of salinity at the easternmost stations represents the effect of the Skeena and Nass Rivers in Chatham Sound.

Compositional differences of phytoplankton occurred to the east and west of Station 15. Diatoms were <10% (as numbers) of the total phytoplankton on the shelf (Stations 16 and 17), whereas in deeper water at stations 15, 14 and 13 they comprised 31, 57 and 81% respectively. Table VIII presents proportional similarity indices for Cruises 10 and 11 calculated according to Kohn and Riggs (1982) using the number L^{-1} of centric and pennate diatoms at each station. The panel for Cruise 10 (northern transect) indicates the stations can be separated into two groups, Stations 16 and 17 in the western mixed region, and 15, 14 and 13 in the stratified region. The most common diatom at all stations in the transect was *Skeletonema costatum* (<10 μm diameter).

The central transect of Cruise 10 (Fig. 21) resembled the northern transect. Maximum concentrations of chlorophyll and diatoms occurred in the stratified waters of central Hecate Strait adjacent to the western mixed region. *S. costatum* was again the numerically dominant phytoplankton group, although the composition of diatoms varied along the transect (low proportional similarity between Stations 16 and 19, see Table VIII). The influence of the Skeena River was apparent at the eastern end of the transect from low salinity and high nitrate

TABLE VIII. Proportional similarity of stations based on their centric and pennate diatom compositions using the sample-size independent index of Kohn and Riggs (1982):

$$PS_i = 1-0.5\ \Sigma_{i=1}^{s} |P_{x,i} - P_{y,i}|$$

where P*xi* is the proportion of taxonomic group *i* in sample *x*, similarly with P*yi* for sample *y*, and s is the total number of taxonomic categories.

CRUISE 10 (NORTH) - DIATOMS

STN	17	15	14	13
16	0.59	0.46	0.45	0.51
17		0.48	0.54	0.45
15			0.73	0.86
14				0.81

CRUISE 10 (CENTRAL) - DIATOMS

STN	17	18	19
16	0.59	0.46	0.23
17		0.56	0.40
18			0.34

CRUISE 11 - DIATOMS

STN	16	15	14	13
17	0.38	0.30	0.29	0.09
16		0.47	0.41	0.05
15			0.69	0.34
14				0.34

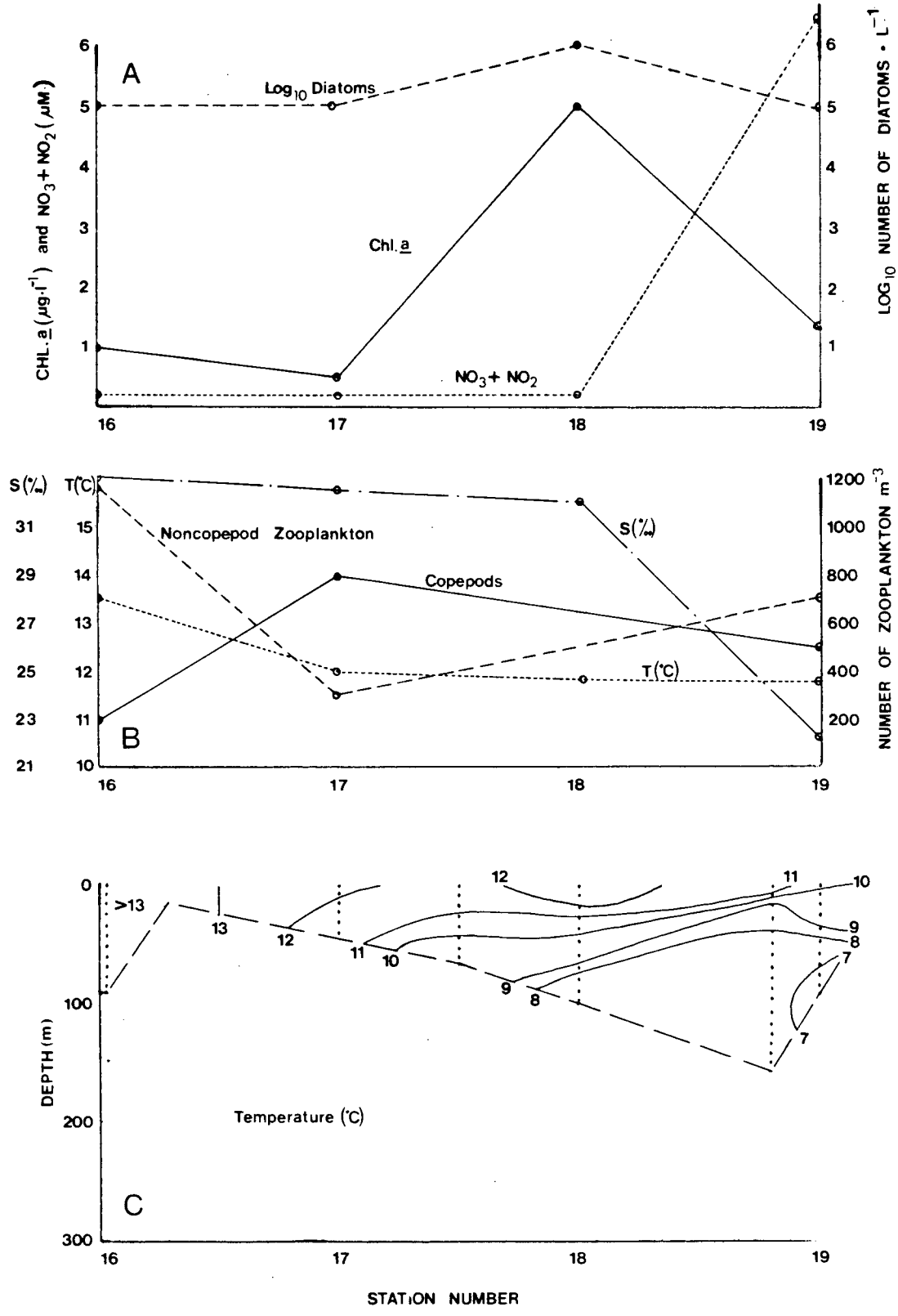

FIGURE 21. Cruise 10, central transect from Sandspit to Prince Rupert, 28 June 1979. Details of A, B, C as for Fig. 20.

concentrations.

In July 1979 (Cruise 11, Fig. 22), diatom and chlorophyll concentrations were lower than the previous month. Nitrate remained low throughout the surface waters of Hecate Strait, except in Chatham Sound near the Skeena River. A strong thermal front apparently occurred at the edge of the western shelf (Fig. 22C) considering the previous month's vertical temperature distribution for the western strait. Diatoms comprised 26% of the total number of phytoplankton at Station 15, 39% in the Skeena River outflow (Station 13), and 10% at all other stations. Stations 14 and 15 in central and east Hecate Strait were most similar in terms of their diatom composition, whereas Stations 17 and 13, at opposite ends of the transect, were least similar (Table VIII).

Data from early June 1980 (Cruise 14, Fig. 23) indicated that chlorophyll and copepods were high in eastern Hecate Strait, although peak concentrations did not occur at the same station. The numerically dominant copepods in Hecate Strait were the same as during Cruise 10 in June 1979. *Acartia longiremus* and *Centropages abdominalis* comprised over 90% of the total number of copepods identified from the stations near the frontal region on these two cruises (data in Perry *et al.* 1981). Non-copepod zooplankton were not abundant except in June 1979 (Cruise 10) and 1980 (Cruise 14) near the Queen Charlotte Islands. In 1979, decapod larvae dominated with over 1100 individuals m^{-3} (97% of the total noncopepod zooplankton),

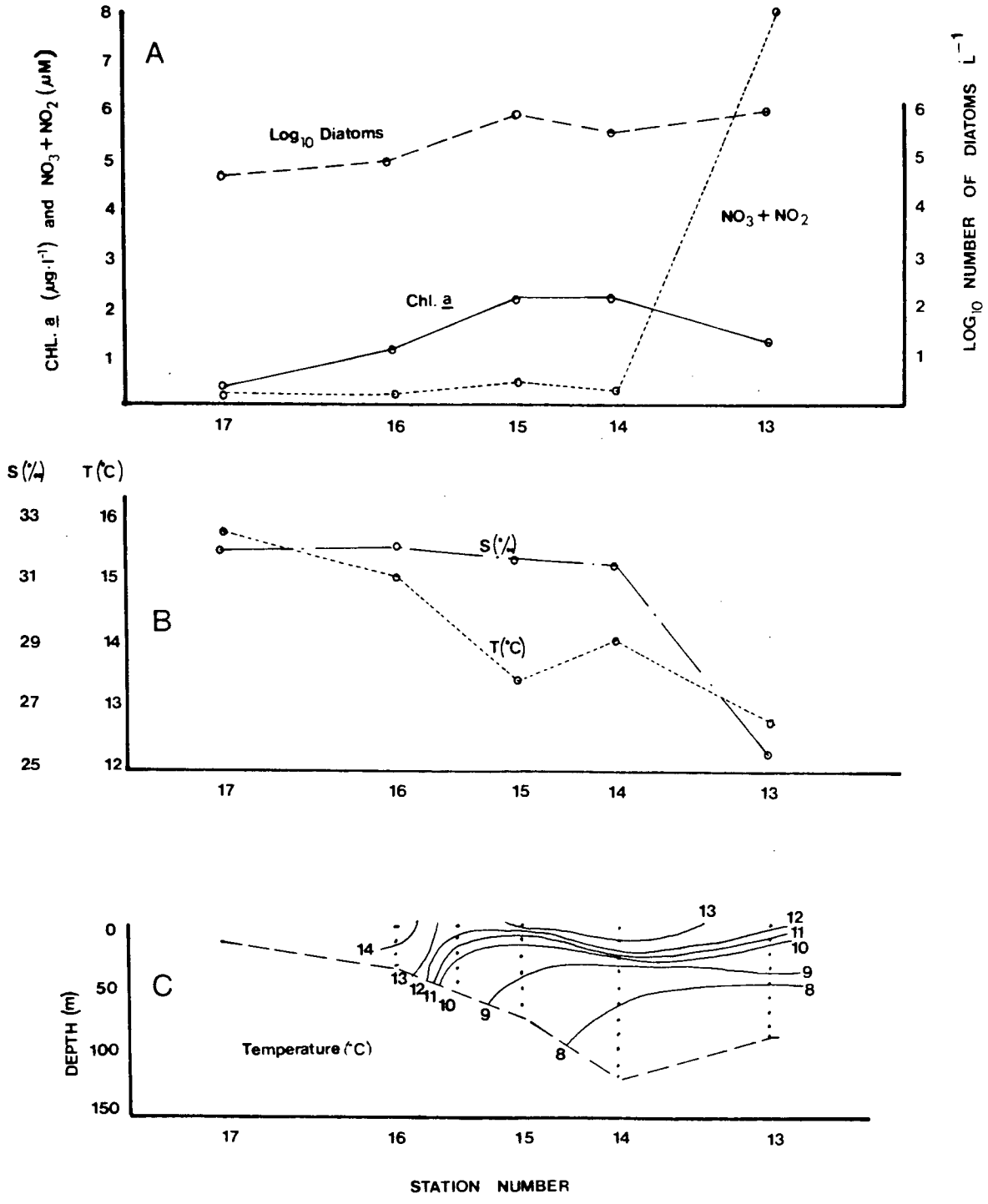

FIGURE 22. Cruise 11, 24 July 1979. Details of A, B, C as for Fig. 20.

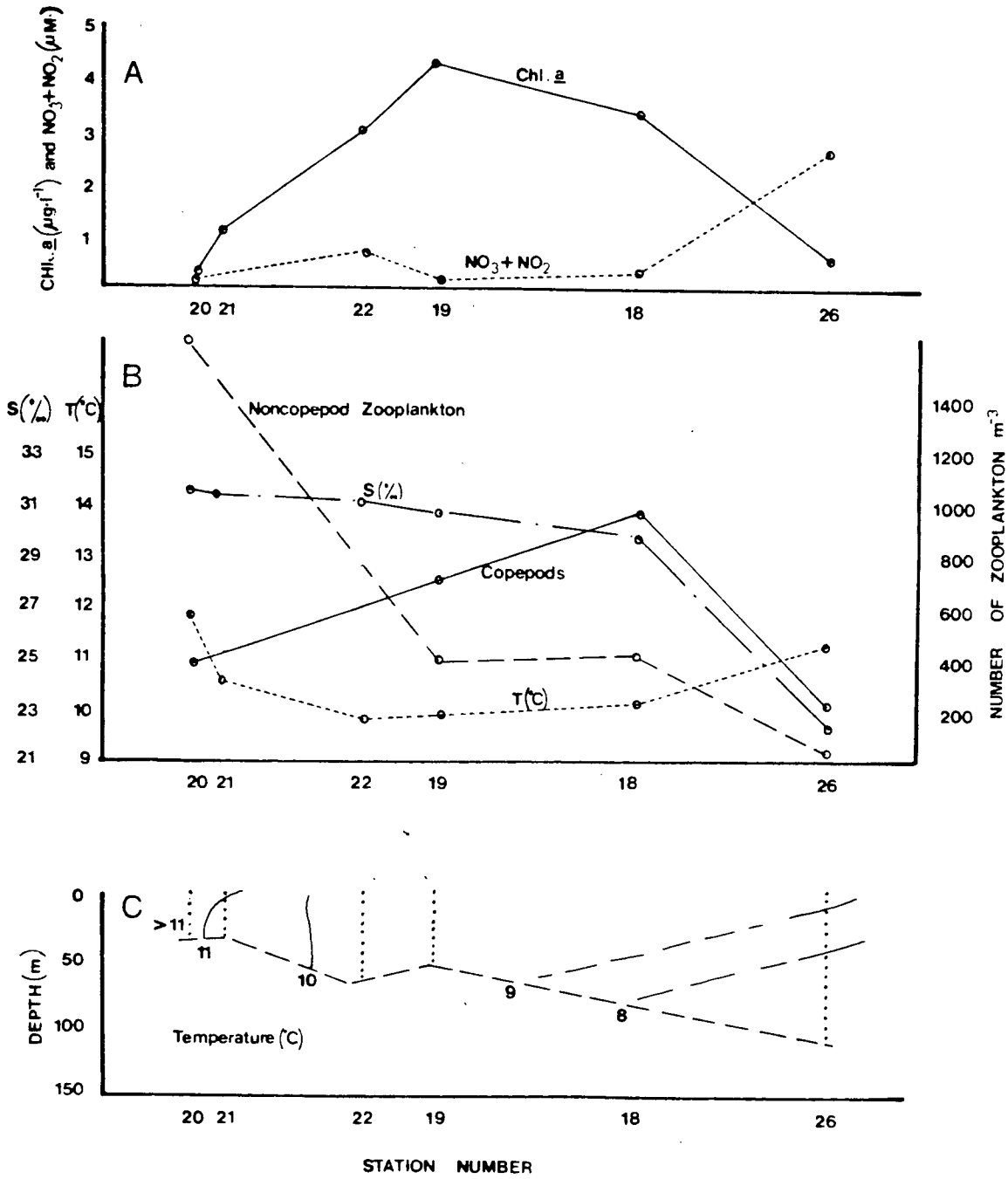

FIGURE 23. Cruise 14, 2-4 June 1980. Details of A, B, C as for Fig. 20.

whereas in 1980 brachyuran zoea were most abundant (98% by number). Brachyuran zoea were still a significant component of the non-copepod zooplankton (35% by number) at Station 19 on the edge of the western shelf in 1980.

Figure 24 presents continuous measurements of horizontal chlorophyll fluorescence, temperature, and approximate bathymetry across central Hecate Strait for Cruise 15 (August 1980). Chlorophyll fluorescence was roughly inversely related to bathymetry and surface temperature, being low over the western shelf and higher to the east. The vertical temperature distribution shows the increase in fluorescence was coincident with the onset of vertical stratification. Note the two major peaks of fluorescence appear to correspond to slightly warmer surface temperatures and increases in the water depth. A continuous transect of chlorophyll fluorescence in June 1980, following the same route, presented similar results. Fluorescence was low over the western shelf, peaked at the western edge of the deep trough, then dropped sharply and remained low to the east of the trough.

The problem of smearing and the inability to resolve small spatial features in horizontal transects using a seachest intake system (discussed in Section III.9.) have been avoided in the presentation of these transects. Typically, ship's speed was 20 km h^{-1} (10 knots), and with a digitizing interval of 3 min this represents a spatial interval of 0.9 km (0.5 nautical miles), within the resolution of such a system.

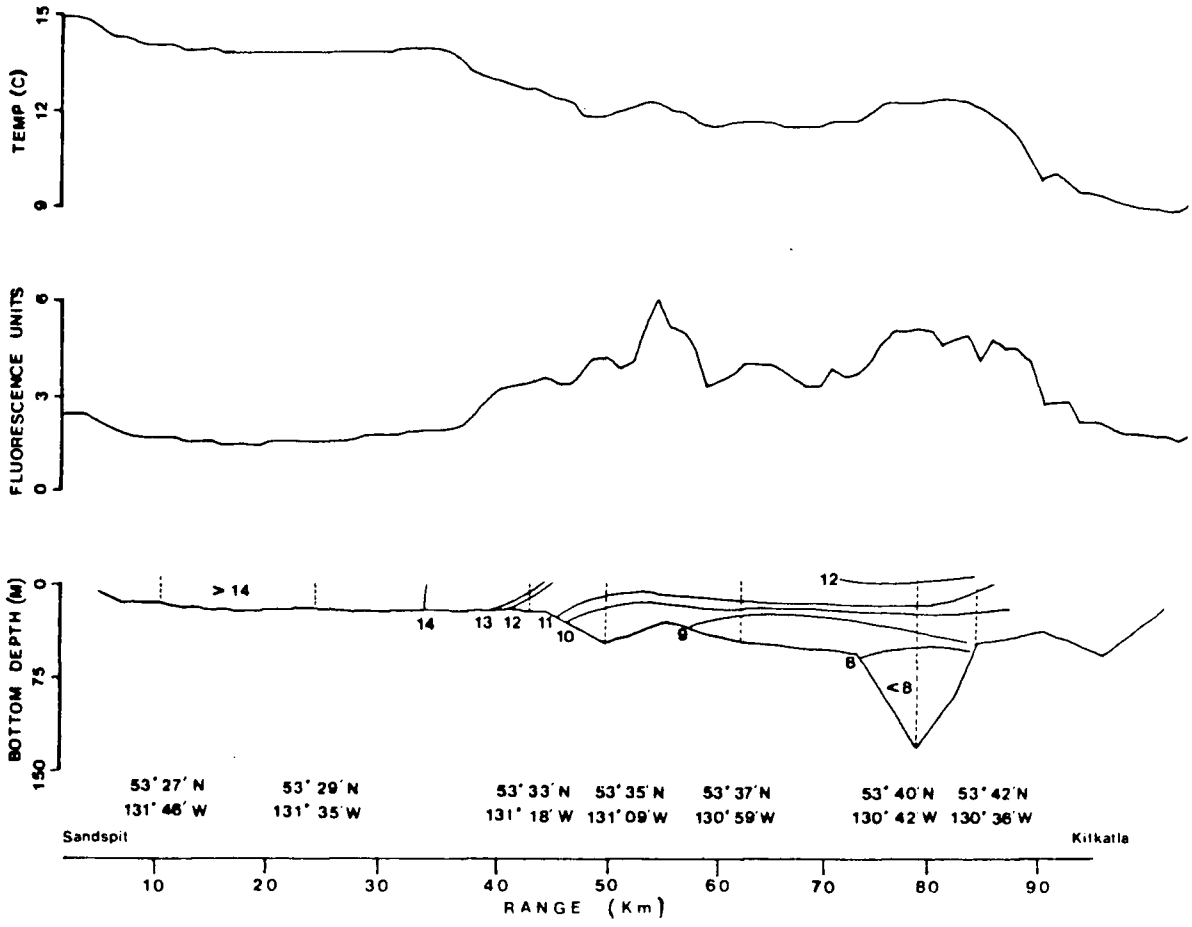

FIGURE 24. Cruise 15, 30 August 1980. Continuous transect from Sandspit, Queen Charlotte Islands, to Kitkatla, indicated on Fig. 15. Top: near surface (3 m) temperature. Middle: near surface relative fluorescence. Bottom: vertical temperature structure (°C) from XBT profiles (vertical dots) and the approximate bathymetry.

D. DISCUSSION

Observations in Hecate Strait in 1979 and 1980 are consistent with the locations of mixed and stratified water masses predicted by the Simpson-Hunter stratification parameter (Fig. 18). Vertical temperature profiles indicate mixed conditions over the shallow western strait and stratified conditions to the east. Chlorophyll concentrations and diatom numbers are lowest in the mixed region, higher in the stratified region, but highest in the central strait with the onset of vertical stratification. This is the transition zone and is expected to have the highest phytoplankton biomass according to the tidal front model. Continuous transects of near-surface fluorescence in June and August 1980 show sharp changes of fluorescence and temperature across Hecate Strait which are likely to indicate locations of fronts within this transition zone.

Zooplankton parallel the pattern for phytoplankton except for the large numbers of decapod and crab larvae sampled in June near the Queen Charlotte Islands. These may be remnants of the spring bloom, which presumably had dispersed or settled to the bottom by midsummer. In this region, crab larvae are known to become free swimming during April, with the larval stage lasting about four months (Butler 1956).

The correspondence between field data and predicted mixing characteristics is found even without considering the effects of

freshwater input. The tidal front model assumes the surface buoyancy flux is due solely to surface heating, but freshwater also increases the buoyancy of the surface layer and reduces the effect of bottom mixing. Hecate Strait is influenced by freshwater in summer, especially from the Skeena River in the north and to a lesser extent along the mainland shore to the east. As noted in the introduction to this chapter, the tidal front model does apply to areas where salinity effects are important, although it may shift the critical value of S. In their study in the Gulf of St. Lawrence, Iles and Sinclair (1982) noted the parameter may indicate relative degrees of mixing in areas with considerable freshwater influence rather than precise locations of fronts. Freshwater added to eastern Hecate Strait would serve to emphasize the effect of stratification, rather than dampen the tidal mixing effect which is dominant over western Hecate Strait.

However, there are two important aspects of the data which are not consistent with the shallow sea tidal front model as presented in the literature. Near surface temperatures were consistently higher on the well-mixed western shelf than in eastern Hecate Strait, often with a minimum in central Hecate Strait at the stations in the frontal zone; and nitrate plus nitrite concentrations on the western mixed side were unusually low for a typical tidal front (see Pingree 1978; Pingree *et al.* 1978).

The simplest explanation for these discrepancies is the very shallow depth of western Hecate Strait. Most of this region is considerably less than 30 m, and well-mixed from surface to bottom according to the vertical temperature profiles. Tabata (1958), in a study of the annual heat budget about Triple Island in eastern Dixon Entrance, has estimated that heat gained by the sea in summer would be sufficient to raise the temperature of a 50 m water column by 0.8°C per month if advective effects were neglected. In western Hecate Strait, this amounts to continually heating the entire water column, whereas eastern Hecate Strait would experience mixing of cooler, deeper water into the stratified layer with the passage of occasional storms. Lower temperatures may also result with the addition of runoff from the mainland shore.

Nutrient concentrations in western Hecate Strait are low because either the region has low nutrients all year, or becomes depleted before summer and remains so until fall. Data in Dilke *et al.* (1979) and Perry *et al.* (1981), and presented in Chapter 4, show that nitrate plus nitrite concentrations in western Hecate Strait in winter (January 1979, February 1980) are between 10 and 20 μM NO_3, decreasing to less than 3 μM NO_3-N during the spring bloom. This rules out the first possibility, and it is therefore suggested ambient nitrate concentrations remain low in summer due to rapid uptake by phytoplankton. This should result in increased phytoplankton (or zooplankton) biomass. However, as measured biomass was low in the western

strait, nutrient supply to this region must be limited, probably by the shallow depth of the shelf and the presence of Graham Island.

The usual tidal mixing model, however, suggests phytoplankton biomass will be low on the mixed side because of lower mean light intensities resulting from deeper vertical mixing. To determine whether phytoplankton in western Hecate Strait are likely to be light limited, the critical depth was calculated. The equation followed Parsons *et al.* (1984), with I_0 (1784 J cm^{-2} d^{-1}) the normal incident solar radiation for June at Sandspit corrected for surface reflection due to sun angle (see Appendix II), and the attenuation coefficient (k) determined as the mean of $1.45/Z_s$ (Walker 1980), where Z_s was the Secchi disk depth measured in western Hecate Strait during June (seven measurements: Strickland 1958, P.O.G. 1959, 1962). The compensation light intensity (I_c = 58 J cm^{-2} d^{-1}, Hobson 1981) was the same as used in Chapter 4. With a mean attenuation coefficient of 0.178 m^{-1} the calculated critical depth for western Hecate Strait in June was 83 m, with a standard deviation of 34 m based on variation in Secchi depth measurements. Data for July indicate similar depths. This is considerably deeper than the depth of the western shelf and suggests phytoplankton will not be light limited in this region. It is also consistent with the observation that in very shallow environments, high mixing may not lead to light limitation of phytoplankton growth (Legendre 1981).

Tidal mixing therefore appears to be a plausible mechanism for promoting mixed conditions over the shallow western region of the strait and stratified conditions on the eastern side. Phytoplankton concentrations were low in summer in both these areas as a result of nutrient limitation. However, nutrients may be mixed sporadically into the surface waters of the stratified region with the passage of local storms. For example, the depth of the wind mixed surface layer can be estimated from the equation (Pond and Pickard 1983)

$$D_E = \frac{4.3\ W}{(\sin|\phi|)^{\frac{1}{2}}}$$

where D_E is the Ekman depth, W the wind speed, and ϕ the latitude. Using a maximum hourly wind speed of 12 m s^{-1} recorded from opposite sides of Hecate Strait (Sandspit and McInnes Island) on August 22, 1980 (Atmospheric Environment Service 1980), the calculated wind mixed layer was about 58 m. Such potential vertical mixing may account for the higher near-surface fluorescence of eastern Hecate Strait apparent in Fig. 24.

Considering the mixed side has low measured nutrient concentrations, what sustains the high plankton biomass in the frontal region of central Hecate Strait? One possibility is the existence of a front between northern Hecate Strait and Dixon Entrance parallel to the rather steep bathymetry. Few nutrient

data are available from this area, although three stations north of Graham Island sampled in July 1979 indicated nitrate plus nitrite concentrations were greater than 1-2 μM, whereas concentrations in Hecate Strait itself were less than 0.5 μM (Fig. 22). The transect from Sandspit through eastern Dixon Entrance to Chatham Sound (Fig. 20) shows anomalously high nitrate at Station 15 near Rose Spit, in the area that frontal activity might be expected.

A second possible source of nutrients for central Hecate Strait surface waters is episodic upwelling along the rapid change of bathymetry from the eastern trough to the western shelf. Such a mechanism has been proposed to account for the high productivity of a front off Nova Scotia (Fournier *et al.* 1977), where nutrient-rich slope water is advected onto the shelf at the shelf break. Sandstrom and Elliot (1984) have estimated that mixing by solitary waves of the internal tide at this shelf break is sufficient to supply the required nutrient flux calculated by Fournier *et al.* (1977). Sandstrom and Elliot (1984) further suggest such interactions of the internal tide with topography are likely to occur at other sites along continental shelves and banks. Denman *et al.* (1981) describe zones of high phytoplankton biomass and productivity on the continental shelf off the west coast of Vancouver Island. They suggest these zones result from advection of nutrient-rich deep water onto the shelf due to the interaction of alongshore currents, including the California Undercurrent, with the

complicated bathymetry of the area. Gardner (1981b) indicated that Pacific Equatorial Water does occur in Hecate Strait using temperature and salinity characteristics and the occurrence of normally subtropical zooplankton species in 1977.

When deep water flows into the trough in eastern Hecate Strait, it may be advected onto the western shelf by upwelling induced by a longshore current, as described by Hsueh and O'Brien (1971) and applied to the southern Nova Scotian coastline by Garrett and Loucks (1976). This upwelling may be aided by tidal mixing effects generating a bottom Ekman (well-mixed) layer along the edge of the shelf.

It is interesting to speculate on the effects a frontal system in central Hecate Strait might have on fish production. Considering the depth of western Hecate Strait, it is reasonable to expect substantial sedimentation of upper layer primary production to the benthos. The amount of material that will sediment to the bottom depends on the water depth, the depth of surface mixing, and the concentration of biomass. More material sediments to the bottom in shallow rather than deep environments (Mills 1980), under shallow mixed layer depths (Hargrave 1973), and when upper layer primary production is high (Parsons *et al.* 1977). In western Hecate Strait, considerable biomass could be expected to sediment to the benthos because of its depth. However, during summer the phytoplankton biomass is evidently low, and mixing may keep such material in suspension for some time.

In the frontal region of the shelf break, the above three criteria appear to be optimal. The water depth is relatively shallow, although as the bathymetry changes rapidly in the east-west direction this depends on location. Mixed layer depths are shallower than over the western shelf, reflecting the onset of vertical stratification, and phytoplankton biomass is relatively high, all suggesting the possibility of considerable transfer of material to the benthos.

Given such a scenario, it is perhaps not surprising to find Hecate Strait is the most productive groundfish region of the B.C. coast, with Pacific cod (*Gadus macrocephalus*) the greatest proportion of the catch. Of all Pacific cod landed from Hecate Strait between 1958 and 1978, 83% were caught along the edge of the western shelf at approximately the 40 m isobath, and at similar depths between Hecate Strait and Dixon Entrance (Stocker 1981).

A potential energy budget for a system similar to that described here, involving shallow depths, tide and wind mixing, and a deepwater nutrient supply, has been outlined by Cohen *et al.* (1982) for Georges Bank. They found that high primary production throughout the summer was able to sustain both high pelagic fish production and high demersal fish production via a pathway through the macro- and micro-benthos. Little is known, however, of the productivity or biomass of benthic organisms in Hecate Strait, and whether they might form a link between high plankton biomass at the front and high groundfish production.

E. SUMMARY

Distributions of plankton, chlorophyll and nutrients were examined across northern Hecate Strait during summer 1979 and 1980 and compared with tidal mixing characteristics. Calculations of the Simpson-Hunter (1974) tidal stratification parameter ($h\ U^{-3}$) indicate most of Hecate Strait and Dixon Entrance are potentially stratified during summer in the absence of excessive wind mixing, with a well-mixed region over the shallow shelf adjacent to the Queen Charlotte Islands. These mixing zones were confirmed by XBT temperature profiles from the *Imperial Tofino*.

Plankton distributions and biomass differed between east and west sides of the strait, consistent with predictions of the tidal mixing model. Near surface concentrations of chlorophyll *a*, nutrients, diatoms, and copepods were lower in the mixed region than the stratified region, but highest in the boundary between these two zones. However, cross-strait nutrient distributions and mean light intensities in the mixed region were not consistent with the tidal mixing model. It is suggested that low phytoplankton biomass in the mixed region is due to nutrient rather than light limitation, while sporadic wind mixing of the stratified region and possible vertical advection along the edge of the western shelf may support the higher biomass of the eastern side and at the front.

VI. MECHANISMS OF SEASONAL PLANKTON BLOOMS IN HECATE STRAIT

A. INTRODUCTION

Coastal regions during summer are richly patterned by biological, physical, and chemical patchiness. Chapter 4 has indicated the B.C. northern shelf can have considerable coarse scale biological and physical heterogeneity, especially during spring and summer. A consequence of such patchiness is the presence of boundaries, which may be either strong or weak. River plumes and tidal fronts are examples of strong boundaries which clearly distinguish different biological and physical characteristics. Weak boundaries can be identified with upwelling zones and the island mass effect (e.g. Simpson *et al.* 1982), where the gradation between different characteristics occurs over larger spatial scales. Coarse scale (10-100 km) patterns of physical and biological characteristics across Hecate Strait in summer were described in Chapter 5, with tidal mixing variations suggested as the principal mechanism.

This interaction of tidal mixing and bathymetry must occur in all seasons, however, its influence on plankton production at times other than summer has not been widely considered. In winter, coastal seas tend to be well-mixed by seasonal winds and with low production due to inadequate light intensities. During spring, the development of the phytoplankton bloom depends upon the formation of the seasonal thermocline and establishment of a

shallow surface mixed layer. Pingree *et al.* (1976) and Fasham *et al.* (1983) describe the development of the bloom in the Celtic Sea, which occurs in April in areas of weak tidal mixing coincident with the onset of temperature stratification. Throughout the seasonal study by Pingree *et al.* (1976), no phytoplankton bloom was observed in tidally well-mixed regions, while Fasham *et al.* (1983) noted that significant variations in the rate of development of the bloom could occur on horizontal scales of the order of 50 km.

However, the question of whether a bloom will be produced at any time is not a matter solely of the intensity of mixing. Rather, it is the effect of such mixing on the light and nutrients available to the phytoplankton. The tidally well-mixed region may experience a spring diatom bloom if some mechanism exists which provides higher light intensities before the onset of seasonal stratification. Similarily, the stratified region may bloom during summer if nutrients are added to the surface mixed layer from some external source.

In this chapter I examine the seasonal patterns of phytoplankton biomass, taxonomic composition, and spatial organization across Hecate Strait, and consider whether the coarse scale differences apparent in summer (Chapter 5) are maintained during winter and spring. Physical mechanisms organizing the observed patterns are proposed, and the seasonal importance of tidal mixing variations to plankton dynamics in Hecate Strait is discussed.

B. METHODS

Data were collected as described in Chapter 3, with station locations for Cruises 12 and 13 indicated on Fig. 25. Phytoplankton abundance estimates have been converted to a biomass index using a relative size coefficient as described in Chapter IV.B.2. Identified taxonomic groups, mean abundances from Hecate Strait samples, and their relative size coefficients for cruises in winter, spring, and summer are presented in Table IX. Histograms of relative composition of major taxa (Fig. 28) were calculated by separating stations from each cruise into eastern and western regions based on bathymetry and geographic location, then calculating the weighted biomass percent of that taxon in all samples from that area for that cruise. Thus (after Mackas and Sefton 1982)

$$\text{weighted \% all samples} = (\Sigma_{j=1}^{N} B_{ij}) / (\Sigma_{i=1}^{P} \Sigma_{j=1}^{N} B_{ij}) * 100$$

where N is the number of stations in that region for that cruise, P the number of taxonomic groups, and B_{ij} the estimated biomass index (abundance*size coefficient) of taxon i in sample j. Data for Station 24 of Cruise 13 (April 1979) have been left out of the histogram calculations as flagellate counts were incomplete.

In order to compare taxonomic composition between stations, and to obtain a distance measure of composition for use in the

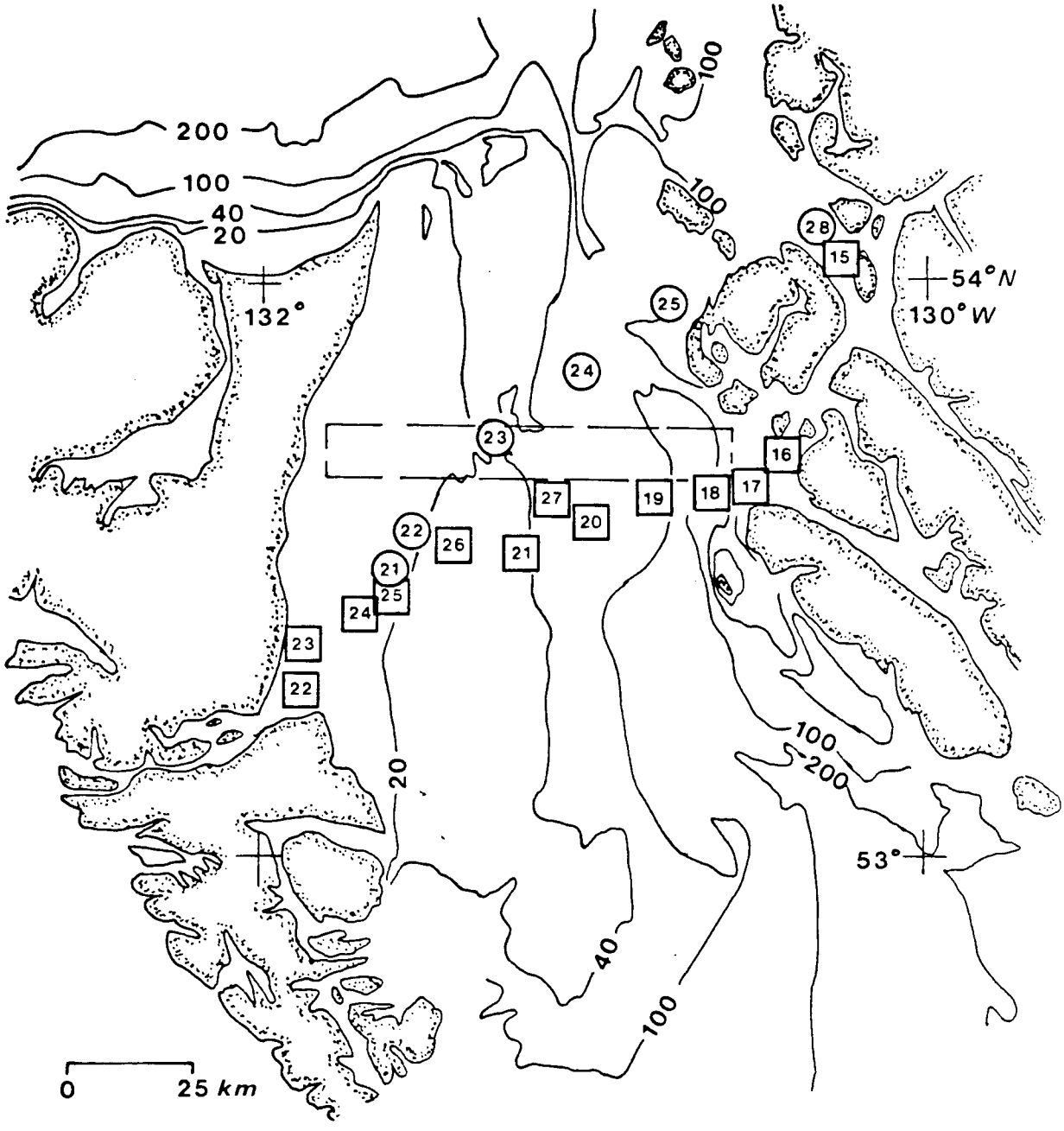

FIGURE 25. Hecate Strait bathymetry (depths in meters) and station locations for Cruise 12 (squares) and Cruise 13 (circles). Dashed box across Hecate Strait indicates the area averaged for the satellite zonal IR brightness section.

TABLE IX. Phytoplankton taxonomic groups, relative size coefficients and mean abundances for Cruises 10 (June 1979), 12 (Feb. 1980) and 13 (April 1980).

TAXA	REL. SIZE COEF.	MEAN ABUNDANCE per 0.1 mL		
		10	12	13
Bacteriastrum delicatula	2.0	0.13	-	
Biddulphia spp.	5.0	-	-	0.06
Cerataulina bergonii	2.5	0.15	-	
Chaetoceros spp. (4-15 μm)	0.9	7.45	0.03	40.30
Chaetoceros spp. (16-25 μm)	2.0	2.93	-	7.89
Corethron hystrix	2.5	-	-	0.12
Coscinodiscus spp.	2.5	-	0.02	0.68
Coscinodiscus spp. (>50 μm)	5.0	-	-	0.12
Ditylum brightwellii	4.5	-	0.01	0.13
Lauderia borealis	3.0	-	-	1.14
Leptocylindrus danicus	1.5	-	-	0.09
Melosira spp.	3.5	-	0.07	0.01
Rhizosolenia delicatula	2.0	0.85	-	1.17
R. fragilissima	3.0	-	-	0.27
R. setigera	2.5	0.25	-	
R. stolterfothii	3.0	0.04	-	1.62
Skeletonema costatum (<10 μm)	1.0	12.26	0.28	6.24
S. costatum (>10 μm)	3.0	13.44	-	3.03
Stephanopyxis palmeriana	5.0	-	-	0.33
Thalassiosira spp. (5-20 μm)	1.2	0.15	0.41	1.11
Thalassiosira spp. (21-40 μm)	3.0	0.31	0.17	1.38
Thalassiosira spp. (41-60 μm)	5.0	0.04	-	0.18
Asterionella japonica	2.0	0.04	-	0.54
Nitzschia delicatissima	1.5	0.23	0.04	
N. longissima	2.0	-	0.09	0.35
N. pungens	2.0	1.40	-	
Thalassionema nitzschiodes	2.5	0.12	0.04	0.59
Ceratium lineatum	4.5	0.04	0.01	
Peridinium spp.	5.0	-	-	0.38
unid. dinoflagellates (16-50 μm)	3.0	0.19	-	0.25
unid. flagellates (<5 μm)	0.2	55.25	12.06	50.95
unid. flagellates (6-15 μm)	1.0	12.72	3.03	13.21
Distephanus speculum	2.0	-	0.01	0.08
Microzooplankton	3.0	0.32	0.04	0.15

clustering routine. I calculated a version of the euclidean distance dissimilarity metric (Orloci 1978, Legendre and Legendre 1979)

$$e(j,k) = [\ \Sigma_i\ (B_{ij} - B_{ik})^2\ ]^{\frac{1}{2}}$$

with B, i, j, k as defined below. However, as discussed by Mackas and Sefton (1982), to isolate compositional patchiness from biomass patchiness it is first necessary to normalize this distance measure to biomass. This chord distance was calculated directly by (Orloci 1978)

$$C(j,k) = \{2(1-q_{jk}/(q_{ii}\ q_{kk})^{\frac{1}{2}})\}^{\frac{1}{2}}$$

with $q_{jk} = \Sigma_i\ B_{ij}\ B_{ik}$, $q_{ii} = \Sigma_i\ B^2_{ij}$, and $q_{kk} = \Sigma_i\ B^2_{ik}$ where B is the biomass index, i represents each taxon, and j and k represent the station pairs being considered. In this form, $C(j,k)$ represents the normalized chord distance of taxonomic composition between stations j and k, with values ranging from 0 for station pairs with identical proportions of biomass in each taxon, to $\sqrt{2}$ for complete dissimilarity. This chord distance measure has the advantage of being a multivariate analog (Mackas 1984) of the structure function for spatial autocorrelation.

Chord distances were also used to cluster stations across time and space on the basis of taxonomic composition. The NT-SYS Numerical Taxonomy System of Multivariate Statistical Programs

(Rohlf, J. F., J. Kispaugh and D. Kirk. 1980. Dept. of Ecology and Evolution, State University of New York, Stony Brook, N.Y.) TAXON routine was used for the analyses following the unweighted pair-group method using arithmetic averages (see Sneath and Sokal 1973 for details).

To estimate coarse scale spatial variability across Hecate Strait, I used the spatial structure function concept. It is a measure of the mean square difference of the value of a variable at several spatial separations (see e.g. Wyrtki 1967, Lutjeharms 1981, Deschamps *et al.* 1981)

$$D(h) = \frac{1}{n} \Sigma^{n} [f(X+h) - f(X)]^2$$

where f is some property that varies as a function of distance X, h is the spatial separation scale, and n the number of data pairs at that scale. Where the estimated structure function is reasonably flat, no strong spatial features would be expected. However, where the structure function shows a peak, it distinguishes specific features or exchanges of energy (Deschamps *et al.* 1981) at that scale. The advantage of using the structure function rather than spectral density curves is that assumptions of stationarity and regular spacing of the data are not as rigorous. Deschamps *et al.* (1981) recommend detrending the data before calculating structure functions if the field is inhomogeneous. The *Tofino* data show consistent trends across the strait which have been removed using a least

squares linear fit.

Critical depths, mixed layer depths, and mean bottom depths were calculated by month to determine the phytoplankton growing season separately for east and west Hecate Strait. Surface mixed layer depths were calculated from σ_t - depth profiles collected on cruises to the region from 1954-1971 following the procedure described in Chapter 4. Critical depths were also calculated as described in Chapter 4, using for I_0 the normal daily solar radiation values for each month as measured at Sandspit airport.

C. RESULTS

1. FIELD DATA

Chapter 5 has described typical plankton distributions across Hecate Strait in summer and their correspondence with zones of tidal mixing and stratification. However, distributions in spring showed quite a different pattern (April 13-14 1980; Fig. 26). Concentrations of chlorophyll *a* and diatoms were highest, and nutrients lowest (as represented by NO_3+NO_2), on the western well-mixed side of Hecate Strait. Although low in chlorophyll, Station 21 adjacent to Graham Island had the highest phaeopigment (2.66 μg L^{-1}) and diatom concentrations of any station on this cruise. Zooplankton were more abundant in western than central Hecate Strait, with up to 244 zooplankton m^{-3} at Station 22 compared to 80 m^{-3} at Station 24. Species composition also varied, with *Neocalanus pacificus*,

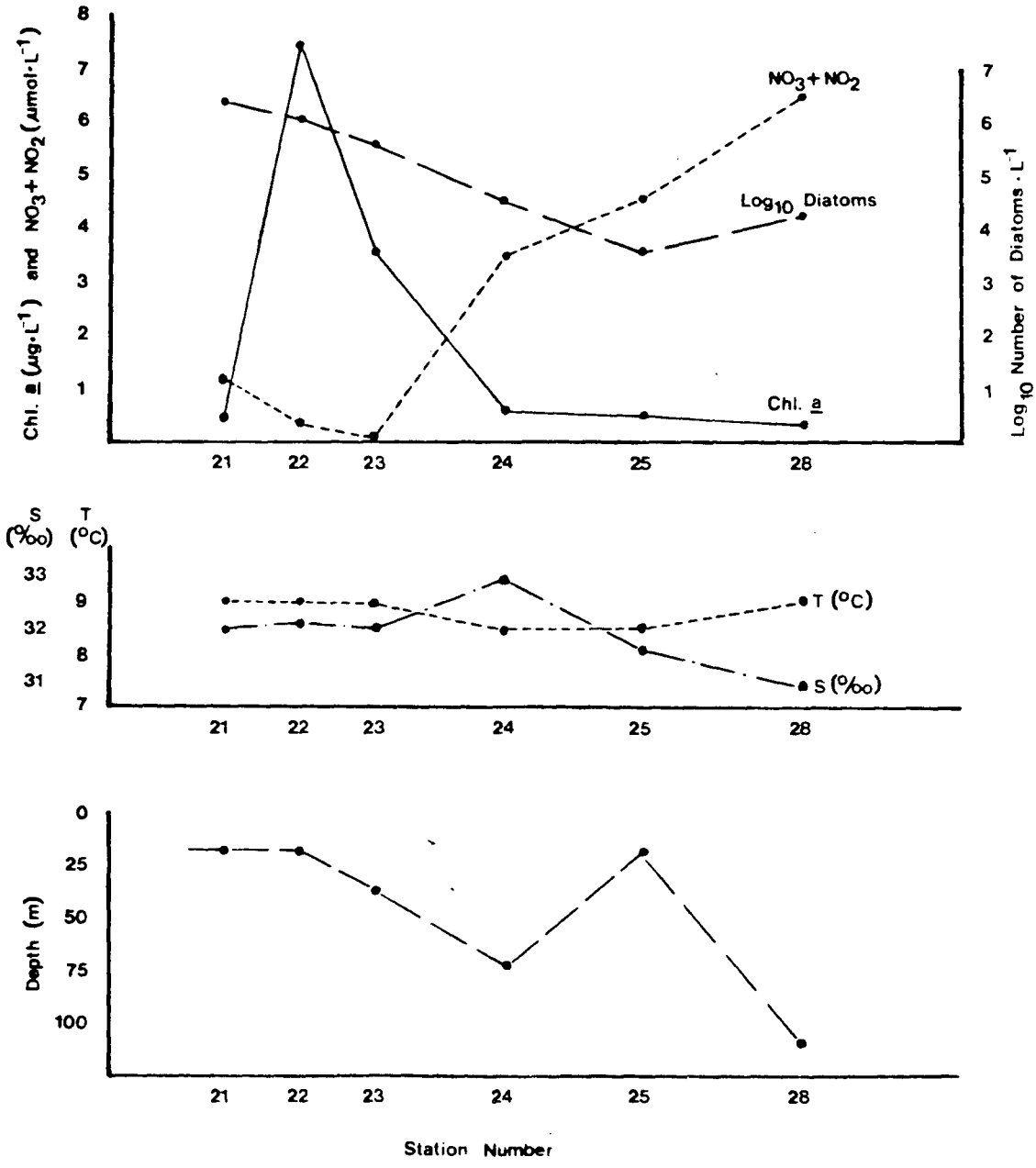

FIGURE 26. Discrete station data for Cruise 13 (13-14 April 1980) across Hecate Strait. Station locations as in Fig. 25. Top: 3 m chl. *a*, NO_3+NO_2, diatom abundance; Middle: 3 m temperature and salinity; Bottom: maximum depth at each station.

Pseudocalanus minutus, euphausiid larvae and brachyuran zoea all abundant numerically at Station 22, while *Metridia pacifica* was abundant at Station 24. It is apparent spring bloom conditions prevailed in western Hecate Strait at this time.

During winter (February 3-4 1980, Fig. 27), biological characteristics also differed between east and west Hecate Strait. Diatom concentrations were low across the strait, while chlorophyll was significantly ($p<0.05$) greater in western (mean 0.23 $\mu g\ L^{-1}$) than eastern (mean 0.12 $\mu g\ L^{-1}$) regions. Zooplankton were also low with $<6\ m^{-3}$ at Station 27 in mid-strait. These chlorophyll differences are rather surprising considering average wind speeds in winter are 7-10 $m\ s^{-1}$, which would be expected to ensure reasonably well-mixed conditions.

2. PHYTOPLANKTON TAXONOMIC COMPOSITION

Phytoplankton taxonomic composition was also different between the eastern and western sides of the strait during these three seasons. In winter (Fig. 28A), the total biomass index of phytoplankton in the western region (normalized per station) was twice that in the east, with a significant contribution by diatoms, especially *Thalassiosira*. In the eastern strait, the relative biomass of this genus was considerably less.

In spring (Fig. 28B), phytoplankton composition across the strait showed the same trend as during winter, although with much greater diatom biomass which agrees with the bloom conditions suggested by Fig. 26. The normalized phytoplankton

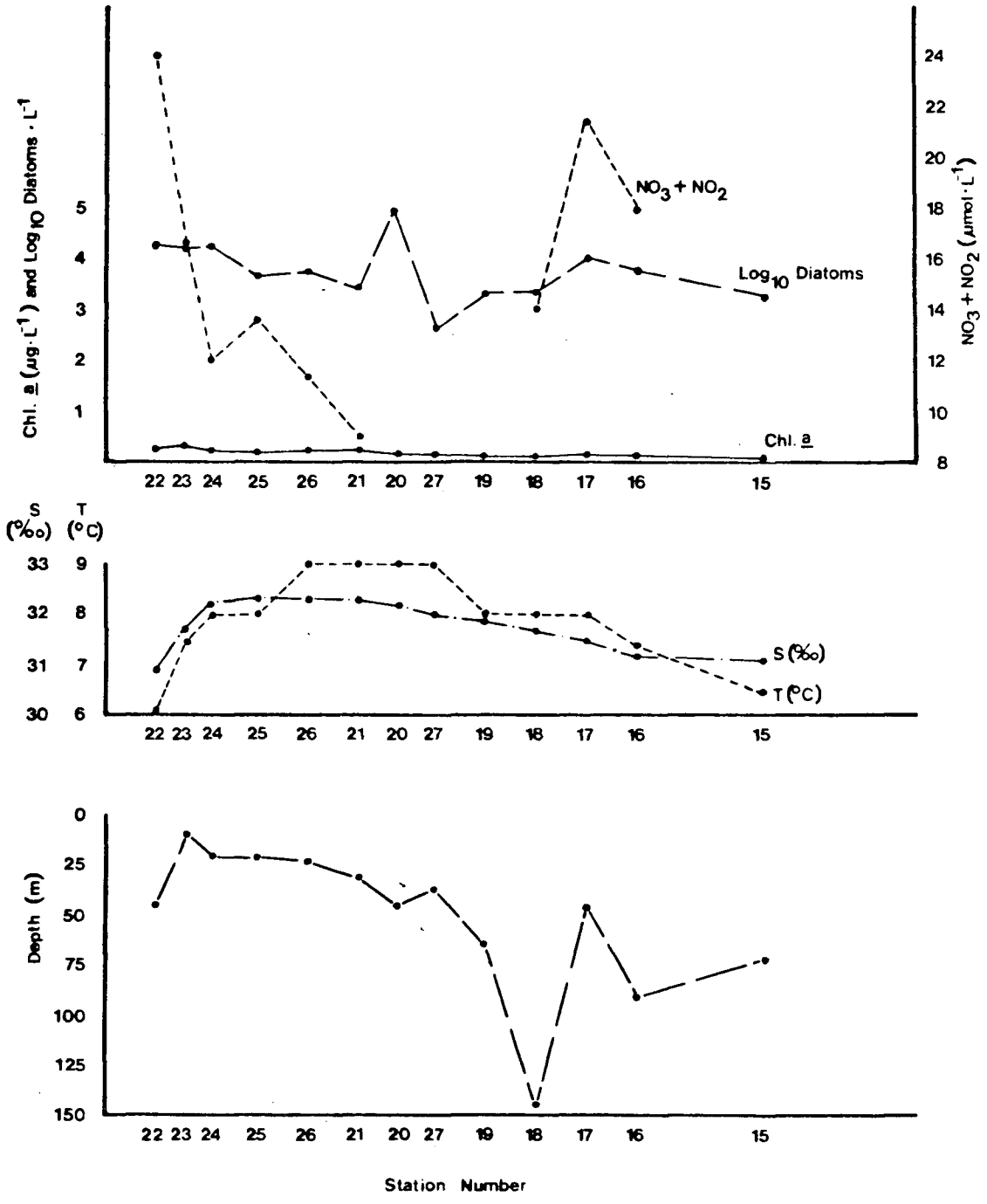

FIGURE 27. Discrete station data for Cruise 12 (3-5 February 1980) across Hecate Strait. Station locations as in Fig. 25. Top: 3 m chl. *a*, NO_3+NO_2, diatom abundance; Middle: 3 m temperature and salinity; Bottom: maximum depth at each station.

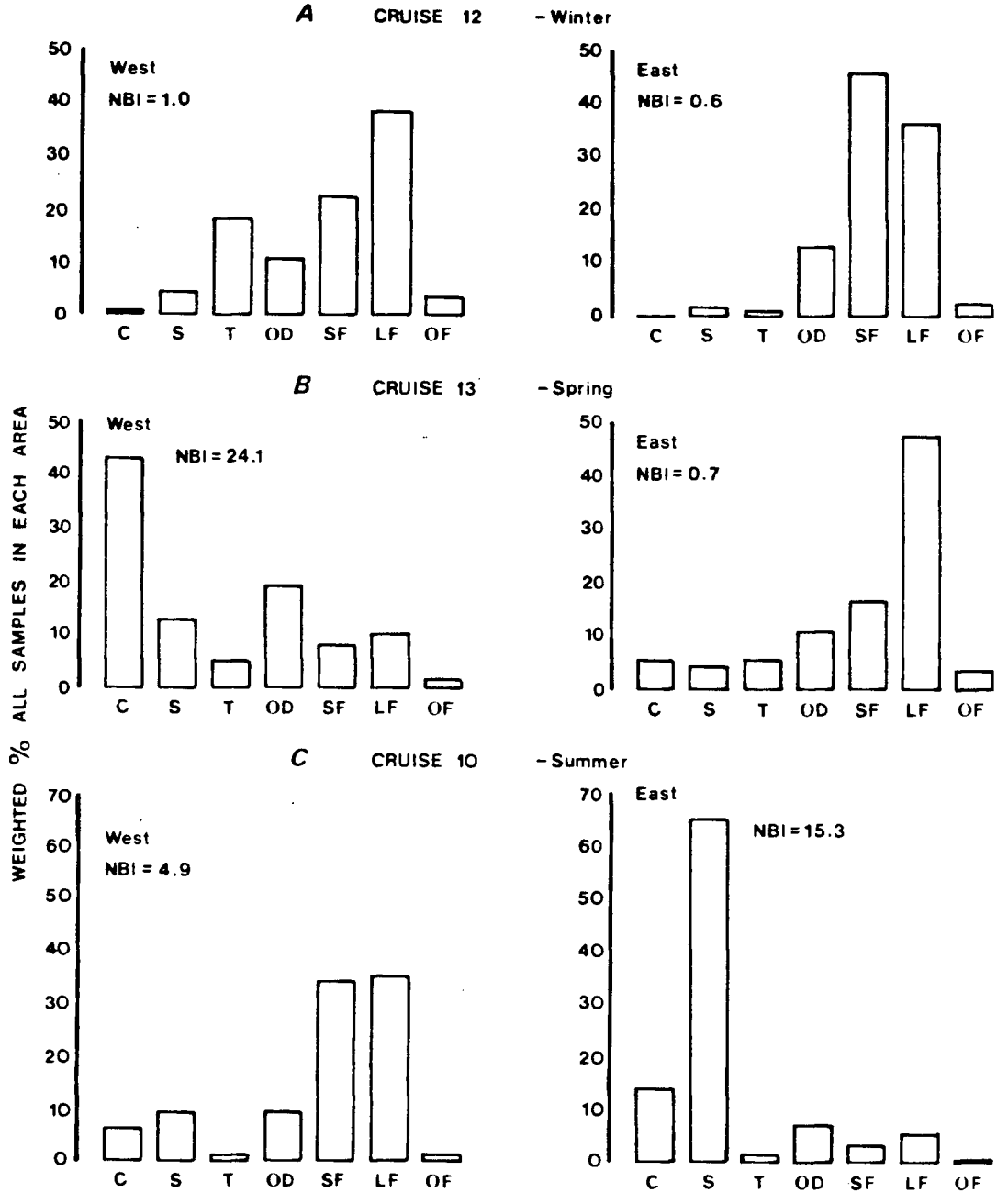

FIGURE 28. Phytoplankton taxonomic composition histograms for east and west Hecate Strait during winter 1980 (A), spring 1980 (B) and summer 1979 (C). See text for discussion of weighted biomass index calculated from abundance and relative size. NBI: Normalized (per station in each area) Biomass Index ($x10^5$); C: *Chaetoceros* spp.; S: *Skeletonema costatum*; T: *Thalassiosira* spp.; OD: other diatoms; SF: small flagellates (<5 μm); LF: large flagellates (6-15 μm); OF: other flagellates (including dinoflagellates).

biomass index in the west was over 35 times that in the eastern strait. There had been a twenty-fold increase of total biomass in western Hecate Strait between winter and spring which coincided with a shift from *Thalassiosira* to *Chaetoceros*. Hollibaugh *et al*. (1981) have noted species of *Chaetoceros* can form resting spores under adverse conditions of light, nutrients or grazing, and that successful germination of these spores is initiated by light intensities ≥100 $\mu E\ m^{-2}\ s^{-1}$ ($=2 \times 10^{-3}\ J\ cm^{-2}\ s^{-1}$ using the conversions in Strickland (1958b) and λ=550 nm) at a temperature range of 7°C to 21°C. Such light and temperature ranges occur in western Hecate Strait at the start of the spring bloom (see Fig. 34). Eastern Hecate Strait remained dominated by flagellates and at the same biomass index as that during winter.

During summer the taxonomic composition pattern was opposite to that during winter and spring. Western Hecate Strait had become the flagellate-dominated region while the stratified eastern side was dominated by diatoms, specifically *Skeletonema costatum* (Fig. 28C). According to Turpin and Harrison (1979) the observed spring-summer switch from *Chaetoceros* to *Skeletonema* is predictable if nutrient (specifically NH_4) patchiness increases, as might occur on the eastern side with sporadic storm mixing of deeper water to the surface. Between June and July 1979 (Cruises 10 and 11), the normalized biomass index for both western and eastern regions approximately doubled, apparently due to an increase of small flagellates. Absolute diatom biomass in the western region decreased between these two cruises, while little

change occurred in the east.

3. SEASONAL COMPOSITION PATTERNS

Phytoplankton composition patterns between seasons and between regions can be examined by clustering stations using their taxonomic chord distances. The resulting cluster phenogram is presented in Fig. 29. Several distinct clusters form at chord distances less than 0.90. Cluster I groups stations in western Hecate Strait during winter, but includes the two spring stations in eastern Hecate Strait. This suggests phytoplankton taxonomic composition during spring in the eastern strait and winter in the western strait were similar, possibly resulting from comparable mixing and light characteristics. Cluster II is composed of stations located in the eastern region during winter, mainly flagellate-dominated with little contribution of diatoms to total biomass, while Cluster III is distinctly the spring bloom stations of western Hecate Strait.

Cluster IV groups stations sampled during summer, but distinguishes two sub-clusters at chord distances less than 0.65. Sub-cluster IVa is formed by three stations in the boundary or frontal region of Hecate Strait between the stratified eastern and mixed western regions, as outlined in Chapter 5. Cluster IVb is formed by stations from Chatham Sound and eastern Dixon Entrance. Note the two summer cruises in June and July 1979 are not separated on the basis of their taxonomic composition. Stations in western Hecate Strait do not form a

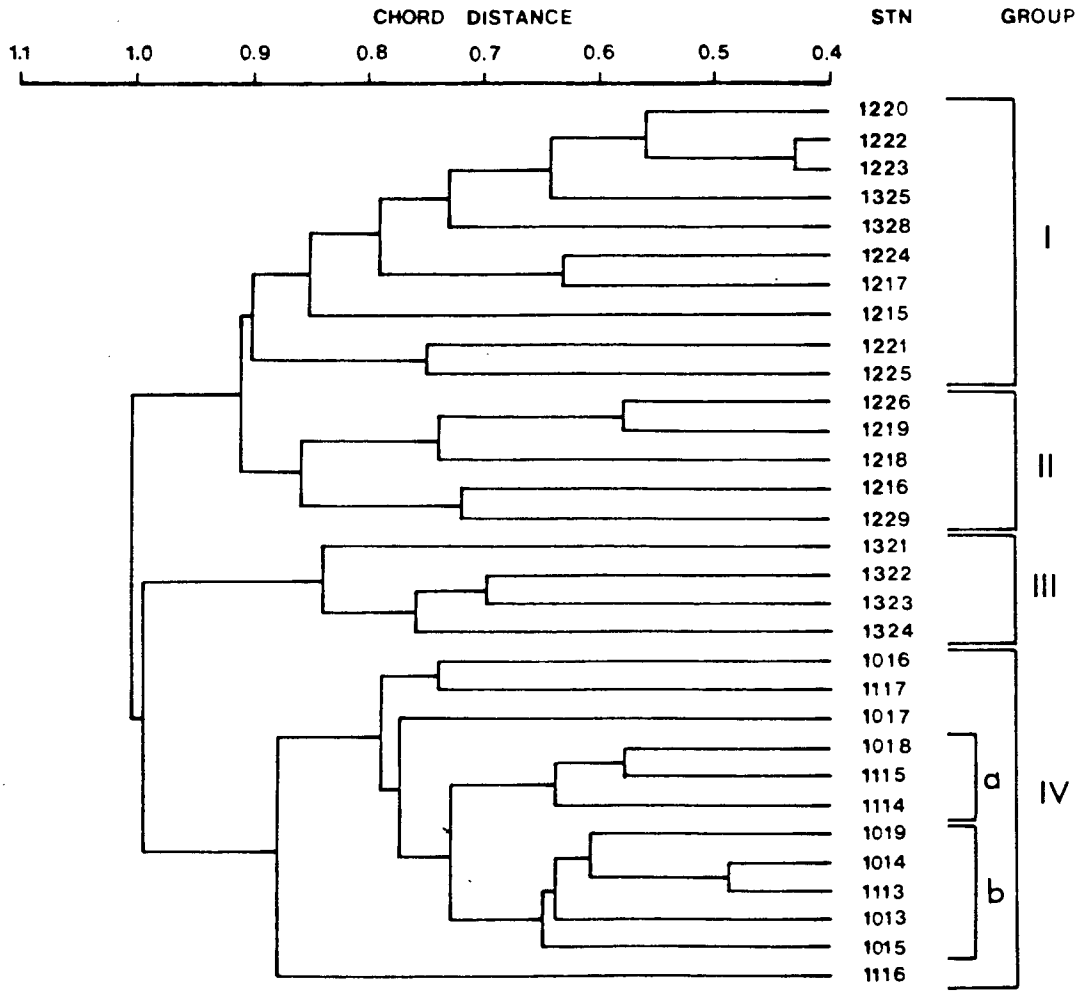

FIGURE 29. Cluster phenogram of stations sampled in Hecate Strait during summer 1979, winter and spring 1980 using chord distances calculated from phytoplankton taxonomic composition. Stations are identified by cruise number (first two digits) then station number. Groups have been assigned from a chord distance of 0.90.

distinct cluster, instead joining sub-clusters IVa and IVb individually.

4. SPATIAL SCALE ESTIMATES

Physical and biological parameters across Hecate Strait will vary on scales consistent with their underlying organizing mechanisms. Any similarity of scales between seasons suggests such mechanisms may be regular features of the region with predictable effects. Sea surface infrared (AVHRR) data measured across Hecate Strait during late summer (12 September 1980) by the TIROS-N satellite (Fig. 30A) show a marked temperature front 30-40 km from the Queen Charlotte Islands, indicating cooler water in mid-strait. Another front is located about 80 km from the western shore. Note that IR brightness values are inversely related to temperature such that warmer water registers as darker shades. Pixels were averaged meridionally across an 80x10 km box (see Fig. 25) to produce this zonal series of brightness values.

Near surface temperature and fluorescence data collected on a transect across Hecate Strait two weeks prior to the image of Fig. 30 are presented in Chapter 5 (Fig. 24). It clearly shows this decrease of temperature and an increase of fluorescence 30-40 km from the Queen Charlotte Islands, coincident with the transition from mixed to stratified water masses. However, fluorescence continued to increase with distance, peaking in mid-strait 60 km from the western shore.

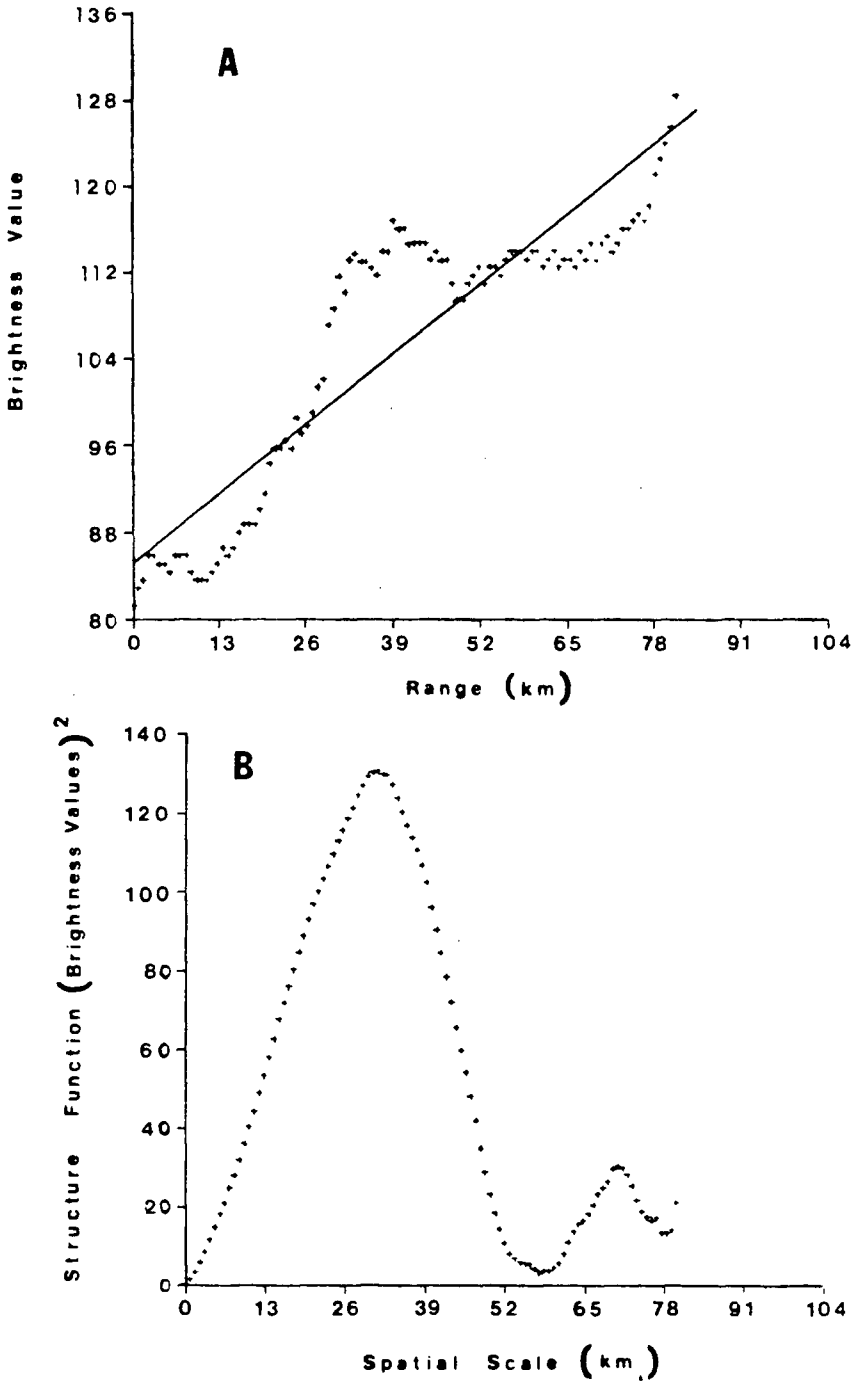

FIGURE 30. TIROS-N (orbit number 9882) AVHRR sea surface infrared brightness values across Hecate Strait on 12 Sept. 1980. A. Zonal section of averaged values from the boxed area in Fig. 25. Line is the linear least square fit to detrend the data. B. Structure function estimates from the detrended data in A.

During spring, Fig. 26 indicates warmer water occurred in the western strait, with a decrease of temperature between 40 and 70 km coincident with the decrease of phytoplankton biomass. Infrared brightness data collected by the NOAA-7 satellite during spring (25 March) 1983 indicate a pattern very similar to that of Fig. 30A. Relatively warm water occurred in western Hecate Strait, with an abrupt transition to cooler water approximately 50 km from the western edge of the strait, followed by another front at 70 km. Although recorded three years later, the pattern resembles the transect data of Fig. 26.

These scales for temperature and fluorescence are also indicated by structure functions calculated from the original data. The structure function derived from a sine (or cosine) wave will have a trough at λ and a peak at $\lambda/2$. Detrending the satellite data produces an approximate sine wave, suggesting for the TIROS brightness data (Fig. 30B) the trough at 60 km represents λ, with peak variability at 30 and 70 km during summer. Calculations of structure functions for the continuous transect temperature data of Fig. 24 and spring 1983 NOAA-7 brightness data show wavelengths and peak variability at scales similar to Fig. 30B. The continuous transect fluorescence data of Fig. 24 shows different scales of variability however (Fig. 31). The wavelength of the detrended series is estimated to be 100 km, which approximates the distance across northern Hecate Strait, with peak variability at a scale of 60 km.

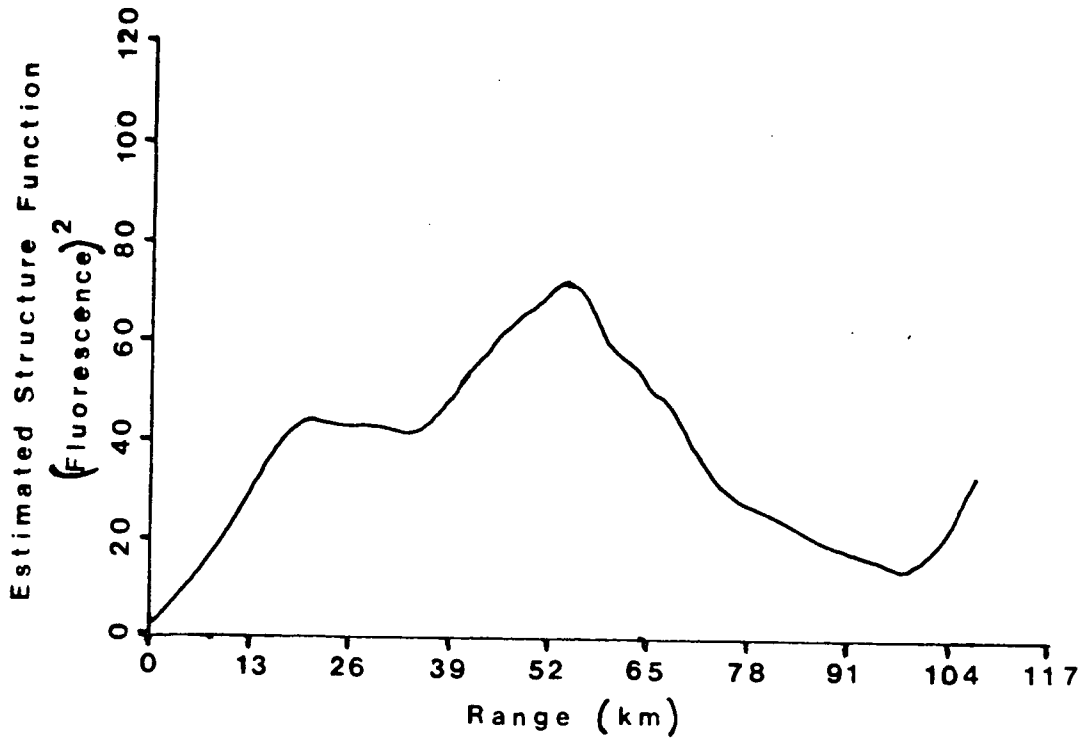

FIGURE 31. Structure function estimates of continuous 3 m fluorescence across Hecate Strait measured on 30 August 1980. Original data shown in Fig. 24.

Continuous data are not available for the winter and spring cruises, so structure functions were estimated by grouping station pairs into categories based on their separation distances. Results are presented in Table X, where a large change suggests spatial variability at that scale. Estimates for summer (Cruise 11) generally agree with the broad spatial scales of temperature and chlorophyll suggested by the satellite and transect data collected one year later. Especially noteworthy is the apparent structure of diatom biomass at scales >60 km which does not appear in flagellate biomass. Differences of spatial organization between these groups have also been noted by Farmer *et al.* (1982) for the winter-spring phytoplankton bloom in Narragansett Bay. In spring (Cruise 13), neither chlorophyll nor the diatom biomass index show any apparent structure at large scales after the removal of the strong cross-strait trends. This suggests the edge of the spring bloom is rather diffuse, compared with the marked tidal front that occurs during summer.

5. RELATION TO BATHYMETRY

The bathymetric profile for the transect from Lawn Point (Graham Island) to Browning Entrance (Fig. 24) is shown in Fig. 32. The shallow (western) and deep (eastern) regions are clearly indicated, with the edge of the shelf occurring in mid-strait at about 50 km. The precise dimension of the shelf varies with location, but 50-60 km from the Queen Charlotte Islands is typical.

TABLE X. Estimated structure functions for parameters measured at discrete stations and grouped into distance categories. Cruise 11, July 1979; Cruise 13, April 1980. Distance categories are in km.

	CRUISE					
	11			13		
	20-40	40-60	>60	20-40	40-60	>60
Number of Pairs	3	3	4	5	4	5
Temperature	0.94	0.16	0.23	0.10	0.25	0.10
Chlorophyll	0.70	0.83	0.66	6.72	9.51	12.03
Log_{10} Flagellate Biomass Index	0.13	0.11	0.14	0.03†	0.02‡	0.01
Log_{10} Diatom Biomass Index	0.16	0.31	0.63	0.60	0.51	0.66

† Number of station pairs = 3 ‡ Number of station pairs = 1

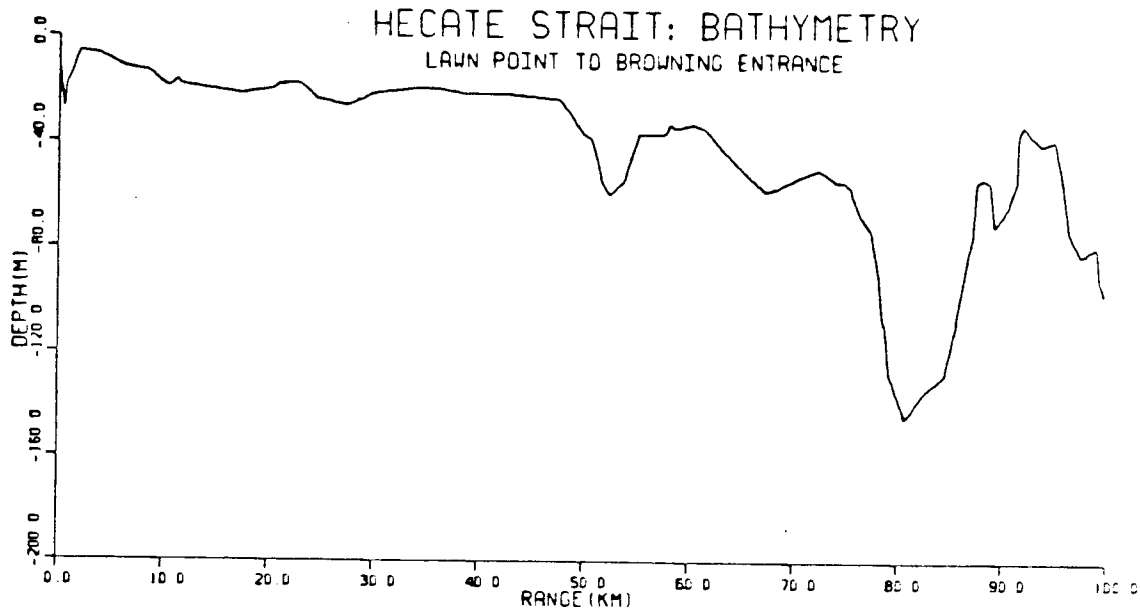

FIGURE 32. Bathymetric profile across Hecate Strait from Lawn Point (Queen Charlotte Islands) to Browning Entrance, 30 August 1980. This is the same transect on which Fig. 24 data were recorded.

No distinct bathymetric feature appears to be related to the temperature front at a range of 30-40 km during summer, although the 40-50 km range during spring is likely related to the edge of the western shelf. Data from the discrete transects suggest major variations of biological and physical properties occur at ranges between 40-70 km in spring (Fig. 26, between Stations 23 and 24) and about 60 km in winter (Fig. 27, Stations 20 and 27). The range of 60 km at which the continuous fluorescence profile peaks can be related to the edge of the western shelf. The second front at 80 km occurs close to the eastern shore and is probably a result of local runoff and to a certain extent the rebound of isopycnals depressed during winter onshore transport, as suggested by Barber (1957).

Such scales, apparent in the original data and confirmed by the structure function estimates, suggest temperature variations may be related to the cross-shelf dimension, while phytoplankton biomass (as measured by fluorescence) may be related to the cross-strait dimension. The temperature front occurs at the edge of the shelf, but will fluctuate horizontally with the intensity of stratification on the eastern side and the strength of the tidal currents over the shelf. During spring, the front will be formed by more intense heating of the shallow water as discussed in Chapter 5. The fluorescence maximum is also related to the shelf dimension: during spring the higher biomass occurs over the whole of the western side, while in summer it occurs in mid-strait where the bathymetry deepens into the eastern trough.

It is here that summer stratification is likely to be more constant, being eastward of the fluctuations of the thermal front over the shelf. Studies of plankton distributions about continental shelf break regions in summer (Denman *et al.* 1980, Pingree and Mardell 1981) also find that phytoplankton biomass is often associated with the edge of the slope rather than the shelf or deep basin.

6. SPRING BLOOM INITIATION

The importance of bathymetry to regions of tidal mixing is clear with its inclusion in the $h\ U^{-3}$ model of Simpson and Hunter (1974). Bathymetry also plays a crucial role in the initiation of the spring bloom of phytoplankton by limiting the depth of mixing and subsequently increasing the mean light intensity to which cells will be exposed. This can be demonstrated for Hecate Strait by calculating surface mixed depths separately for the shallow western and deep eastern regions (Fig. 33). The critical depth remains deeper than the bottom (the effective limit of the mixed layer) from March to August or September in the western strait, while in the east the bottom is too deep to directly influence the surface mixed depth. The "growing season" for the eastern region is therefore predicted to be May to August or September. This prediction is substantiated by the data of Fig. 26, which further indicates that the spring phytoplankton bloom should occur about March or April in western Hecate Strait as a result of its shallow depth.

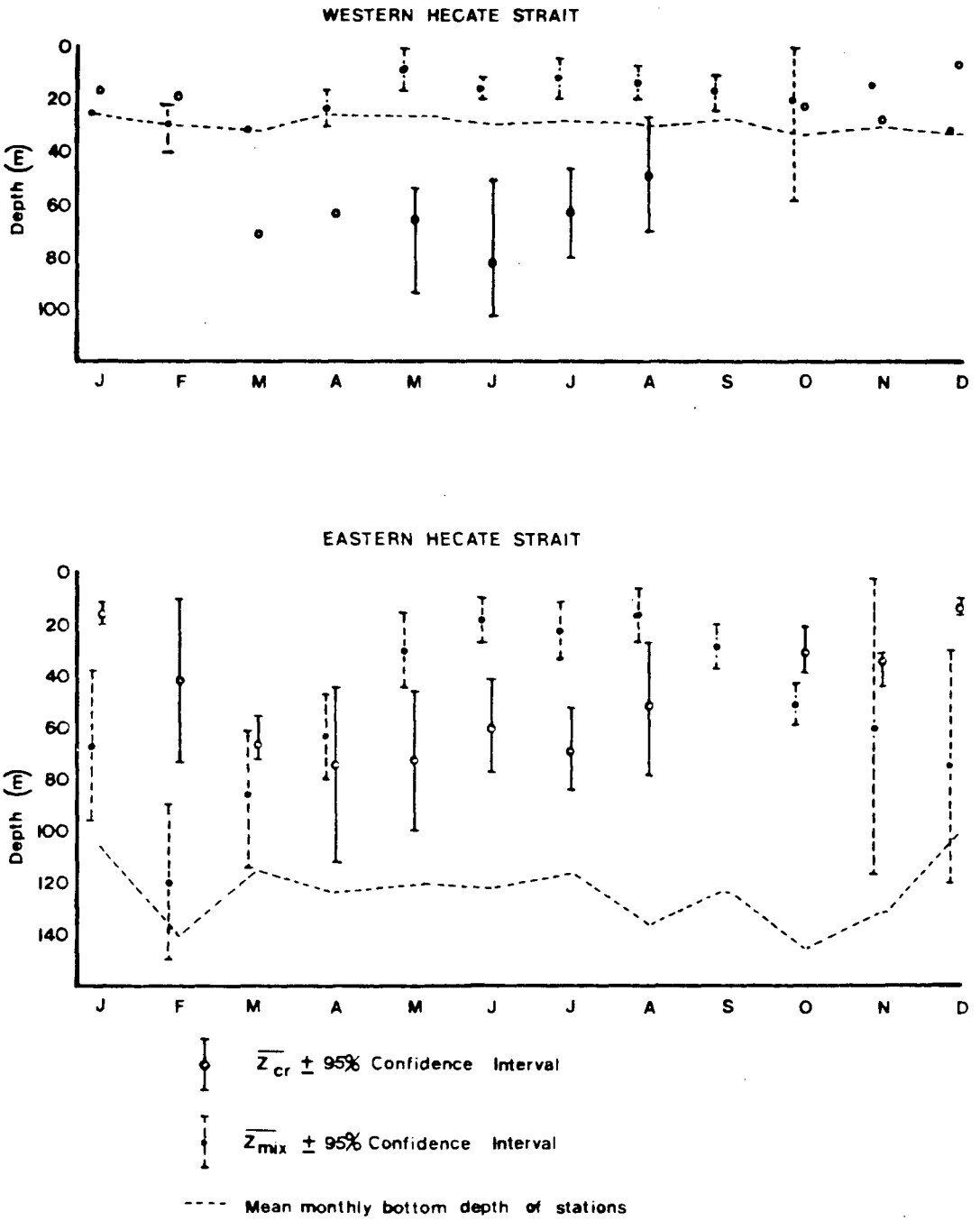

FIGURE 33. Hecate Strait critical depth - mixed depth model results calculated as described in text. Horizontal dashed line represents mean bottom depth of the set of stations sampled that month. Data are a composite from 1954 to 1971.

These monthly-composite mixed layer depths (MLD) can also be used in the equation

$$\bar{I}_{MLD} = \frac{0.5\ I_o}{k\ MLD}\ (1-e^{-k\ MLD})$$

(Parsons *et al.* 1984) to estimate the mean light intensity available throughout the surface mixed layer. Fig. 34 indicates these values for east and west Hecate Strait and compares them with the mean light intensity proposed by Gieskes and Kraay (1975) for a net increase of spring phytoplankton production in Dutch coastal waters. This figure suggests the same timing of the spring bloom as proposed by the critical depth model, with the bloom in the western region occurring early in the spring. However, during summer the difference of mean light intensities expected by the tidal mixing hypothesis, which suggests that phytoplankton on the mixed side are light-limited, does not occur. The shallow depth of the mixed region, plus weak stratification at its eastern edge, produce light conditions sufficient to support net phytoplankton growth. This conclusion was also noted in Chapter 5, where it was suggested nutrients rather than light were the limiting resource.

D. DISCUSSION

A seasonal progression of phytoplankton production and the importance of tidal mixing can now be proposed for Hecate

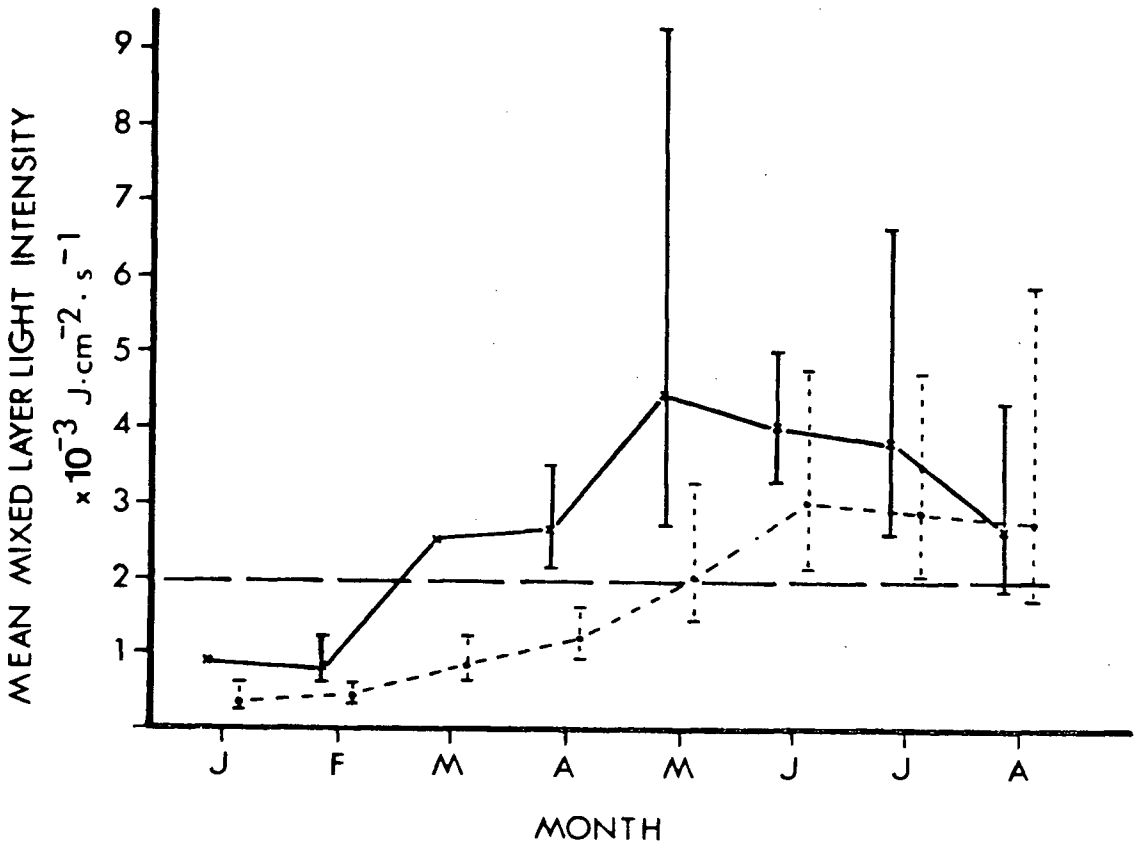

FIGURE 34. Monthly mean mixed layer light intensities for west (solid line) and east (short dashed line) Hecate Strait. Vertical bars represent 95% confidence intervals of the mean. Long dashed line represents the light intensity suggested by Gieskes and Kraay (1975) as the critical intensity for phytoplankton blooms.

Strait. During winter, the larger proportion of diatoms on the western side of the strait results from adequate nutrient concentrations and higher mean light intensities due to the shallow depth of mixing. Examples of such increases during winter due to shoaling of the mixed layer have been shown for chlorophyll (Fournier *et al.* 1979) and diatoms (Reid *et al.* 1983). In Long Island Sound, Schnitzer (1979, quoted in Farmer *et al.* 1982) observed that in well mixed waters the ratio of 1% light depth to maximum depth can be used to predict the dominant phytoplankton group, i.e. microflagellates if this ratio is <0.5, and diatoms if >0.5. In the mixed waters of western Hecate Strait this ratio is likely to be greater than 0.5 in winter, resulting in diatom-favourable conditions.

With increasing solar radiation in spring, the phytoplankton outburst occurs first on the western side. Tidal mixing does not play a role in initiating this bloom, as the whole strait will tend to be well-mixed by average winds of 8-10 m s^{-1} (Environment Canada 1975). Moreover, there will be insufficient solar radiation for stratification (Tabata 1958). The difference in timing between eastern and western sides is a result of the different bathymetry and its effect on limiting the mixed depth and increasing mean light intensities above critical levels. The presence on the western side of greater diatom biomass over winter may also act as a source of seed stock.

Such a predictable mechanism influencing the development of the spring bloom in western Hecate Strait may have important consequences for the distribution and survival of larval fish. Mason *et al.* (1981) sampled across Hecate Strait in April 1980 less than one week after the data of Fig. 26 were collected, and found greater diversity and over ten times greater abundance of fish larvae on the western side than the eastern side of the strait. Ketchen (1956) has suggested that English sole *(Parophyrs vetulus)* larvae drift northwards to settle on these shallow banks about April. Such a mechanism may increase larval survival by matching their arrival in western Hecate Strait with a bloom of potential food items.

In summer, mean mixed layer light intensities across the strait are similar according to the limited data on mixed depths and attenuation coefficients summarized in Fig. 34. The western region appears to be sufficiently shallow, with depths comparable to the surface mixed layer of the stratified side, to eliminate growth differences due to light limitation. As suggested in Chapter 5, the low biomass of the mixed side during summer probably results from nutrient limitation and lack of a deep reserve pool, while higher biomass on the eastern side may occur from nutrient input via upwelling along the shelf edge in the central strait (e.g. due to the longshore current, Hsueh and O'Brien 1971), or sporadic storm mixing as discussed for the New York Bight by Walsh *et al.* (1978). Data presented in Fig. 28C, showing dominance of flagellate biomass on the western side

relative to diatom biomass in the east, are consistent with this interpretation.

During winter, spring and summer, the cross-strait feature that consistently influences phytoplankton spatial organization and composition is bathymetry. It influences the water column mean light intensity during winter and spring, and the degree of tidal mixing and potential for nutrient resupply to surface waters during summer. Tidal mixing variations across Hecate Strait appear to be important to plankton organization only in summer, however, in such shallow water the influence of wind mixing must also be considered. If we postulate conditions of no tidal mixing, then typical wind velocities during summer of 4-6 m s^{-1} (Thomson 1981) suggest mixed layer depths of about 20 m, similar to actual mixed depths for the eastern strait in summer and maximum depths of much of the western shelf. The actions of tidal mixing and wind mixing may essentially overlap in the western region with the mixing effect of the tides equivalent to that of winds blowing about 5 m s^{-1}.

This is also shown from theoretical considerations, where the actions of tidal mixing and wind mixing are equivalent if they have equivalent energy dissipation rates per unit mass (Kullenberg 1983)

$$\frac{C_d\ U^3}{h} = \frac{\rho_a\ C_s\ k\ W_{10}^3}{\rho_w\ h} \quad .$$

Bottom and surface drag coefficients are C_d and C_s (2.5×10^{-3} and 2×10^{-3} respectively), h is the water depth, ρ_a and ρ_w are air and water densities, **U** the vertically-averaged tidal velocity, k the wind factor (3×10^{-2}) and W_{10} the wind velocity 10 m above the surface. Using conventional values as indicated (from Kullenberg 1983), it can be shown that average wind velocities of 5-7 m s^{-1} correspond to average tidal currents of 0.2-0.3 m s^{-1}, similar to those derived from the tidal model of Chapter 5 for waters of western Hecate Strait shallower than 20 m. Therriault *et al.* (1978), studying a shallow coastal embayment, concluded that phytoplankton spatial variability was dominated by physical processes when wind speeds were >5 m s^{-1}. Tidal mixing was not considered in their study.

The effects of wind and tidal action in mixing a shallow water column will differ on both temporal and spatial scales, however. In general, mixing by tides during summer will be more important at shorter scales. Its intensity will vary with the semi-diurnal or diurnal cycle, and will vary also with the fortnightly neap-spring cycle. In contrast, the intensity of wind mixing will decrease from winter to summer with the decrease in frequency of extra-tropical cyclones in the northeast Pacific. Fissel (1975), in a study of wind data from Ocean Station 'Papa' (50°N, 145°W), found periods between maximal winds during winter of 2.5 days, and 4.5 days during summer. Spectral analysis of oceanic wind data measured during summer 1979 and 1980 off the west coast of Vancouver Island

suggest similar periods (Thomson 1983). Spatial scales of wind and tide action also differ, with significant tidal mixing confined to the shallow western region and varying with the bathymetry, while wind mixing will vary with topography, showing much less small scale variation over the open strait. There is, however, an increasing gradient of wind speed from west to east, with winds at Bonilla Island in the eastern strait about twice as strong as those at Sandspit (Environment Canada 1975).

Little is known about benthic communities in Hecate Strait. Especially in western Hecate Strait, with the shallow depth and probable sedimentation of the spring bloom, the benthic community may be quite extensive, although it is likely to vary with bottom tidal stress (see e.g. Warwick and Uncles 1980). Pomroy *et al.* (1983) estimated that nutrient efflux from sand sediments in a bay adjacent to the Bristol Channel should satisfy the nitrogen demand of the phytoplankton when productivity is low, but meet only 16% of the demand during peak productivity in June. If nutrients are released from the sediments in western Hecate Strait, then tidal mixing will have a greater impact on their vertical and horizontal distributions than wind mixing. The maximum action of tidal mixing is at the bottom, while for wind mixing the maximum stress occurs at the surface. However, if nutrient release from the sediment was slow, it may not meet the phytoplankton demand on the western side compared with the frequency of storm mixing and injection of nutrients in the east.

E. SUMMARY

Phytoplankton spatial organization and taxonomic composition across Hecate Strait, B.C. were examined seasonally. The pattern was similar in winter and spring with the highest biomass and a greater contribution by diatoms on the shallow western shelf. The spring bloom occurred by April in the west, but later on the eastern side. Bathymetry is the key difference, limiting the mixed depth of the western side and increasing mean light intensities. A critical depth model which includes these bathymetric variations correctly predicts this pattern.

The biomass and composition pattern during summer was opposite to that in winter and spring. Chapter 5 has suggested plankton distributions in summer are driven by tidal mixing and nutrient, not light, limitation. Taxonomic composition patterns agree with this interpretation, although wind mixing of shallow (<30 m) water columns must also be considered. The predictability and small scales of tidal mixing suggest that it may be more important in distributing nutrients vertically, especially if benthic regeneration occurs.

Scales of variation of temperature and fluorescence appear to be related to dimensions of the shallow shelf. I conclude bathymetry is the major feature across Hecate Strait influencing plankton organization and composition seasonally by reducing the mixed layer in winter, and maintaining the mixed layer and preventing nutrient accumulations in summer. Although present in

all seasons, tidal mixing does not appear to determine plankton blooms in winter or spring.

VII. GENERAL CONCLUSIONS AND SUMMARY

1. CONCLUSIONS

The British Columbia northern shelf includes Queen Charlotte Strait and Sound, Hecate Strait, Dixon Entrance, and their contiguous waters. It is the largest region of the B.C. coast, with oceanographic properties that reflect both coastal and oceanic characteristics. It is also a region that has been poorly studied oceanographically, yet has potentially valuable living and non-living resources.

One such resource, petroleum, is expected to occur in commercially exploitable quantities. Ten years ago a moratorium was imposed on petroleum exploration activities in this region, principally to allow time for collection of environmental data and assessment of its sensitivity to such activities. However, during this time very few oceanographic data were actually collected. The ship of opportunity project on which this thesis is based was therefore initiated to provide such information, which has since proven useful in the Initial Environmental Evaluations for the region (e.g. Petro-Canada 1983).

The scope of this thesis was expanded, however, to become the first routine investigation of the biological oceanography of the B.C. northern shelf. In addition to providing baseline information on plankton and areas potentially sensitive to petroleum exploration, its findings will also be of use in multi-species fisheries management models, and in examining

basic biological responses to physical oceanographic processes.

The general physical oceanography of the northern shelf was not examined directly in this study. Instead, results from previous studies were used (reviewed in Chapter 2), although they are by no means complete. The most serious lack is of detailed knowledge of the circulation patterns. For example, a weak gyre over the shallow banks of western Hecate Strait was implied by the model studies of Bell (1963), although it has not been substantiated yet by direct measurements. The subsurface current patterns are also almost completely unknown. Current meters have been installed at various locations on the northern shelf to resolve these questions, and results should be available in the near future (Dr. Bill Crawford, Institute of Ocean Sciences, Sidney, B.C., personal communication). Such detailed information will be very useful in predicting processes like current-driven upwelling and dispersal of plankton patches.

The theoretical pattern of initiation of the spring phytoplankton bloom for the B.C. coast was calculated in this thesis using a critical depth - mixed depth model (Sverdrup 1953) which included bathymetry. It predicted a general northward progression in the time of the outburst following the seasonal increase of solar radiation. However, this progression was not entirely sequential between adjacent regions, particularily Queen Charlotte Sound and Hecate Strait. Conditions in the northern Strait of Georgia were predicted to be appropriate for a bloom during February - March, in Queen

Charlotte Sound by May or late April, Hecate Strait in April, and Dixon Entrance in May. Observations of the actual spring increase of plankton by the ship of opportunity program confirmed this predicted pattern, although found there was little difference in timing between Queen Charlotte Sound and Hecate Strait, both of which had blooms during April in 1979 and 1980.

Diatoms were the major phytoplankton component contributing to the spring bloom, with taxonomic composition on the northern shelf similar to that in the Strait of Georgia (i.e. *Skeletonema costatum, Thalassiosira* spp. and *Chaetoceros* spp.). Zooplankton were more abundant in areas of phytoplankton blooms, with occasional local outbursts of barnacle nauplii and decapod larvae near shore in specific areas.

The similar timing of the diatom spring increase in Queen Charlotte Sound and Hecate Strait was not what was expected, considering the distance they span along the coast. However, spatial variation of plankton biomass within any one region was considerable, which made precise definition of the timing of the bloom rather difficult. The earliest spring blooms on the northern shelf during the two years of study occurred in western Hecate Strait and southeastern Queen Charlotte Sound. In this latter region, the spring diatom increase occurred by April in Fitz Hugh and Milbanke Sounds, then advanced towards Cape Caution and open Queen Charlotte Sound as spring progressed. This lead to a zone of increased plankton biomass at the mouth

of Fitz Hugh Sound during spring and summer, while Queen Charlotte Strait rarely showed evidence of a phytoplankton bloom in this study. Vertical temperature profiles and river discharge statistics suggest this bloom may be initiated by freshwater runoff and stratification, and maintained by nutrients supplied through entrainment of deeper water into the surface layer, although this mechanism was not tested in this thesis. The development of this bloom and zone of high biomass may be important for the survival of juvenile salmonids in this area. As this bloom occurred earlier than at most stations in oceanic Queen Charlotte Sound, it may account for the discrepancy between the observed timing of the spring bloom and that predicted for Queen Charlotte Sound by the critical depth model.

Northern Hecate Strait was the other region of the northern shelf in which the spring diatom increase was first observed to occur. Specifically, it was the western part of the strait where the phytoplankton outburst occurred as early as the second week of April in 1980. During summer however, the area of high plankton biomass switched to the central and eastern sections of the strait. The principal characteristic distinguishing Hecate Strait is bathymetry, with a shallow bank (depths <30 m) on the western side, while a deep trough occurs on the eastern side. It is this cross-strait variation of bathymetry which is responsible for the different biological characteristics of east and west Hecate Strait.

A critical depth model calculated separately for eastern and western Hecate Strait correctly predicted the observed development of the spring phytoplankton bloom in April on the western side. This early bloom occurred because the shallow water depth limited the depth of the mixed layer, and so increased the mean light intensities to which cells were exposed relative to the more deeply mixed eastern side. This extensive shelf is the reason why the regional critical depth calculations predicted a spring bloom in Hecate Strait earlier than Queen Charlotte Sound, and why the bloom was observed to occur in April in Hecate Strait along with the bloom in southeastern Queen Charlotte Sound.

The switch between spring and summer, from high plankton biomass and a taxonomic composition dominated by diatoms on the western side to the eastern side of Hecate Strait, can also be attributed to the effect of bathymetry. While during spring the shallow depths promoted conditions favourable for phytoplankton growth, once seasonal winds decreased and the eastern side became stratified during summer, these same shallow depths created less favourable growth conditions. Calculation of the Simpson - Hunter (1974) stratification parameter, based on water depth and mean tidal velocities, predicted the deep eastern side was likely to be stratified and the shallow western side well-mixed or transitional during summer. Vertical temperature profiles recorded by the *Imperial Tofino* and calculation of a bulk stratification parameter, confirmed these characteristic

mixing zones. This implies a front should occur between these zones, particularily in northwestern Hecate Strait where the mixing - stratification gradient is sharpest. Plankton biomass distributions conformed to the typical pattern about fronts in the Celtic Sea (e.g. Pingree 1978), and were low in the well-mixed region, higher in the stratified region, and highest in mid-strait at the edge of the western shelf. It is also interesting to note that the richest groundfish fishing areas of Hecate Strait occur on the slopes of the western shelf, somewhat related to the zone of highest biomass. Consideration of the cross-strait dimensions of the shallow shelf, and the dimensions of both spring and summer plankton blooms, confirmed the importance of bathymetry in the development and location of these blooms, although by different mechanisms. It was also clear that, although present throughout the year, tidal mixing was an important mechanism initiating plankton blooms only during summer.

Hecate Strait can therefore be included as another example of the ability of the shallow sea tidal front model to predict mixed and stratified water masses during summer, even when there is some degree of freshwater influence. Other such areas studied to date include Long Island Sound (Bowman and Esaias 1981, Bowman *et al.* 1981), Hudson Bay (Griffiths *et al.* 1981), and the Gulf of St. Lawrence (Iles and Sinclair 1982). However, there are two aspects of the system in Hecate Strait which are not characteristic of the usual tidal front model: the near surface

waters of Hecate Strait were consistently low in nutrients during summer, and it was the stratified side which had the higher diatom biomass rather than the mixed side, as described by Holligan *et al.* (1984). Calculations of critical depths and mean light intensities during summer for western Hecate Strait indicate there appears to be adequate light for net phytoplankton growth, and it is therefore suggested phytoplankton in this well-mixed region are limited by the supply of nutrients onto the shelf. The greater biomass of diatoms on the eastern side are likely supplied with nutrients by sporadic mixing of deeper water into surface layers due to the passage of storms, while the western side is prevented from accumulating a deep nutrient pool by its more vigorous tidal mixing.

This may be an important distinction between the tidal mixing model as applied to straits and to continental shelf seas. In areas where the water depth is shallow enough to prevent light limitation, limitation of phytoplankton growth by nutrients may become important. However, where this shallow mixed region occurs within an open sea or as a narrow strip adjacent to the shore, nutrients may be supplied from the surrounding deep water by advection onto the bank as suggested for Georges Bank by Cohen *et al.* (1982). In the case of the strait, especially where the shallow bank is extensive and bounded on one or more sides by land, such advection of deep, nutrient-rich water will be restricted and may not be sufficient

to resupply the whole of the shelf. Plankton biomass in the mixed region during summer would then become limited by the rate of nutrient resupply, either by advection, or by benthic or *in situ* regeneration.

2. FUTURE STUDIES

This study is the first to examine spatial and temporal distributions of plankton on the B.C. northern shelf, and potential physical mechanisms regulating these distributions. It has begun to answer such questions as the kinds of organisms that occur and how they vary. These answers are incomplete, however, as the ship of opportunity program sampled only certain areas of the northern shelf with any consistency, and even then with a temporal resolution that was monthly at best. They do form a basis on which to make predictions about areas of the region that were poorly sampled, both in terms of their plankton distributions and underlying physical processes.

Central Queen Charlotte Sound is an area with important fishing sites, for example Goose Island Bank and Cook Bank north of Vancouver Island, and with considerable bathymetric variation, yet was poorly sampled in this study. In these chacteristics it is similar to Hecate Strait, although without the protection from direct oceanic influence provided by the Queen Charlotte Islands. Similar processes may therefore be operating in both areas, with temporal plankton distributions in Queen Charlotte Sound predictable from study of Hecate Strait.

The Goose Island Bank area may also resemble Georges Bank, where advective effects, both onto and off the bank, can become very important (e.g. Cohen *et al.* 1982). Future studies in the northern shelf region would do well to examine this area in detail with these predictions as background.

Although studied fairly intensively in this program, plankton dynamics in northern and central Hecate Strait are still not completely known. Much better temporal resolution over a longer period is required to clearly identify factors initiating the spring bloom, as well as its interannual variability and spatial extent. During summer, when tidal mixing is the dominant physical process, better spatial resolution is required to establish the precise locations of frontal and transition zones, the extent of their fluctuations, and their influence upon plankton productivity and distributions. A suggestion for such a study would be to use the B.C. ferries which travel between Prince Rupert and Sandspit several times per week as ships of opportunity. The SHOP techniques of Royer and Emery (1982) and Boyd (1984), as well as the present study, would be most appropriate.

Other areas of the northern shelf poorly studied in this program, yet of interest for further study, are Dixon Entrance and southern Hecate Strait. Dixon Entrance is of considerable importance as a prime migration route for salmon between the Skeena River and northeast Pacific Ocean, yet has marked oceanographic and biological differences between both northern

and southern, and eastern and western areas (e.g. LeBrasseur 1956) which have been poorly studied. Southern Hecate Strait is a similar area.

In addition to such regional questions and hypotheses, this study also introduces several theoretical questions concerning precise mechanisms of increased biological productivity about frontal zones. No productivity values were estimated during this study, an important omission which needs to be corrected in future work. Especially necessary are primary productivity estimates within the frontal and high biomass regions of Hecate Strait and southeastern Queen Charlotte Sound. This would help develop a more detailed description of the processes by which frontal zones produce higher biomass by advection or *in situ* production.

The results of this study also question the classic description of low biomass on the well-mixed side of a tidal front due to light limitation. In western Hecate Strait, the water depth appears to be sufficiently shallow to prevent light limitation compared with the stratified side. What are needed are measurements of the actual rates of vertical mixing in both mixed and stratified waters, and of the resultant mean light intensities experienced by phytoplankton. Denman and Gargett (1983) have made a start on such studies, although measurements in specific frontal systems are still needed.

Nutrient uptake and regeneration rates by phytoplankton are other rate process that need to be measured in frontal systems.

Measurements of ambient nutrient concentrations are not entirely satisfactory for determining biological processes. For example, nutrients are low in near surface waters during summer across Hecate Strait, yet there is considerable variation of biomass. Such biomass is presumably supported by rapid uptake of nutrients as they become available, with the limiting process the rate at which such nutrients are injected into, or regenerated within, the surface layers (or appropriate light regime). In the case of Hecate Strait such nutrients appear to be injected more frequently on the eastern than western sides. In their study of frontal zones in the English Channel, Holligan *et al.* (1984) also noted low ambient nutrient concentrations (<1 μM NO_3-N) throughout the mixed region, which still supported higher phytoplankton biomass than the stratified side.

3. GENERAL SUMMARY

This study is the first to examine the spatial and temporal biological oceanographic characteristics of the British Columbia northern shelf. Consequently, its objectives were rather broad, concerned more with a first overview of the region and the general physical processes initiating plankton blooms in spring and summer than with specific details of local spatial or temporal interest. Its findings are intended to serve as background to fishery management models and environmental sensitivity analyses, and suggest further questions and research opportunities for more detailed studies.

The two general objectives were:

1. To examine the spatial and temporal distributions of plankton blooms on the B.C. northern shelf, including their physical and chemical properties, phytoplankton and zooplankton biomass fluctuations and taxonomic composition; and
2. To investigate potential physical mechanisms initiating plankton blooms and regulating their observed spatial and temporal distributions on the B.C. northern shelf.

The conclusions of this study have been summarized in this chapter, and in the summaries at the end of each specific chapter. The principal conclusions are as follows:

- temporal patterns of plankton are typical of other temperate latitude coastal areas (Chapter 4).
- spatial patterns of bloom initiation are highly variable within any one region due to local oceanographic and bathymetric characteristics. This in turn complicates the temporal pattern of bloom outbreak within each area (Chapter 4).
- the general pattern of initiation of the spring bloom is the Strait of Georgia, Queen Charlotte Sound and Hecate Strait, Dixon Entrance. This was both observed and predicted with a critical depth model, although a discrepancy occurred with Queen Charlotte Sound perhaps due to the incomplete sample observations in this region (Chapter 4).
- tidal mixing is an important physical mechanism regulating biomass distributions and blooms across Hecate Strait in

summer. The shallow western region is tidally the most energetic, and consequently had the lowest biomass. Phytoplankton production is suggested to be nutrient rather than light limited. The front occurred in the central strait, with high biomass also on the eastern side (Chapter 5).

- tidal mixing is not an important mechanism influencing plankton distributions in winter or spring in Hecate Strait. Instead, bathymetry was concluded to be the major feature influencing seasonal plankton composition by decreasing the mixed layer in winter, and maintaining it during summer (Chapter 6).

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APPENDIX I

Station locations for each cruise of the *Imperial Tofino* ship of opportunity program. Original data are available in Dilke *et al.* (1979) for Cruises 1 to 8, and Perry *et al.* (1981) for Cruises 9 to 14.

CRUISE 1 13 - 20 March 1978

STATION	DAY/MO/YR	TIME	POSITION
01	13/03/78	1600	54°29'N 131°17'W
02	14/03/78	0200	53°39'N 133°11'W
03	14/03/78	1500	53°46'N 133°12'W
04	16/03/78	0300	53°59'N 130°13'W
05	18/03/78	1400	50°42'N 126°49'W
06	19/03/78	2100	50°42'N 126°33'W
07	20/03/78	1020	49°25'N 123°50'W

APPENDIX I (Continued)

CRUISE 3 24 July - 3 August 1978

STATION	DAY/MO/YR	TIME	POSITION
01	24/07/78	1830	50°21'N 125°08'W
02	24/07/78	2300	50°22'N 124°22'W
03	25/07/78	1000	51°17'N 127°43'W
04	25/07/78	1900	51°23'N 127°49'W
05	26/07/78	0800	51°46'N 127°55'W
06	26/07/78	1250	52°15'N 128°17'W
07	26/07/78	1630	52°34'N 128°29'W
08	26/07/78	1900	52°58'N 128°31'W
09	26/07/78	2245	53°19'N 128°56'W
10	27/07/78	0715	54°09'N 130°20'W
11	27/07/78	2300	53°56'N 130°54'W
12	28/07/78	0030	53°45'N 131°14'W
13	28/07/78	1500	53°29'N 131°30'W
14	28/07/78	2400	53°40'N 130°25'W
15	29/07/78	1900	54°18'N 130°34'W
16	30/07/78	0600	54°51'N 130°13'W
17	31/07/78	2355	53°22'N 129°19'W
18	02/08/78	0615	52°20'N 127°05'W
19	02/08/78	1810	51°37'N 127°53'W
20	03/08/78	0630	51°00'N 128°00'W
21	03/08/78	1810	50°40'N 127°13'W
22	03/08/78	2345	50°29'N 126°11'W

APPENDIX I (Continued)

CRUISE 4 12 - 27 August 1978

STATION	DAY/MO/YR	TIME	POSITION
01	12/08/78	0840	50°00'N 124°51'W
02	12/08/78	1530	50°25'N 124°30'W
03	12/08/78	1840	50°11'N 124°35'W
04	12/08/78	2335	49°32'N 124°06'W
05	13/08/78	1135	48°25'N 124°10'W
06	13/08/78	1735	48°50'N 125°10'W
07	14/08/78	1235	49°40'N 126°12'W
08	14/08/78	1635	49°46'N 126°28'W
09	15/08/78	0635	49°50'N 127°02'W
10	15/08/78	1240	50°00'N 127°32'W
11	15/08/78	1646	50°30'N 128°20'W
12	16/08/78	0006	50°47'N 127°30'W
13	16/08/78	0930	51°06'N 127°48'W
14	16/08/78	1252	51°17'N 127°20'W
15	16/08/78	1800	51°18'N 127°41'W
16	16/08/78	2321	51°34'N 127°34'W
17	17/08/78	1530	51°55'N 127°54'W
18	17/08/78	1730	52°10'N 128°08'W
19	18/08/78	0620	53°13'N 128°46'W
20	18/08/78	1240	53°23'N 129°17'W
21	19/08/78	1123	54°17'N 131°22'W
22	19/08/78	1400	54°06'N 131°48'W
23	19/08/78	1830	54°10'N 132°28'W
24	19/08/78	2340	53°46'N 133°12'W
25	20/08/78	1600	54°11'N 132°45'W
26	21/08/78	0630	53°17'N 131°53'W
27	21/08/78	1930	53°26'N 131°46'W
28	22/08/78	0615	53°55'N 130°14'W
29	22/08/78	1840	54°13'N 130°24'W
30	22/08/78	2340	54°37'N 130°41'W
31	24/08/78	1930	52°34'N 128°30'W
32	25/08/78	0930	52°23'N 127°27'W
33	25/08/78	1700	52°16'N 127°17'W
34	26/08/78	2130	50°36'N 127°01'W
35	27/08/78	0700	50°08'N 125°20'W
36	27/08/78	1200	49°35'N 124°23'W
37	27/08/78	1500	49°25'N 123°45'W

APPENDIX I (Continued)

CRUISE 5 11 - 27 September 1978

STATION	DAY/MO/YR	TIME	POSITION
01	11/09/78	2200	48°57'N 123°20'W
02	12/09/78	0600	48°25'N 124°22'W
03	12/09/78	1300	49°06'N 125°55'W
04	14/09/78	0715	49°51'N 127°13'W
05	14/09/78	2210	49°18'N 126°30'W
06	15/09/78	0330	48°39'N 125°09'W
07	15/09/78	1050	48°18'N 123°28'W
08	16/09/78	2305	49°49'N 124°34'W
09	17/09/78	1600	50°20'N 125°09'W
10	17/09/78	2330	50°33'N 126°45'W
11	18/09/78	1600	51°27'N 127°50'W
12	19/09/78	1400	53°18'N 129°04'W
13	20/09/78	1145	54°32'N 130°32'W
14	21/09/78	1145	53°24'N 132°36'W
15	22/09/78	0900	53°33'N 131°45'W
16	22/09/78	2340	53°32'N 131°22'W
17	24/09/78	1230	53°49'N 130°19'W
18	24/09/78	1505	53°41'N 129°47'W
19	25/09/78	0930	52°53'N 128°32'W
20	25/09/78	1830	52°16'N 127°43'W
21	26/09/78	1205	52°05'N 128°06'W
22	27/09/78	0600	50°41'N 127°15'W
23	27/09/78	1245	50°26'N 125°56'W
24	27/09/78	1730	49°57'N 125°07'W

APPENDIX I (Continued)

CRUISE 6 18 - 26 October 1978

STATION	DAY/MO/YR	TIME	POSITION
01	18/10/78	2100	54°07'N 131°49'W
02	18/10/78	2345	54°11'N 132°25'W
03	19/10/78	0300	54°09'N 133°10'W
04	19/10/78	0600	53°41'N 133°09'W
05	19/10/78	1815	53°46'N 133°12'W
06	20/10/78	0630	53°54'N 131°34'W
07	20/10/78	0900	53°32'N 131°45'W
08	20/10/78	2315	53°32'N 131°18'W
09	21/10/78	1320	54°13'N 130°24'W
10	21/10/78	2110	54°32'N 130°32'W
11	22/10/78	2135	53°52'N 130°03'W
12	22/10/78	2310	53°41'N 129°47'W
13	23/10/78	1500	53°20'N 129°00'W
14	23/10/78	1645	53°12'N 128°40'W
15	23/10/78	2330	52°18'N 128°30'W
16	24/10/78	1430	51°46'N 127°56'W
17	24/10/78	1545	51°23'N 127°50'W
18	24/10/78	1845	50°58'N 127°32'W
19	24/10/78	2015	50°44'N 127°17'W
20	25/10/78	1130	50°29'N 126°13'W
21	25/10/78	2210	50°21'N 125°07'W
22	26/10/78	0330	49°39'N 124°14'W

APPENDIX I (Continued)

CRUISE 7 2 - 7 January 1979

STATION	DAY/MO/YR	TIME	POSITION
01	02/01/79	1815	49°43'N 124°43'W
02	02/01/79	2330	50°22'N 125°44'W
03	03/01/79	0622	50°47'N 127°27'W
04	03/01/79	1136	51°08'N 128°47'W
05	03/01/79	2345	52°09'N 131°28'W
06	04/01/79	1810	53°29'N 132°59'W
07	05/01/79	0635	53°56'N 131°34'W
08	05/01/79	2400	53°16'N 131°13'W
09	07/01/79	1708	50°21'N 125°07'W

APPENDIX I (Continued)

CRUISE 8 30 March - 8 April 1979

STATION	DAY/MO/YR	TIME	POSITION
01	30/03/79	2300	50°21'N 125°07'W
02	01/04/79	0330	50°45'N 127°08'W
03	01/04/79	1130	50°48'N 127°06'W
04	01/04/79	2100	51°09'N 127°48'W
05	02/04/79	0100	51°53'N 127°57'W
06	02/04/79	0830	52°18'N 129°06'W
07	02/04/79	1415	52°48'N 130°33'W
08	02/04/79	1910	53°22'N 131°42'W
09	03/04/79	1245	54°10'N 130°24'W
10	04/04/79	0830	54°18'N 130°36'W
11	05/04/79	2230	53°18'N 128°54'W
12	06/04/79	1000	52°18'N 128°29'W
13	07/04/79	0100	51°27'N 127°46'W
14	08/04/79	0330	50°32'N 126°40'W
15	08/04/79	0700	50°24'N 125°53'W
16	08/04/79	1100	49°58'N 125°09'W
17	08/04/79	1230	49°46'N 124°47'W
18	08/04/79	1500	49°33'N 124°18'W
19	08/04/79	1700	49°23'N 123°44'W

APPENDIX I (Continued)

CRUISE 9 8 - 17 May 1979

STATION	DAY/MO/YR	TIME	POSITION
01	08/05/79	2230	49°38'N 124°12'W
02	09/05/79	1225	50°20'N 125°06'W
03	09/05/79	1815	50°30'N 126°23'W
04	10/05/79	1630	50°56'N 127°42'W
05	10/05/79	2015	51°47'N 127°55'W
06	11/05/79	0440	52°20'N 128°30'W
07	11/05/79	1015	53°11'N 128°48'W
08	11/05/79	1900	53°05'N 130°02'W
09	12/05/79	0035	53°24'N 131°33'W
10	12/05/79	2015	54°00'N 130°46'W
11	12/05/79	2215	54°11'N 130°21'W
12	13/05/79	1720	54°51'N 130°13'W
13	13/05/79	2355	54°34'N 130°30'W
14	14/05/79	2030	53°42'N 129°47'W
15	15/05/79	0330	53°24'N 129°13'W
16	15/05/79	1420	53°11'N 129°48'W
17	15/05/79	2130	52°21'N 128°31'W
18	16/05/79	0700	51°24'N 127°50'W
19	16/05/79	1545	51°09'N 127°48'W
20	17/05/79	0030	50°22'N 125°41'W
21	17/05/79	1010	49°35'N 124°05'W

APPENDIX I (Continued)

CRUISE 10 19 June - 1 July 1979

STATION	DAY/MO/YR	TIME	POSITION
01	19/06/79	2200	49°43'N 124°20'W
02	20/06/79	0020	49°23'N 124°00'W
03	20/06/79	0620	49°14'N 123°44'W
04	20/06/79	0705	49°17'N 123°32'W
05	21/06/79	1900	50°21'N 125°07'W
06	21/06/79	2400	50°21'N 125°32'W
07	23/06/79	0530	50°42'N 127°16'W
08	23/06/79	2015	51°10'N 127°50'W
09	24/06/79	0730	51°23'N 127°49'W
10	24/06/79	2030	51°47'N 127°55'W
11	25/06/79	1415	53°11'N 128°43'W
12	26/06/79	0315	53°22'N 129°13'W
13	27/06/79	0730	54°36'N 130°32'W
14	27/06/79	1030	54°30'N 131°05'W
15	27/06/79	1210	54°14'N 131°16'W
16	27/06/79	1805	53°18'N 131°56'W
17	28/06/79	0845	53°42'N 131°17'W
18	28/06/79	1035	53°53'N 130°59'W
19	28/06/79	1300	54°09'N 130°24'W
20	30/06/79	0800	52°17'N 128°29'W
21	01/07/79	0800	50°25'N 125°53'W
22	01/07/79	1215	49°55'N 125°03'W
23	01/07/79	1730	49°25'N 123°52'W

APPENDIX I (Continued)

CRUISE 11 13 - 29 July 1979

STATION	DAY/MO/YR	TIME	POSITION
01	13/07/79	2120	49°40'N 124°17'W
02	14/07/79	1430	50°21'N 125°08'W
03	16/07/79	0200	50°45'N 127°10'W
04	17/07/79	0300	51°15'N 127°49'W
05	17/07/79	1000	51°47'N 127°55'W
06	18/07/79	1225	52°25'N 128°30'W
07	21/07/79	0955	54°15'N 131°47'W
08	21/07/79	1145	54°13'N 132°26'W
09	21/07/79	1745	53°46'N 133°12'W
10	22/07/79	0355	53°25'N 132°40'W
11	22/07/79	1530	54°18'N 131°16'W
12	23/07/79	2145	54°51'N 130°13'W
13	24/07/79	1750	54°09'N 130°23'W
14	24/07/79	1930	54°00'N 130°46'W
15	24/07/79	2040	53°52'N 131°00'W
16	24/07/79	2200	53°41'N 131°21'W
17	24/07/79	2400	53°25'N 131°52'W
18	26/07/79	1210	53°10'N 129°06'W
19	26/07/79	1520	53°10'N 128°39'W
20	27/07/79	2400	51°10'N 127°52'W
21	28/07/79	1630	50°20'N 125°25'W
22	28/07/79	1850	49°55'N 125°03'W
23	29/07/79	0010	49°25'N 123°52'W

APPENDIX I (Continued)

CRUISE 12 30 January - 9 February 1980

STATION	DAY/MO/YR	TIME	POSITION
01	30/01/80	1130	49°29'N 124°08'W
02	30/01/80	1220	49°35'N 124°24'W
03	30/01/80	1400	49°46'N 124°45'W
04	30/01/80	1500	49°57'N 124°58'W
05	30/01/80	1550	49°58'N 125°10'W
06	30/01/80	2400	50°28'N 126°10'W
07	31/01/80	0200	50°29'N 126°20'W
08	31/01/80	1500	51°02'N 127°48'W
09	31/01/80	1530	51°07'N 127°49'W
10	31/01/80	1600	51°11'N 127°49'W
11	01/02/80	0130	51°32'N 127°52'W
12	01/02/80	0330	51°47'N 127°55'W
13	01/02/80	2000	52°16'N 128°25'W
14	01/02/80	2030	52°21'N 128°31'W
15	02/02/80	1130	54°08'N 130°19'W
16	03/02/80	0315	53°43'N 130°25'W
17	03/02/80	0345	53°41'N 130°34'W
18	03/02/80	0415	53°39'N 130°42'W
19	03/02/80	0445	53°37'N 130°51'W
20	03/02/80	0515	53°36'N 130°59'W
21	03/02/80	0615	53°32'N 131°14'W
22	04/02/80	0100	53°17'N 131°54'W
23	04/02/80	0200	53°25'N 131°50'W
24	04/02/80	0230	53°27'N 131°41'W
25	04/02/80	0300	53°29'N 131°37'W
26	04/02/80	0400	53°33'N 131°21'W
27	04/02/80	0500	53°37'N 131°07'W
28	05/02/80	1100	54°25'N 130°34'W
29	05/02/80	1225	54°12'N 130°28'W
30	05/02/80	1640	53°41'N 129°49'W
31	05/02/80	1920	53°21'N 129°14'W
32	06/02/80	0820	53°38'N 128°35'W
33	06/02/80	1500	52°18'N 128°28'W
34	06/02/80	2230	51°30'N 128°15'W
35	06/02/80	2345	51°17'N 128°18'W
36	07/02/80	2050	50°52'N 128°13'W
37	09/02/80	0715	50°21'N 125°08'W
38	09/02/80	1210	49°39'N 124°13'W

APPENDIX I (Continued)

CRUISE 13 10 - 16 April 1980

STATION	DAY/MO/YR	TIME	POSITION
01	10/04/80	1140	50°21'N 125°07'W
02	10/04/80	1300	50°28'N 125°21'W
03	10/04/80	1500	50°28'N 126°00'W
04	10/04/80	1600	50°30'N 126°18'W
05	10/04/80	1800	50°34'N 126°51'W
06	11/04/80	0120	50°53'N 127°36'W
07	11/04/80	0230	51°00'N 127°51'W
08	11/04/80	0330	51°05'N 128°07'W
09	11/04/80	0430	51°09'N 128°19'W
10	11/04/80	0530	51°13'N 128°34'W
11	11/04/80	1130	51°39'N 130°03'W
12	11/04/80	1300	51°45'N 130°22'W
13	11/04/80	1400	51°46'N 130°25'W
14	11/04/80	2200	52°44'N 132°15'W
15	11/04/80	2300	52°52'N 132°25'W
16	12/04/80	1700	53°45'N 133°12'W
17	12/04/80	1915	54°08'N 133°11'W
18	12/04/80	2200	54°13'N 132°26'W
19	12/04/80	2300	54°14'N 132°09'W
20	13/04/80	0100	54°16'N 131°30'W
21	13/04/80	2100	53°30'N 131°40'W
22	13/04/80	2200	53°36'N 131°30'W
23	13/04/80	2300	53°44'N 131°18'W
24	14/04/80	0000	53°51'N 131°02'W
25	14/04/80	0100	53°59'N 130°47'W
26	14/04/80	1815	54°31'N 130°31'W
27	14/04/80	1900	54°24'N 130°34'W
28	14/04/80	2045	54°06'N 130°22'W
29	15/04/80	1445	53°07'N 128°35'W
30	15/04/80	2145	52°20'N 128°30'W
31	16/04/80	1600	51°52'N 127°55'W
32	16/04/80	1745	51°22'N 127°50'W
33	16/04/80	2045	51°11'N 127°58'W
34	16/04/80	2125	51°05'N 128°05'W
35	16/04/80	2155	51°00'N 128°10'W
36	16/04/80	2235	50°54'N 128°17'W
37	16/04/80	2255	50°51'N 128°22'W

APPENDIX I (Continued)

CRUISE 14 30 May - 7 June 1980

STATION	DAY/MO/YR	TIME	POSITION
01	30/05/80	1155	49°30'N 123°57'W
02	30/05/80	1432	49°47'N 124°30'W
03	30/05/80	2031	50°11'N 124°38'W
04	31/05/80	0920	50°27'N 125°16'W
05	31/05/80	0950	50°27'N 125°25'W
06	31/05/80	1201	50°28'N 126°00'W
07	31/05/80	1245	50°29'N 126°09'W
08	31/05/80	1416	50°32'N 126°41'W
09	31/05/80	1910	50°40'N 127°14'W
10	31/05/80	2354	50°54'N 127°37'W
11	01/06/80	0451	51°39'N 127°54'W
12	01/06/80	0546	51°47'N 127°55'W
13	01/06/80	1120	52°13'N 128°09'W
14	01/06/80	1305	52°23'N 128°30'W
15	01/06/80	1932	53°10'N 128°38'W
16	01/06/80	2139	53°19'N 129°08'W
17	02/06/80	0630	54°07'N 130°18'W
18	02/06/80	1600	53°59'N 130°48'W
19	02/06/80	1800	53°46'N 131°15'W
20	02/06/80	2030	53°29'N 131°47'W
21	03/06/80	1155	53°28'N 131°33'W
22	03/06/80	1400	53°33'N 131°02'W
23	03/06/80	1935	53°50'N 130°19'W
24	04/06/80	0838	54°37'N 130°42'W
25	04/06/80	1535	54°20'N 130°34'W
26	04/06/80	1730	54°10'N 130°23'W
27	04/06/80	2145	53°35'N 129°40'W
28	05/06/80	1345	52°17'N 128°27'W
29	06/06/80	0101	51°26'N 127°49'W
30	06/06/80	0239	51°07'N 128°00'W
31	06/06/80	0515	50°46'N 128°26'W
32	06/06/80	2000	50°40'N 128°23'W
33	07/06/80	0120	50°51'N 127°44'W
34	07/06/80	1935	50°22'N 127°32'W
35	07/06/80	2150	49°58'N 125°09'W

APPENDIX II

Calculation of regional critical depths and mixed depths for B.C. coastal waters. Regions are defined as the Strait of Georgia (Lat >49°N), Queen Charlotte Sound (50°10'N < Lat ≤ 52°N), Hecate Strait (52°N < Lat ≤ 54°10'N and Long < 132°W), and Dixon Entrance (Lat > 54°10'N). Each page represents a successive step in the calculations; results are presented in Fig. 3 (Chapter 4).

Normal Daily Radiation Values

These values represent the normal daily total radiation for each month, $\bar{I}_0$ in J cm^{-2} d^{-1}, recorded for Sandspit (Dixon Entrance and Hecate Strait), Cape St. James (Queen Charlotte Sound), and Nanaimo (the Strait of Georgia), and available in the Monthly Radiation Summary, Atmospheric Environment Service, Ottawa. The Proportion Transmitted through Sea Surface is from Parsons *et al*. (1966) and is based on the seasonal sun angle.

	SANDSPIT	CAPE ST. JAMES	NANAIMO	Proportion Transmitted through Sea Surface
Jan	242.4	264.5	291.4	.80
Feb	491.4	519.3	612.7	.87
Mar	901.6	904.1	1048.6	.92
Apr	1362.7	1398.4	1649.8	.95
May	1822.4	1915.6	2119.6	.96
Jun	1783.7	1974.7	2226.8	.96
Jul	1723.6	1916.1	2380.3	.96
Aug	1510.3	1667.0	1965.7	.95
Sep	1362.5	1221.8	1404.4	.93
Oct	589.5	665.3	775.3	.90
Nov	411.7	325.5	316.0	.85
Dec	181.1	379.3	234.1	.78

APPENDIX II (Continued)

Critical Depths

Critical depths were calculated using the equation from Parsons *et al.* (1984):

$$Z_{cr} = \frac{0.5\ \bar{I}_o}{k\ \ I_c}$$

with $\bar{I}_o$ the normal daily radiation by month for each area, $\bar{I}c$ the compensation light intensity (58 J cm^{-2} d^{-1} from Hobson 1981), and k the attenuation coefficient as calculated from Secchi depths measured in the region (see Section IV.B.2.). A critical depth was calculated for each available measurement of k, then the means ($\bar{Z}cr$) and standard deviations (s) were determined for each month and area (depths in meters).

	Dixon Entrance			Hecate Strait			Queen Charlotte Sound			Georgia Strait		
	n	$\bar{Z}cr$	s	n	$\bar{Z}cr$	s	n	$\bar{Z}cr$	s	n	$\bar{Z}cr$	s
Jan	11	15.2	3.9	4	17.8	2.5	5	22.0	5.6	3	14.9	2.1
Feb	3	27.6	9.7	4	52.1	15.4	8	35.2	7.4	12	27.2	7.7
Mar	23	69.3	12.3	5	67.0	8.5	17	74.3	13.2	18	52.3	21.6
Apr	5	68.8	33.1	5	92.9	13.2	12	67.7	25.7	20	66.0	17.8
May	16	91.8	56.0	18	96.5	46.2	17	99.9	34.3	18	47.3	19.1
Jun	12	65.5	25.0	13	80.6	29.2	12	82.2	26.5	21	74.7	42.1
Jul	17	56.3	27.7	21	82.0	27.9	26	84.1	25.5	18	74.8	24.4
Aug	17	46.8	14.7	7	59.1	20.4	11	65.6	25.7	17	62.8	14.8
Sep		-			-		2	54.4	0.0	9	71.4	30.3
Oct	8	28.3	7.0	6	34.8	10.5	11	35.1	14.7	17	37.4	10.3
Nov	9	24.5	8.1	2	31.8	2.4	6	20.5	0.9	14	15.4	3.3
Dec	8	9.8	2.7	4	7.9	4.1	4	19.3	2.2	4	10.2	5.5

APPENDIX II (Continued)

Critical Depth 95% Confidence Intervals

Confidence intervals of critical depths for B.C. coast regions were placed on monthly mean critical depths using the equation from Sokal and Rohlf (1981):

$$95\% \text{ Confidence Interval} = \bar{Z}_{cr} \pm t_{0.5,(n-1)} \frac{s}{\sqrt{n}} .$$

The following table presents the monthly ranges in meters.

	Dixon Entrance	Hecate Strait	Queen Charlotte Sound	Georgia Strait
Jan	12.6 - 17.8	13.8 - 21.8	15.0 - 29.0	9.7 - 20.1
Feb	3.5 - 51.7	27.6 - 76.6	29.0 - 41.4	22.3 - 32.1
Mar	64.0 - 74.6	56.4 - 77.6	67.5 - 81.1	41.6 - 63.0
Apr	27.7 - 82.2	76.5 -109.3	51.5 - 83.9	57.7 - 74.3
May	62.1 -121.6	73.5 -119.5	84.0 -119.2	37.8 - 56.8
Jun	49.8 - 81.2	63.0 - 98.9	65.5 - 98.9	55.6 - 93.8
Jul	42.1 - 70.5	69.3 - 94.7	73.8 - 94.4	62.7 - 86.9
Aug	39.3 - 54.3	40.2 - 78.0	48.3 - 82.9	55.2 - 70.4
Sep	-	-	54.4	48.1 - 94.7
Oct	22.6 - 34.2	23.8 - 45.8	25.3 - 45.0	32.1 - 42.7
Nov	18.3 - 30.7	10.2 - 53.4	19.6 - 21.4	13.5 - 17.3
Dec	7.5 - 12.1	1.4 - 14.4	15.8 - 22.8	1.8 - 19.0

APPENDIX II (Continued)

Mixed Depth Summary Statistics

Summary statistics for surface mixed depths calculated as described in Section IV.B.2. using data collected during the 1950's and 1960's for the northern shelf (cruise numbers listed in Appendix III), and during 1968 in the Strait of Georgia (Crean and Ages 1971). The 95% confidence intervals on mean mixed depths ($\bar{Z}mix$) were calculated as (Sokal and Rohlf 1981):

$$95\% \text{ Confidence Interval} = \bar{Z}_{mix} \pm t_{0.5,(n-1)} \frac{s}{\sqrt{n}} .$$

with n the number of stations for that region and month, and s the standard deviation. All depths are in meters.

DIXON ENTRANCE

	n	$\bar{Z}mix$	s	95% C.I. (m)
Jan	24	79.6	61.5	53.5 -105.7
Feb	27	104.7	60.6	80.6 -128.8
Mar	43	102.8	75.7	79.6 -126.0
Apr	38	56.9	70.7	33.6 - 80.2
May	19	23.0	31.2	8.1 - 37.9
Jun	45	17.4	20.9	11.2 - 23.6
Jul	25	17.4	25.8	6.7 - 28.1
Aug	36	34.8	55.5	16.2 - 53.4
Sep	107	24.8	27.8	19.5 - 30.0
Oct	111	42.8	28.5	37.5 - 48.1
Nov	23	36.6	43.7	17.7 - 55.5
Dec	22	67.0	52.4	43.7 - 90.3

APPENDIX II (Continued)

HECATE STRAIT

	n	$\bar{Z}$mix	s	95% C.I. (m)
Jan	8	96.5	40.5	62.7 -130.3
Feb	26	114.6	54.9	92.4 -136.8
Mar	23	116.7	47.2	96.4 -137.0
Apr	61	50.5	45.8	38.7 - 62.3
May	32	33.6	35.2	20.9 - 46.3
Jun	64	15.9	21.1	10.7 - 21.1
Jul	27	23.9	25.2	14.0 - 33.8
Aug	26	15.5	16.8	8.7 - 22.3
Sep	28	25.9	16.9	19.3 - 32.5
Oct	51	50.9	25.0	43.9 - 57.9
Nov	6	64.8	59.0	2.8 -126.8
Dec	17	61.6	67.9	26.6 - 96.6

APPENDIX II (Continued)

QUEEN CHARLOTTE SOUND

	n	$\bar{Z}$mix	s	95% C.I. (m)
Jan	19	74.2	40.5	54.7 - 93.7
Feb	47	76.3	42.3	63.8 - 88.8
Mar	60	93.3	50.0	80.5 -106.1
Apr	75	67.9	41.7	58.3 - 77.5
May	20	33.3	42.8	13.2 - 53.4
Jun	42	15.6	16.9	10.4 - 20.8
Jul	43	21.8	28.0	13.1 - 30.5
Aug	24	17.4	32.3	3.7 - 31.1
Sep	25	28.6	22.3	19.3 - 37.9
Oct	96	44.3	25.8	39.1 - 49.5
Nov	11	72.5	52.6	37.1 -107.9
Dec	23	72.2	49.2	51.0 - 93.4

STRAIT OF GEORGIA

	n	$\bar{Z}$mix	s	95% C.I. (m)
Jan	43	38.8	24.6	31.2 - 46.4
Feb	43	13.1	16.4	8.1 - 18.1
Mar	43	9.0	5.8	7.2 - 10.8
Apr	46	15.4	9.9	12.5 - 18.3
May	46	7.2	4.1	6.0 - 8.4
Jun				
Jul	92	7.4	4.5	6.5 - 8.3
Aug	47	9.9	6.5	8.0 - 11.8
Sep				
Oct	45	12.1	7.2	9.9 - 14.3
Nov	46	12.1	8.4	9.6 - 14.6
Dec	86	34.2	32.7	27.2 - 41.2

APPENDIX III

Original cruise identifications and their corresponding Marine Environmental Data Service (MEDS) cruise numbers for B.C. northern shelf cruises whose data were used to estimate mixed layer depths and bulk surface stratification values. Archived data are available from the Marine Environmental Data Service, Dept. of Fisheries and Oceans, 240 Sparks St., Ottawa, Ont.

ORIGINAL ID	MEDS CRUISE NUMBER
H-54-1	180254688
H-54-2	180254689
H-54-3	180254690
H-54-4	180254691
H-55-1	180255694
H-55-2	180255695
H-55-3	180255699
C-57-4	180257716
CS-58-1	180258730
CS-59-1	180259733
CS-59-2	180259735
CS-59-3	180259740
SW-60-1	180260754
SW-61-1	180261759
MR-61-2	180261769
MR-61-3	180261774
MR-61-4	180261775
MR-62-1	180262778
MR-62-2	180262781
MR-62-3	180262790
11 Sept - 5 October 1967	180267008
16 - 27 April 1968	180268006
30 Sept - 16 October 1968	180268008
1 - 16 October 1969	180269021
5 - 15 March 1970	180270012
5 - 21 March 1971	180271015

APPENDIX IV

Complete taxonomic identifications for those species discussed in the text are as follows:

PHYTOPLANKTON

Centric Diatoms

Bacteriastrum delicatula Cleve 1897
Ceratulina bergonii Peragallo 1892
Corethron hystrix Hensen 1886
Ditylum brightwellii Grunow 1885
Lauderia borealis Gran 1900
Leptocylindrus danicus Cleve 1894
Skeletonema costatum Cleve 1878
Stephanopyxis palmeriana Grunow 1884

Pennate Diatoms

Asterionella japonica Cleve 1878
Thalassionema nitzschiodes Grunow 1885

Flagellates

Ceratium lineatum Cleve 1899
Distephanus speculum Haeckel 1899

ZOOPLANKTON

Copepoda

Acartia cf. clausii Giesbrecht 1889
Acartia longiremis Lilljeborg 1853
Calanus pacificus s.l. Brodsky 1948
Centropages abdominalis Sato 1913
Eucalanus bungii Giesbrecht 1892
Metridia pacifica Brodsky 1950
Neocalanus cristatus Kroyer 1848
Neocalanus plumchrus Marukawa 1921
Paracalanus parvus Claus 1863
Pseudocalanus cf. minutus Kroyer 1845
Tortanus discaudatus Thompson and Scott 1897

Chaetognatha

Eukrohnia hamata Mobius 1875
Sagitta elegans Verrill 1873

FISH

Anoplopoma fimbria Pallas 1811
Gadus macrocephalus Tilesius 1810
Hippoglossus stenolepis Schmidt 1904
Onchorhynchus gorbuscha Walbaum 1792

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Parsons, T.R., J. Stronach, G.A. Borstad, G. Louttit and R.I. Perry. 1981. Biological fronts in the Strait of Georgia, British Columbia, and their relations to recent measurements of primary productivity. Mar. Ecol. Prog. Ser. 6: 237-242.

Aranuvachapun, S. and R.I. Perry. 1981. Spectral variations of coastal water irradiance as a measure of phytoplankton pigments. Int. J. Remote Sensing 2: 299-312.

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1. Flavonol Glycosides of Hyginea abysinica. G.K. Pillai and Mulatu D'jote, J. Health Sci., 11:140 (1976).

2. Some Practical Aspects of Test Construction. G.K. Pillai, Indian J. Pharm. Educ., 10:9 (1976).

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4. Outpatient Medication Prescribing Pattersn in a Tropical Teaching Hospital. R.K. Raina and G.K. Pillai, Ind. J. Med. Assoc., 74:62 (1980).

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6. Resolution of Equine Estrogens Using Glass Capillary Columns. G.K. Pillai and K.M. McEralne, J. High Resol. Chromatogr. Comm., 4:70 (1981).

7. Quantitative Determination of Conjugated Estrogens in Formulations by Capillary Gas Chromatography. G.K. Pillai and K.M. McErlane, J. Pharm. Sci., 70:1072 (1981).

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9. Analysis of Indomethacin and its Impurities in Formulations by High Performance Liquid jChromatography. E. Kwong, G.K. Pillai and K.M. McErlane, J. Pharm. Sci., 71:828 (1982).

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11. Gas Liquid Chromatographic Resolution and Assay of Tocainide Enantiomers Using Chiral Capillary Column and Study of Their Selective Disposition in Man. K.M. McErlane and G.K. Pillai, J. Chromatogr., 274:129 (1983).

12. Stereospecific Salivary Excretion of Tocainide Enantiomers in Man. G.K. Pillai, J.E. Axelson and K.M. McErlane, Res. Commun. Chemical Pathol. and Pharmacol., 43:209 (1984).

13. Pharmacokinetics of tocainide enantiomers in healthy volunteers and in patients with renal dysfunction. G.K. Pillai, J.E. Axelson and K.M. McErlane. Manuscript in preparation.