Nearshore Oceanography and Planktonic Prey (Family Porcellanidae) of Gray Whales, *Eschrichtius robustus*, in Clayoquot Sound, British Columbia

by

Kecia Alene Kerr
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ABSTRACT

Gray whales in Clayoquot Sound occasionally feed on dense patches of porcelain crab larvae. The irregular timing and extent of patches prompted interest in factors influencing larval distribution and abundance. Timing of larval release in *Petrolisthes cinctipes* (Randall 1839) was estimated by monitoring egg-carrying crabs. CTD/fluorometer casts and plankton net tows were conducted to document temperature, salinity, chlorophyll fluorescence, distribution and density of porcelain crab larvae. Larval release peaked in early July. A subsequent increase in larvae in the plankton was not detected. Porcelain crab larvae densities were low throughout the season and gray whales were not observed feeding on porcelain crab larvae. Variation in temperature and salinity is driven mainly by upwelling processes. Variation in chlorophyll up to five-fold occurred over short time periods. Spatially discrete phytoplankton blooms and thin vertical layers of chlorophyll fluorescence were documented. This study increases understanding of the relatively unknown nearshore zone of a wave-exposed environment.

Supervisor: Dr. David A. Duffus (Department of Geography)

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CHAPTER 1: GENERAL INTRODUCTION

BACKGROUND AND IMPETUS FOR THIS STUDY

Research in Clayoquot Sound, on the west coast of Vancouver Island, BC, has shown that gray whale habitat use is not uniform, reflecting a patchy distribution of prey in space and time (Meier 2003). Gray whales (*Eschrichtius robustus* Lilljeborg 1861) are relatively asocial animals with geographic separation of their major feeding and breeding grounds. This results in gray whale behaviour while on the foraging grounds being fundamentally driven by the dynamics of their prey. Unlike the primarily benthic feeding behaviour of gray whales that migrate to the Bering and Chuckchi Seas, whales in Clayoquot Sound exploit a variety of benthic, epibenthic and planktonic prey items exhibiting dynamic foraging techniques as they rapidly switch between prey types to make use of short-term availability of energy (Dunham & Duffus 2001, 2002). It appears that whales will first exploit the temporarily available, and less predictable, planktonic prey items such as porcelain crab larvae (Porcellanidae) and epibenthic mysids (Mysidacea), switching to benthic prey such as amphipods (Gammaridea) or ghost shrimp (Thalassinidea) only when the density of crab larvae and mysids fall below a level that is energetically efficient (Dunham & Duffus 2001). Porcelain crab larvae are the most ephemeral of gray whale prey. Similar to other crab larvae, high density patches of porcelain crab larvae occur for periods of only a few days to a week, while bottom orienting and tube-dwelling prey are less likely to be dispersed or swept offshore by currents (Natunewicz & Epifanio 2001, Dunham & Duffus 2001). Observations of gray whales temporarily targeting porcelain crab larvae as prey prompted interest in the factors affecting the timing and extent of porcelain crab larvae patches. Through this study I examine nearshore, small-scale oceanography in conjunction with porcelain crab larvae distribution and density over a three month period.

PLANKTON PATCHINESS AND OCEANOGRAPHY

Patchiness of prey has important consequences for abundance, distribution, feeding success, growth and survival for organisms at higher trophic levels (Coyle *et al.* 1992, Denman & Dower 2001, Piatt *et al.* 1989). Their large size, metabolic requirements as mammals, filter feeding behaviour and concentration of feeding in the summer months necessitates that baleen whales locate high density prey patches to obtain enough energy to sustain themselves, grow and reproduce (Piatt & Methven 1992, Tynan 2004). Thus, the distribution and abundance of whales during the feeding season reflects community structure and biomass of their preferred prey (Tynan 2004, Piatt *et al.* 1989).

Many baleen whale species feed primarily on small crustaceans; some of which themselves are filter feeders, feeding on phytoplankton and detritus. The more direct influence of oceanography on the prey of baleen whales through this short food web results in a stronger link between whales and oceanographic variability compared to other top predators that feed higher up the food web. Thus, while all top predators give indications of the dynamics of the ecosystem through their ecology and behaviour (Davoren & Montevecchi 2003), baleen whales are particularly good species to concentrate on when studying the links between physical factors and top predators.

Although coarse-scale patchiness of plankton distribution has been documented for decades, the drivers of spatial patchiness and seasonal variability of plankton are not well understood (Pinel-Alloul 1995). These factors are difficult to identify and assign importance unequivocally due to the three dimensional aspect of marine habitat and the involvement of numerous physical and biological factors acting on multiple spatial and temporal scales. Much disagreement among researchers as to the relative importance of physical and biological factors at varying scales is apparent in the literature (Daly & Smith 1993, Folt & Burns 1999, Hamner 1988, Mackas *et al.* 1985, 2001). Drivers of phytoplankton patchiness appear to be mainly physical but biological factors such as growth and grazing are also important. Patchiness of zooplankton is even more complex as zooplankton have the ability to aggregate on their own and respond to their surroundings by changing swimming speed or direction thus altering patch dynamics (Hamner 1988, Denman & Dower 2001). In addition, drivers of patchiness of phytoplankton also drive some of the patchiness of zooplankton and the patchiness of phytoplankton can directly drive zooplankton patchiness through predator-prey interactions.

Potential mechanisms for crab larvae patch formation and maintenance include synchronous spawning events, associative larval behavior and aggregative physical processes (Natunewicz & Epifanio 2001). Studies of the timing of reproductive events have shown that many crab species release larvae at particular times within the tidal, lunar and diurnal cycles (Forward 1987, Morgan 1995, 1996). When high densities of adult crabs produce larvae that are synchronously released, a pulse of larvae may be detected in the water column. Adult porcelain crabs, *Petrolisthes cinctipes* Randall 1839, are the most abundant organisms found in developed beds of the mussel *Mytilus californianus* on the outer coasts of the Pacific Northwest, with densities of up to 3933 m^{-2} (Jensen 1990) but studies of the timing of release of larvae have not been conducted.

Very little is known about porcelain crab larvae in general, and even less is known about the ecology of this group. No dedicated field research has been conducted prior to this study. What is known about the larvae of this taxonomic group comes from early laboratory studies describing the larvae, field studies targeting commercially important crab species which mention porcelain crab larvae, and the gray whale feeding study in Clayoquot Sound which documented this group as a gray whale prey item (Dunham & Duffus 2001, 2002, Gonor & Gonor 1973, Jamieson & Phillips 1988, Wing *et al.* 1995, 1998a, 1998b). Therefore, an early but important step in understanding the spatial and temporal patchiness of porcelain crab larvae is the description of variability in factors considered important in determining crab larvae biomass.

Factors which influence survival, growth and development of organisms will impact overall biomass of larvae in the plankton and will influence patchiness directly and indirectly. Physical factors represent the "fundamental constraints to which individuals, populations and communities respond" (Pinel-Alloul 1995 pg 37). Temperature determines the rate of all chemical reactions thereby affecting all biological processes (Kinne 1970). Salinity affects osmotic pressure, altering movement across cell membranes (Kalle 1971). In seawater, both temperature and salinity determine water density which is an important water property for small planktonic organisms. Survival and length of larval development in decapod zoeae is dependent on temperature and salinity as a result of the influence of these factors on basic biology (Anger 2003, McConaugha 1992, Moloney *et al.* 1994). Not only are these effects felt directly, but they are also amplified when in combination with other stressors. In addition, they impact organisms indirectly through effects on lower trophic levels. Knowledge that these physical factors can influence decapod zoeae prompted me to try and link the presence of dense patches of porcelain crab zoeae with present and recent history of oceanographic conditions of the area. For example, if temperature is an important control on growth in porcelain crab larvae, I would expect an increase in the proportion of later stage larvae (zoea II or megalopae) after an increase in temperature.

Food quality and availability also affect larval development and survival (Paulay *et al.* 1985). In particular, there appear to be crucial times during the development of decapod zoeae when starvation for as little as one day drastically increases mortality rates (Anger *et al.* 1981). Evidence for food limitation in the field is lacking but much debate on the potential for food limitation appears in the literature. This thesis assumes that food limitation is possible under natural conditions. Proxy measures of phytoplankton concentration such as chlorophyll fluorescence can be used to assess food availability at the base of the food web. High levels of chlorophyll fluorescence should translate to higher concentrations of prey available to porcelain crab zoeae. If suitable food is available to porcelain crab zoeae at critical times during their development, zoeal survival should be high and I expect this to be expressed as high abundances of porcelain crab larvae.

Thus, in addition to the direct influence of physical factors on porcelain crab larvae, I am also interested in the influence of temperature and salinity on phytoplankton as the base of the food web and whether changes in phytoplankton abundance could be followed up the food web to porcelain crab zoeae. As mentioned above, temperature impacts the metabolic rate of all organisms. Many studies in the lab and the field have found correlations between temperature changes and phytoplankton growth and abundance (Berges *et al.* 2002, Falkowski & Raven 1997). Optimal conditions for phytoplankton growth are a balance between light and nutrient availability (Klausmeier & Litchman 2001). Light availability is influenced by turbidity of the water which is increased by mixing. However, nutrient availability is also increased by mixing or upwelling. Calm, stratified waters may increase light penetration and temperature but nutrients may be limiting. On the other hand, mixing can decrease water temperature, increase turbidity and increase the possibility that phytoplankton are transported out of the photic zone. Thus, phytoplankton abundance and growth is a complex interaction of factors, one of which is temperature. While temperature can directly impact phytoplankton growth it is also an indicator of other water conditions such as water column stratification which can also be important for phytoplankton growth, distribution and abundance.

OCEANOGRAPHY OF THE WEST COAST OF VANCOUVER ISLAND

Macrozooplankton, including porcelain crab zoeae, are the principal food for organisms at several trophic levels including fish, seabirds and marine mammals (McFarlane *et al.* 1997, Mackas & Galbraith 1992). The majority of abundant marine bird species on the west coast of Vancouver Island are either planktivorous or feed on small planktivorous fish (Mackas & Galbraith 1992). Additionally, juvenile fishes tend to be planktivorous regardless of their dietary preferences as adults (Morgan 1990). Specifically, porcelain crab larvae have been important prey items at times for juvenile salmon (I. Perry pers. comm.), Cassin's auklets (G. Jensen pers. comm.), and gray whales (Dunham & Duffus 2002). Macrozooplankton are also the main consumers of large phytoplankton and microzooplankton, placing them in an important intermediate position in the food web (McFarlane *et al.* 1997). Thus, zooplankton community dynamics are likely to play a significant role in the coupling between oceanographic variability and overall community response (Mackas 1995, Bertram *et al.* 2001).

Oceanographic studies of the west coast of Vancouver Island continental shelf have been conducted for decades (Lane 1962). The area is dominated by winds from the northwest during the summer, resulting in upwelling conditions which bring nutrients into the surface waters (Crawford & Thomson 1991, Thomson 1981). This increased nutrient availability combined with surface warming and increased day length result in spring and summer phytoplankton blooms (Thomson 1981, Mackas 1992). The major current at the continental shelf break runs southward in the summer. However, a more nearshore current, the Vancouver Island Coastal Current, driven by freshwater outflow mainly from the Fraser River runs northwest along the coast of the island (Freeland 1992). Despite regular upwelling bringing colder, more saline water to the surface, the warming effects of the sun's increased intensity and longer day length result in increased temperatures to about 50 m depth during the summer months (Mackas 1992). Water temperature for the upper water column generally ranges between 9 and 13 °C annually (Mackas & Galbraith 1992, Mackas *et al.* 2001). Upper water column salinity is lowest during the spring just before upwelling begins and ranges annually between approximately 31 and 32 psu (Mackas *et al.* 2001).

While much has been learned about the continental shelf of Vancouver Island, particularly around the La Perouse Bank and Juan de Fuca eddy regions, most oceanographic sampling is conducted on the scale of several hundred kilometres and once per month or season. Smaller scale changes in oceanography over space and time have been less intensively studied but reversals in seasonal conditions for days to a week are common in the Pacific Northwest (Hickey & Banas 2003). It is these smaller scale temporal changes that are responsible for the multiple phytoplankton blooms that occur throughout the summer months off Vancouver Island. The timing and spatial extent of these blooms could have large implications for zooplankton distribution and abundance.

Over the last several years, studies of baleen whales which incorporate several oceanographic factors and use standard oceanographic equipment that allow sampling of the entire water column or samples at multiple depths have become more common (Murison & Gaskin 1989, Kenney & Wishner 1995, Croll *et al.* 1998, Benson *et al.* 2002, Baumgartner *et al.* 2003). However, these studies have focused on deep water species and follow the general oceanographic procedure of low temporal and spatial resolution sampling. In addition to the relative lack of information on small scale oceanography, there is almost nothing known about oceanographic conditions and variability in the nearshore zone. Gray whales are unique among baleen whales in that they spend the majority of their time in shallow water near shore. In Clayoquot Sound, gray whales forage in water depths less than 30 m and less than 2 km from shore the majority of the time and are regularly observed only a few meters from shore. The interest in understanding the dynamics of porcelain crab larvae as potential gray whale prey required that I gain knowledge of variability in oceanographic factors which may influence porcelain crab larvae distribution and abundance. This, in turn, provided the opportunity to examine oceanography of the relatively unknown nearshore area.

OBJECTIVES AND HYPOTHESES

The objectives of this study are as follows:

1) Document spatio-temporal variation in porcelain crab larvae such as abundance, density, distribution and patch characteristics such as size, location and duration during the gray whale feeding season.

2) Determine the role of pelagic porcelain crab larvae in the spatial determination of foraging gray whales by correlating presence and number of whales with presence and density of larval patches.

3) Document small scale spatial and temporal variability in temperature, salinity and chlorophyll fluorescence of this nearshore area.

4) Examine the relationship between physical oceanographic factors, chlorophyll fluorescence and porcelain crab larvae density.

5) Determine the timing of larval release by adult porcelain crabs in the study area and correlate larval release with the peak in stage I zoeae.

Related to these objectives and based on information available in the literature, I established specific questions and hypotheses to address during this study. First, based on knowledge provided by previous studies in the area, I expect that high densities of porcelain crab larvae will only be present for short periods of time and that the increased density of larvae will be spatially discrete rather than encompassing the entire study area. Second, I hypothesize that gray whales will abandon other prey items to forage on porcelain crab larvae when they are present in high densities. The third objective addresses the oceanographic variability of this exposed nearshore study area. In designing this study I intend to describe the variation in temperature, salinity and chlorophyll fluorescence in the study area, however, I do expect to see some general trends. I expect that temperature will increase over the study period but that significant spatial variation in temperature will not be present. I hypothesize that chlorophyll fluorescence will be high at the beginning of the study period after the spring bloom and that levels will drop off over the season with the exceptions of small blooms.

Fourth, given that temperature and salinity are known to influence survival, growth and development of crab larvae, I ask: is the presence of dense patches of porcelain crab larvae related to physical oceanography of the area? Is there a history of higher temperature or persistent upwelling providing nutrients to the food web prior to the appearance of dense patches? I hypothesize that increased water temperature will lead to an increase in the proportion of stage II zoeae in plankton samples. I also expect that upwelling conditions, expressed as decreases in temperature will be followed by increases in chlorophyll fluorescence. As the base of the food web, phytoplankton ecology influences organisms throughout the web via food availability. Is there a correlation between phytoplankton, measured as chlorophyll fluorescence, and porcelain crab larvae density? I hypothesize that increased levels of chlorophyll fluorescence will result in increased survival of porcelain crab zoeae expressed as higher densities of zoeae in the plankton. Fifth, when high densities of adults produce larvae that are synchronously released, a pulse of larvae may be detected in the water column. Do porcelain crabs release larvae in response to predictable cues? Are patches of porcelain crab larvae controlled by the timing and extent of reproductive events? I hypothesize that an increase in larval release by adult crabs will result in increased densities of porcelain crab zoeae in the water column.

To address these questions and hypotheses, this study consisted of several parts. Gray whale surveys were conducted every few days to monitor the number of whales in the study area and determine the prey type of feeding whales. CTD/fluorometer casts and plankton net tows were conducted at 26 stations approximately once per week to document the oceanographic conditions and distribution and abundance of porcelain crab larvae. Adult *Petrolisthes cinctipes* (Randall 1839) at three locations in mussel beds along the shore were monitored for egg presence and development status to determine the time of larval release.

This thesis is organized into four results chapters. In Chapter 2, I address the variability in temperature, salinity and chlorophyll fluorescence observed over space and time. Chapter 3 focuses on the results of the plankton tows and I make comparisons between environmental conditions and porcelain crab larvae. Chapter 4 consists of the results of the larval release study. Chapter 5 is a short description of an interesting oceanographic phenomenon, thin layers of phytoplankton, which I documented during 3 sampling days.

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CHAPTER 2: OCEANOGRAPHIC VARIABILITY IN AN EXPOSED NEARSHORE ENVIRONMENT OF A GRAY WHALE FEEDING AREA

INTRODUCTION

Previous research in Clayoquot Sound, on the west coast of Vancouver Island, British Columbia has shown that gray whale habitat use is not uniform, reflecting a patchy distribution of prey in space and time (Meier 2003). However, drivers of the spatial patchiness and seasonal variability of gray whale prey, such as mysids (Mysidacea), amphipods (Gammaridea) and porcelain crab larvae (Porcellanidae), are not understood. These factors are difficult to identify and assign importance unequivocally due to the three dimensional aspect of marine habitat and the involvement of numerous physical and biological factors acting on multiple spatial and temporal scales. Therefore, an early but important step in understanding this spatial and temporal patchiness is the description of variability in factors considered important in determining prey biomass.

Prey biomass is determined by survival, growth, reproduction and aggregation and each of these are influenced by many factors themselves. Temperature and salinity directly influence phyto- and zooplankton survival and growth (Anger 2003, Berges *et al.* 2002, Daunt *et al.* 2003, Gessner 1970, Kalle 1971, Kinne 1970, Moloney *et al.* 1994, Reay *et al.* 2001, Spivak 1999). Variation in temperature and salinity can also be used as an indicator of changes in water types, such as fronts, which may act as barriers, transporters or accumulation zones for zooplankton patches (Daunt *et al.* 2003, Franks 1992, Olson *et al.* 1994, Pineda 1991). In addition, phytoplankton distribution and abundance, as the base of the food web, influences growth, survival, distribution and abundance of higher trophic levels through predator-prey interactions. In this study I document the temporal and three dimensional spatial variation in temperature, salinity, and chlorophyll *a* concentration, as a proxy measure of phytoplankton concentration, at a nearshore gray whale (*Eschrichtius robustus*) summer foraging ground.

A fifteen-year study of zooplankton off Vancouver Island found that nearly all zooplankton taxa documented exhibited large year to year variations in abundances which correlated with changes in several environmental indices (Mackas *et al.* 2001).

However, the authors note that small and unpredictable interannual shifts in environmental indices not documented due to the large temporal (once per season) and spatial (100s of km) scale of the study may result in more extreme community changes than those associated with the larger seasonal cycle (Mackas *et al.* 2001). In fact, oceanographic variability on the scale of days to a week is dominant in the Pacific Northwest often reversing seasonal conditions particularly nearshore (Hickey & Banas 2003). Cowles *et al.* (1998) found that small-scale changes in environmental variables and phytoplankton structure were persistent enough to have important impacts on the plankton community. Thus the commonly used large scale spatial and temporal resolution, results in severe limitations in data leaving many questions unanswered and small scale changes described by Cowles *et al.* (1998) undocumented (Daunt *et al.* 2003).

Related to and confounding the issue of scale, is the fact that very little is known about nearshore (<4 km from shore) oceanography, particularly in exposed environments (Narváez *et al.* 2004, Weiters *et al.* 2003). The concentration of oceanography on offshore areas is partially a result of the assumption that the nearshore zone is mostly homogeneous due to wind and wave mixing (Menge *et al.* 2002, and references therein). Recently however, studies of the nearshore zone conducted on spatial scales of 10s of km have shown that temperature and levels of chlorophyll *a* concentration vary significantly both spatially and temporally (St. Lawrence estuary - Archambault *et al.* 1999; Oregon - Menge *et al.* 1997a&b, 2002, Shanks & McCulloch, 2003; New Zealand - Menge *et al.* 2003; Chile - Weiters *et al.* 2003, Narváez *et al.* 2004). Additionally, some of this temporal variation in chlorophyll *a* concentration has been attributed to physical factors including temperature stratification and wind mixing even in waters only 25 m deep (Weiters *et al.* 2003, Yin *et al.* 1996).

The present study was conducted in a shallow, wave exposed environment with a maximum tidal amplitude of 3.6 m during the study period. Much of the water movement in this area is classified as turbulent (Kopach 2004). Given the depth, exposure to wind and waves and large tidal amplitude, the water column should be mixed. Nonetheless, in highly turbulent areas at other locations, small scale heterogeneity in temperature, nutrients and chlorophyll have been found (Seuront *et al.* 2002, Sharples *et al.* 2001). Water column structure such as this can have important implications for plankton concentration and growth. Through the present study I investigate fine (1 to 1000 m) to coarse (1 to 100 km) spatial scale and temporal (days to months) variation of nearshore oceanographic conditions in gray whale feeding habitat in Clayoquot Sound, BC. Specifically I examine temperature, salinity and chlorophyll *a* fluorescence of the water column at stations throughout the study area between June 15 and September 5, 2002 (Figure 1). The questions addressed in this study are: 1) Do temperature, salinity and chlorophyll *a* fluorescence of the nearshore marine environment vary in time and/or two dimensional space? 2) Is the water column mixed or is fine scale vertical structure present and persistent? 3) Is there evidence chlorophyll *a* concentration responds to changes in temperature and salinity on this spatial and temporal scale?

METHODS

THE STUDY AREA

This study was conducted along 12 km of the southwest edge of Flores Island (49°17'N, 126°10'W) in Clayoquot Sound, British Columbia between Dagger Point in the north and the Fitzpatrick Islands in the southeast (Figure 1). The majority of the study area is less than 30 m deep. The coastline is characterized by rocky shores and kelp beds interspersed with sandy beaches and cobblestone bays. This substrate variability results in different habitat types which support three main gray whale prey types: benthic amphipods found in sandy bottom habitat of Cow Bay, hyperbenthic mysids in nearshore areas where kelp forests and boulder substrate occur and planktonic porcelain crab larvae occasionally found in dense patches off Rafael Point (Dunham & Duffus 2001). Most of the study area, excluding the western edge of Cow Bay, is exposed to prevailing summer wind waves from the northwest.

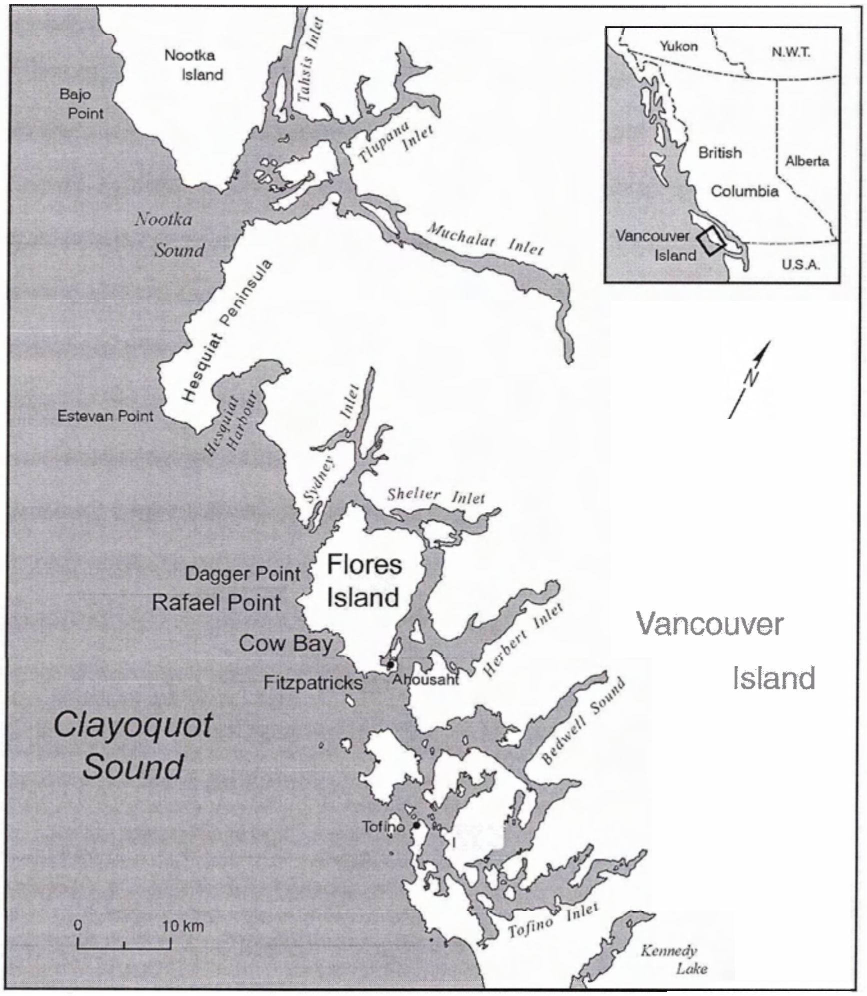


Figure 1: Location of the study area within Clayoquot Sound, BC.

OCEANOGRAPHIC SAMPLING

To determine the variability of oceanographic conditions I measured temperature, salinity and chlorophyll fluorescence using a Seabird *SBE 19plus* SEACAT Profiler CTD and attached WetLabs EcoFL Fluorometer between June 15 and September 5, 2002 at 26 stations located along the southwest edge of Flores Island (Figure 2). Station locations were chosen to coincide with water circulation transects completed in 2001 (Kopach 2004) with the highest concentration of stations placed within areas where porcelain crab larvae have been known to occur (Dunham & Duffus 2001, 2002). Stations off Rafael and Dagger Points were spaced, on average, 549 m apart (SD = 25.5 m). Average water depth of the stations is 17 m (SD = 8.0 m). Vertical profiles of temperature, salinity and chlorophyll *a* fluorescence were obtained for the entire water column at each station. At the beginning of each cast the CTD was raised to allow the sensors to sample within approximately the upper 20 cm of the water column and then was lowered to the bottom at a rate of approximately 1 m/s. Only data from the downcast were used for analysis. Sampling rate of the *SBE 19plus* CTD is 4 Hz (4 samples per second). Accuracy of the *SBE 19plus* is 0.005 °C (range: 5 to 35°C), 0.0005 S/m (translates to 0.0048 psu) and 0.6 m (resolution = 0.012 m) (Sea-bird Electronics 2001). The fluorometer was calibrated prior to the field season at Sea-bird labs in Bellevue, WA. Fluorescence measurements presented as chlorophyll *a* concentration represent relative chlorophyll *a* concentrations as they were not calibrated against extracted chlorophyll *a* samples from the study area. Complete sampling consisted of CTD/Fluorometer casts and plankton samples at all stations. Sampling was conducted approximately once per week, weather permitting, which resulted in 11 full sampling occasions distributed as follows: 2 in June, 4 in July, 4 in August and 1 in September. Periods between sampling occasions ranged from 4 to 13 days.

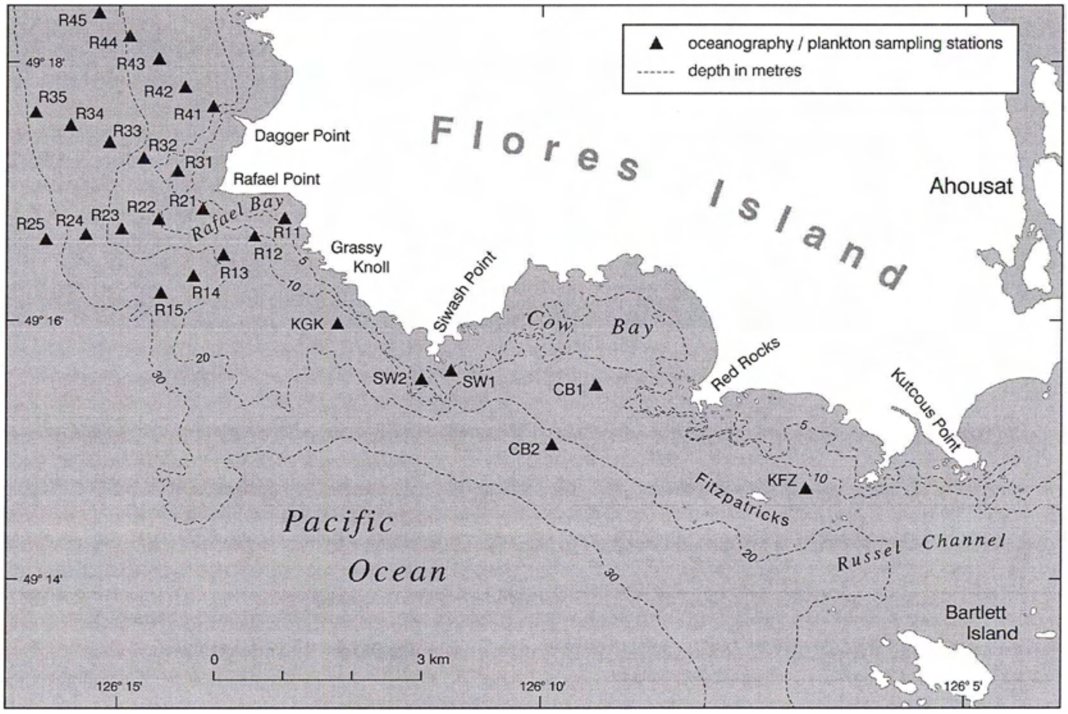


Figure 2: Location of sampling stations within the study area.

DATA ANALYSIS

CTD cast data were processed using Sea-Bird's SBE Data Processing software (Sea-Bird Electronics 2001). Initial data screening included removal of all data points during water pump priming at the surface and data points obtained when the CTD was not moving or was moving upwards due to swell. Based on the shallow depth of the study area, the decision was made to maintain all remaining data as individual data points rather than averaging data over vertical distances prior to analysis. This allows for detection of small scale vertical changes to the limit of the instrument without being overloaded with excessive amounts of data as would be the case if data were not averaged in deep water casts. Vertical profiles of CTD casts were produced by SBE Data Processing Sea Plot function.

Means per sampling date presented in temporal results were calculated by averaging mean per cast of all stations per day. For the spatial results either surface values or the top 10 m of the water column were used to allow direct comparisons between stations while minimising the effect of the depth of the station on the results. When using the top ten metres, 2 stations (R11 and SW2) were excluded from the analyses because the depth of these stations was less than 10 m.

Vertical section plots were produced with Surfer 8 software using Kriging gridding method. No smoothing of contours was introduced. Section plots show depth in metres on the y-axis and station number on the x-axis with most offshore station positioned on the left side and most nearshore station located on the right. Distance between each station and shore is provided in Table 1. Contours represent 0.2 °C and 2 mg/m^3 chlorophyll *a* concentration.

To closely examine spatial variation in chlorophyll *a* concentration, average chlorophyll concentration for the top 5 m of the water column at each station were compared on each sampling date. The top 5 m was selected for two reasons, the shallowest station sampled had a depth of just over 5 m (R11) and the chlorophyll maximum occurred at a depth of less than 5 m in the majority of casts (see vertical results). Contour maps of chlorophyll *a* concentration of the top 5 m were produced using Radial Basis Function Multiquadratic interpolation gridding method without smoothing in Surfer 8. Contours represent 1 mg/m^3 chlorophyll *a* concentration.

To aid in the interpretation of data collected during this study, I also consulted datasets available to the public. Tidal amplitudes were calculated from tidal height predictions in the Canadian Tide and Currents Tables (Fisheries and Oceans Canada, 2002). Upwelling information was obtained from the National Oceanic and Atmospheric Administration's Pacific Fisheries Environmental Laboratory (PFEL) website (www.pfeg.noaa.gov). The PFEL's Daily Coastal Upwelling Index is calculated from six-hourly atmospheric pressure field data for 15 sites along the North American Pacific Coast. PFEL's Upwelling Index average daily values for the two locations nearest to my study area, 48° N 125° W and 51° N 131° W, were downloaded and plotted for comparison with data collected in my study.

RESULTS

1) TEMPORAL AND SPATIAL VARIATION IN NEARSHORE PHYSICAL OCEANOGRAPHY OF FLORES ISLAND

Temporal Variation

Mean water temperature for each cast averaged across all stations varied from a low of 10.37 °C (SE = 0.090) on July 15 to a high of 12.61 °C (SE = 0.163) on September 5 (Figure 3). The temperature increase across the season from 11.36 °C (SE = 0.042) on June 15 to 12.61 °C (SE = 0.163) on September 5 is similar to or smaller than some of the changes in temperature between sampling dates (July 07 to 15 to 19, July 25 to August 01 and August 30 to September 05) (Figure 3).

Average surface temperature generally increased over the season from 11.85 °C (SD = 0.266) on June 15 to 13.78 °C (SD = 0.407) on September 5 (Figure 4). However, decreases in surface temperature of 1 °C or more were evident between July 15 and 19 and August 7 and 20 (Figure 4).

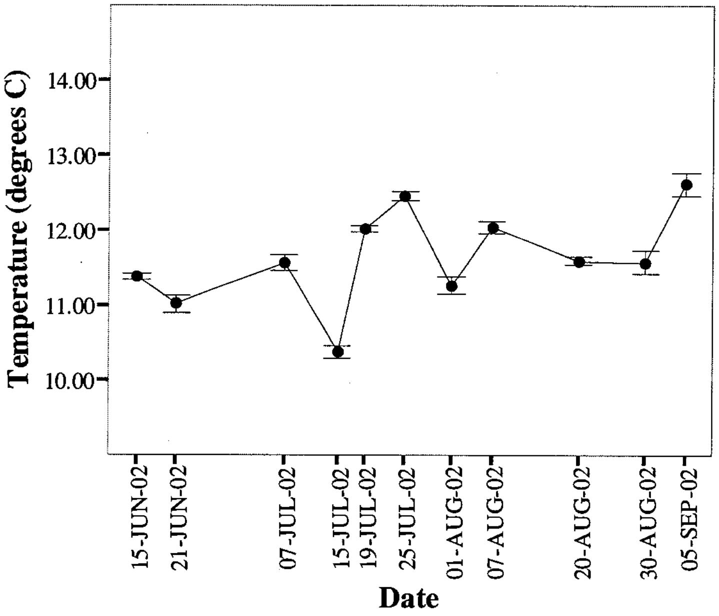


Figure 3: Mean water temperature (error bars = 1 SE) at all stations across the sampling period. Each point is an average of all stations sampled on a particular day (max = 26).

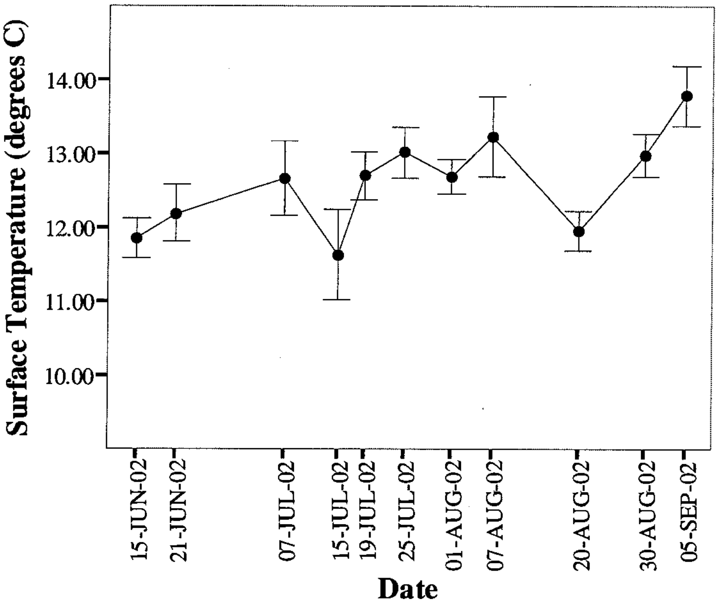


Figure 4: Mean surface temperature of all stations across the sampling period (error bars = 1 SD).

Minimum mean salinity was 31.168 psu (SE = 0.0615) on July 7, while the maximum mean salinity of 31.862 (SD = 0.0525) occurred on July 15, the next sampling date (Figure 5). The minimum mean value per cast, 30.585 psu, occurred on July 7 at SW2 and the maximum, 32.115, at R32 on July 15.

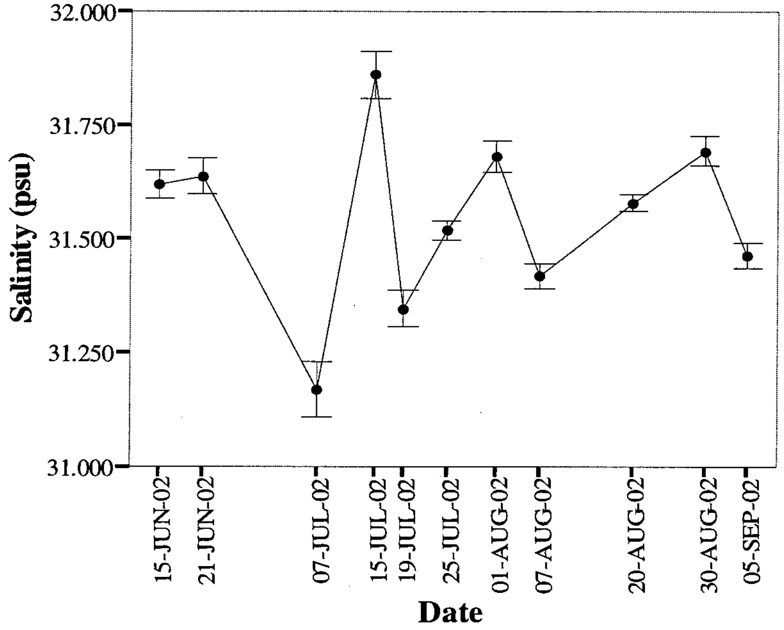


Figure 5: Mean salinity per cast averaged for all stations (error bars = 1 SE) over the field season.

Spatial Variation

When depth of the station was accounted for by including only the top 10 m of the water column, spatial variation in mean temperature pooled across all dates was minimal. However, close examination of surface temperatures on each day indicates that nearshore stations often have a colder surface temperature than stations further offshore (Figure 6). Although very slight on some days, increasing surface temperature with increasing distance from shore was present for some stations on all sampling days (Figure 6). The spatial extent of this trend included up to all 5 stations within a station line with surface temperature increasing from inshore to offshore between 0.23 to 1.69 °C (mean = 0.702, SD = 0.4197).

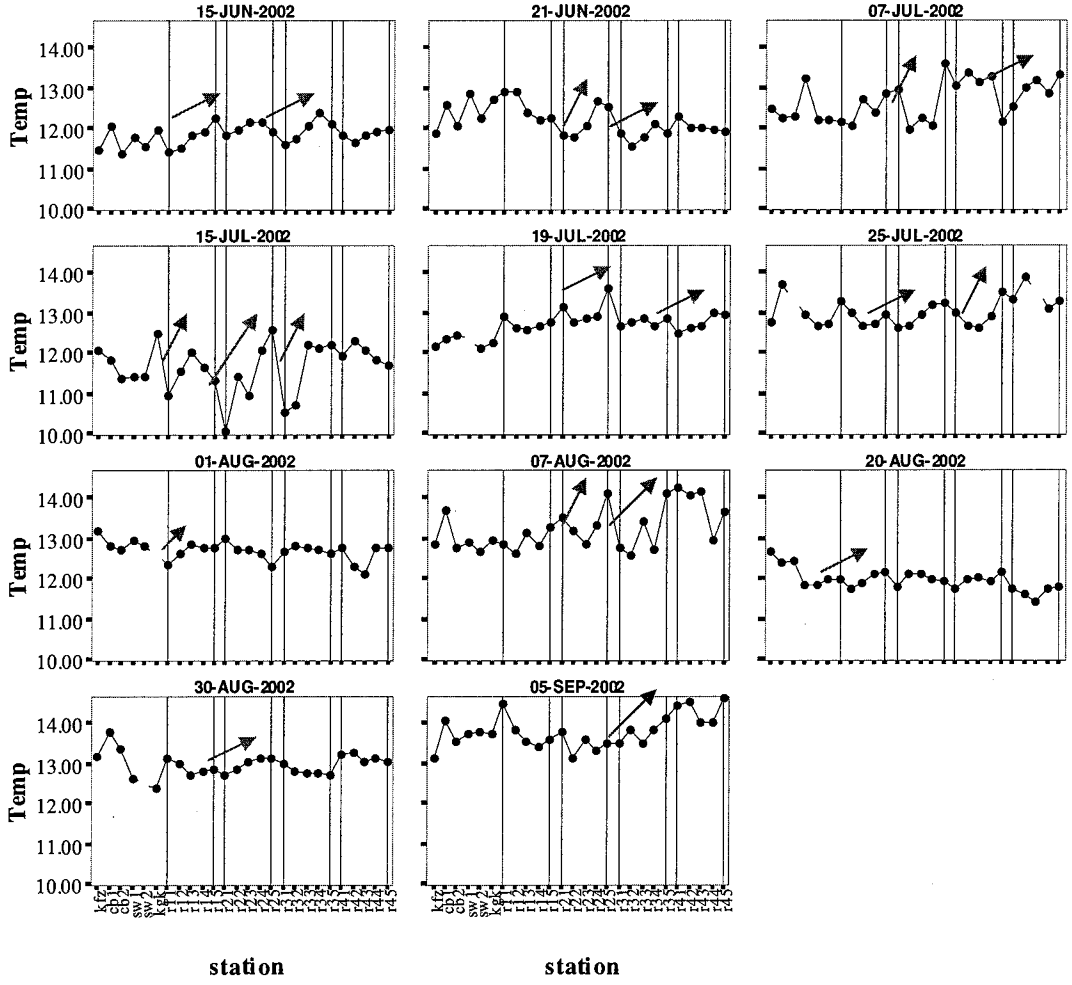


Figure 6: Surface temperature of all stations on each sampling date. Stations are arranged along the x-axis in general order of east to west and inshore to offshore where stations are in the same general east-west location (example CB1, CB2 and SW1, SW2). Reference lines indicate stations R11, R15, R21, R25, R31, R35, R41 and R45 from left to right. Gray arrows (not precisely placed) indicate increasing surface temperature from inshore to offshore.

Spatial variation in mean salinity of the top 10 m pooled across dates was also minimal (Figure 7). The lowest mean salinity for the top 10 m was located at KFZ, the station nearest the entrance to Clayoquot Sound at the southern end of Flores Island (Figure 7).

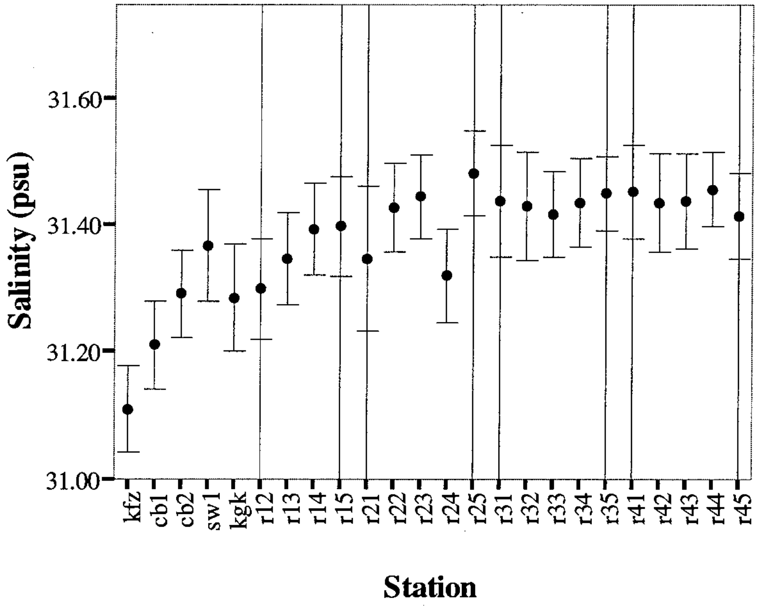


Figure 7: Mean salinity (psu) (error bars = 1 SE) for the top 10 m of each station averaged over the field season. Stations R11 and SW2 were excluded as the depth of these stations are less than 10 m. Reference lines indicate R12, R15, R21, R25, R31, R35, R41 and R45.

Vertical Variation

To determine if the water column was mixed or if vertical structure of physical characteristics was present, vertical variation in temperature and the presence of thermoclines was examined. Water column mixing of the top 20 m was evident on some days (June 15, July 19, 25, August 20), however, despite the area being shallow, exposed to wind, waves, currents and tides, the water column cannot be assumed to be mixed during the summer months (Figure 8).

Water temperature range within a cast differed from a low of 0.02 °C at R21 on July 25 to a high of 4.51 °C at R25 on August 07 (mean = 1.83 °C, SD = 1.134 °C), indicating variation in the water column from mixed to stratified. The lowest average temperature range per day of 0.82 °C (SD = 0.688 °C) occurred on August 20. In contrast, August 1 had the highest mean daily temperature range of 1.54 °C (SD = 0.774 °C) with a maximum temperature difference of 3.31 °C over 26 m at R14. Vertical profiles of individual casts show that the water column was mixed from the surface to approximately 25 m on August 20 (Figure 9 a&b). Stations deeper than 20 m showed a thermocline at 20 to 25 m (Figure 9 b) while stations less than 20 m deep were mixed (Figure 9 a). In contrast, profiles of casts from other days such as August 01 and September 05 showed stratification of the water column (Figure 9 c&d). September 05 also had a relatively high average temperature range of 2.23 °C (SD = 1.234 °C) and a maximum temperature difference of 4.28 °C over 30 m at Station R35 (not shown).

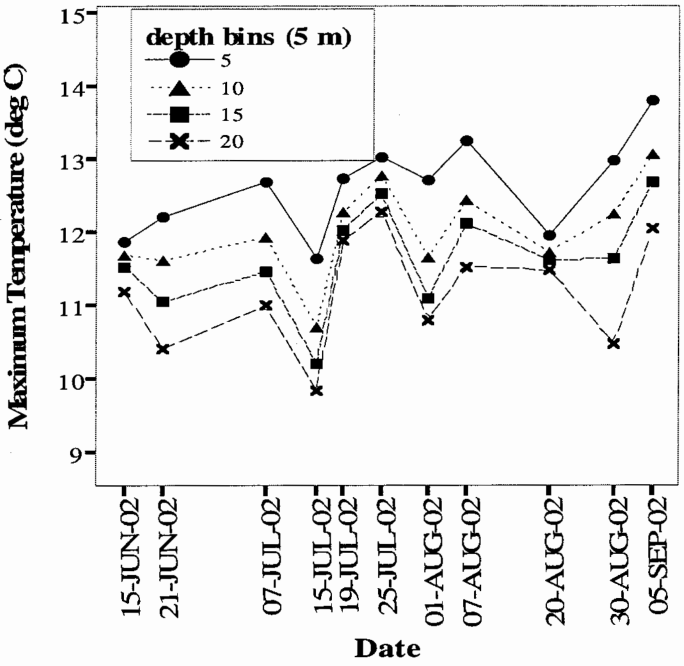
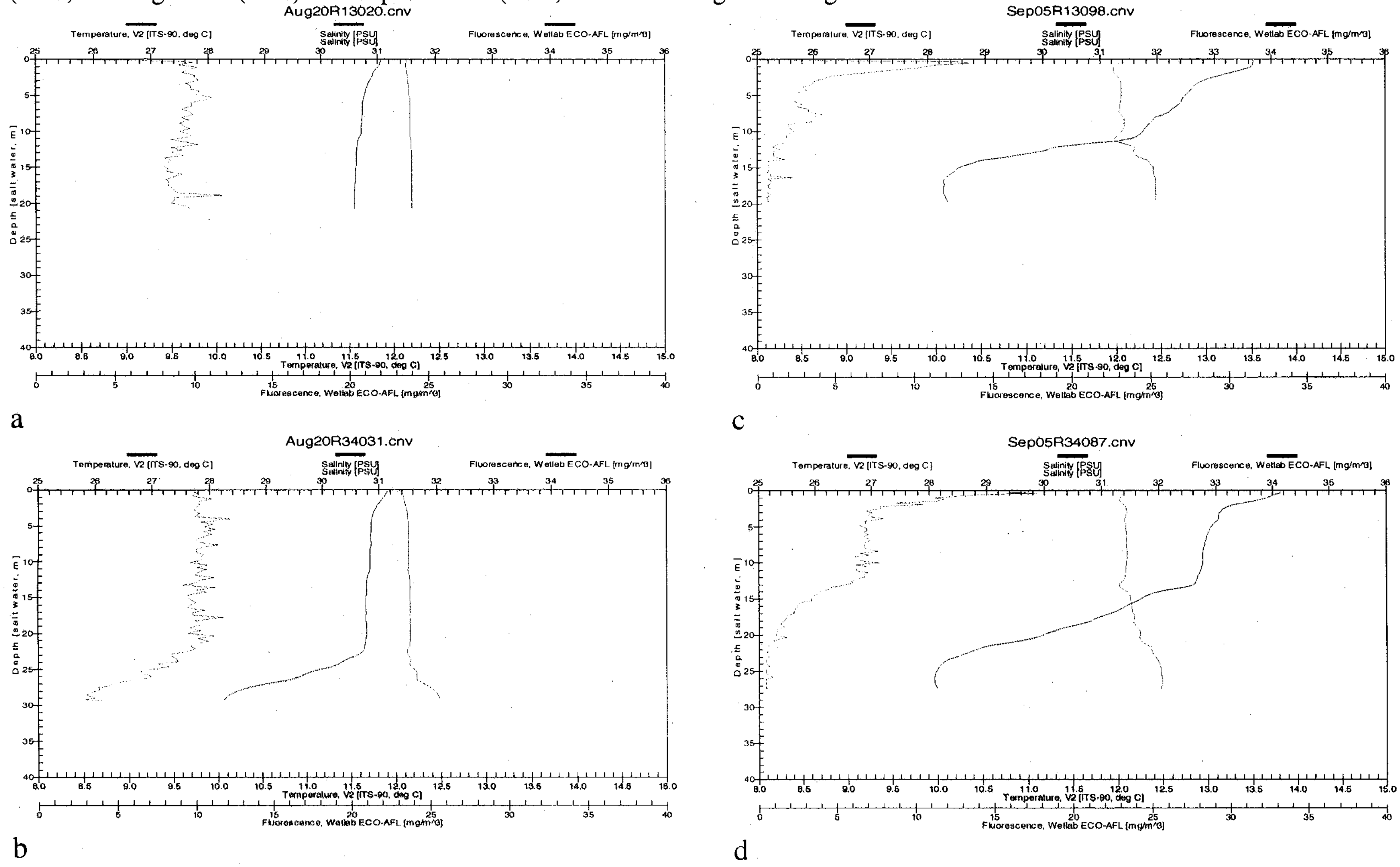


Figure 8: Average maximum temperature within a 5 m depth bin for the top 20 m (N = 14- 26). Depth value listed in the legend is the maximum depth within a bin (ie: 5 = 0-5 m). Depths over 20 m have been excluded due to small sample size.

Figure 9 a-d: Vertical profiles of temperature (blue), salinity (red) and chlorophyll fluorescence (green) at R13 (a&c) and R34 (b&d) on August 20 (a&b) and September 5 (c&d) demonstrating the change from mixed to stratified water column.



To quantitatively assess temperature stratification within the water column, casts were divided into 5 m depth bins and the temperature change within each bin was determined. The average temperature change within the resulting 1218 depth bins was 0.402 °C (SD = 0.3980, min = 0 °C, max 2.014 °C, median = 0.280 °C). Given these values, results of other studies (Narváez *et al.* 2004) and the subjective general definition of a thermocline as a "layer at some depth below the surface where the temperature rapidly decreases with depth" (Baretta-Bekker *et al.* 1992, pg 279) a temperature change of 1.0 °C or more within a 5 m bin was defined as a thermocline. This analysis provides a conservative view of the temperature change within the water column as this method may divide an actual thermocline into two bins decreasing the possibility of detection. Despite this, over one third (106) of the 281 casts were categorized as having a thermocline somewhere within the vertical profile using this definition. Over half of the stations, on June 21, August 1, 30 and September 5 exhibited thermoclines while nearly half the stations had thermoclines on July 15 and August 7 (Figure 10). The spatial distribution of thermoclines shows that deeper stations were classified as having thermoclines more frequently than shallow stations (Figure 11). Six stations were stratified during over half of the sampling occasions and an additional 3 stations were stratified on 5 of the 11 sampling occasions (Figure 11). However, no stations were categorized as having thermoclines on all sampling days (Figure 11). Visual examination of vertical profiles indicates that this is partially due to the method of categorizing the thermocline as mentioned above. Water column mixing appears to influence primarily the top 20 – 25 m as stations deeper than 20 m showed a rapid decrease in temperature below this depth even on days when most of the water column would be considered mixed (Figure 9 b).

Many casts collected from deeper stations exhibited a surface thermocline and a deep thermocline (example: Figure 9 d). As mentioned above, even if mixing was strong in the upper water column a deep thermocline was often present. This deep thermocline could indicate the limit of wind mixing from above, or cold, deeper origin water being pulled along the bottom via upwelling or large amplitude tides.

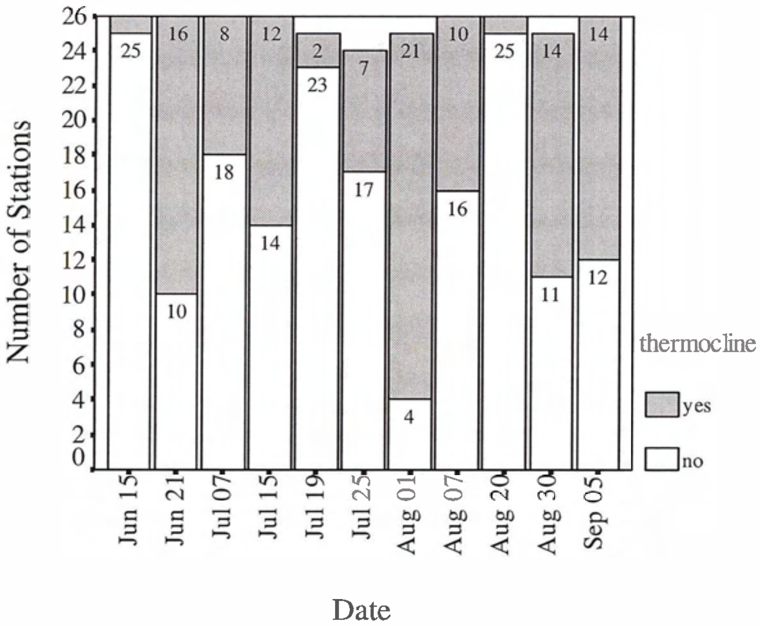


Figure 10: Number of stations with and without thermoclines across the season.

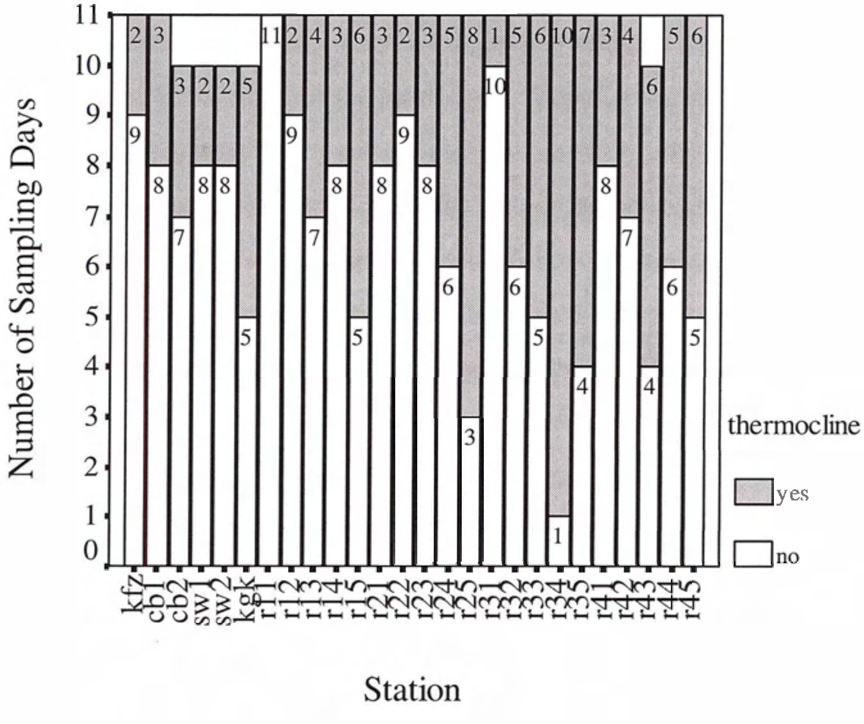


Figure 11: Number of sampling days that the water column was categorized as having a thermocline for each station.

Upwelling/Mixing Events

The nonlinear temporal temperature and water column structure changes observed in this study indicate physical events resulting in mixing or stratification possibly through upwelling and upwelling relaxation. The spatial trend of increasing surface temperature in an offshore direction and the presence of deep water thermoclines discussed above could be evidence of upwelling. To describe the frequency and spatial extent of upwelling in the study area, vertical section plots of water temperature and chlorophyll concentration for the four lines of stations around Rafael and Dagger Point were examined and compared with changes in mean and surface temperature over time (Figures 12, 13 – 23). Chlorophyll concentration results will be discussed in more detail in the next section of this chapter but are discussed here as an additional method of determining water movement. Distance from shore, distance between stations, station numbers and station names are given in Table 1.

Vertical section plots display the thermocline strengthening, weakening and changing position over the course of days (examples: Figures 18, 19, 21, 22). Following the 11°C isotherm over time shows that temperature at a given depth varies by several degrees as the 11 °C isotherm moves up and down within the water column for example, from approximately 5 m depth on July 15 to over 30 m on July 19 (Figure 16 & 17).

The largest drops in mean water temperature occurred between July 7 and 15 (11.56 to 10.37 °C) and July 25 and August 1 (12.45 to 11.25 °C) (Figure 12). Surface temperature dropped from 12.68 °C to 11.63 °C between July 7 and 15, but decreased only minimally between July 25 and August 1 (13.01 to 12.69 °C) (Figure 12). The largest surface temperature decrease of nearly 2 °C occurred between August 7 and 20 (13.23 to 11.35 °C) which was evident as a mean temperature decrease of only 0.44 °C (12.03 to 11.59 °C).

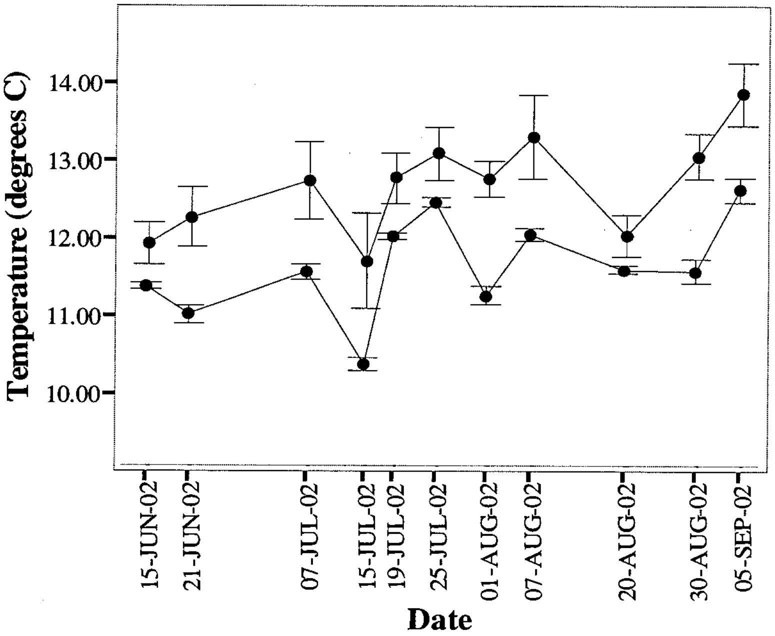


Figure 12: Temporal variation in surface temperature (top line, error bars = SD) and mean water temperature per cast averaged across all stations (bottom line, error bars = SE).

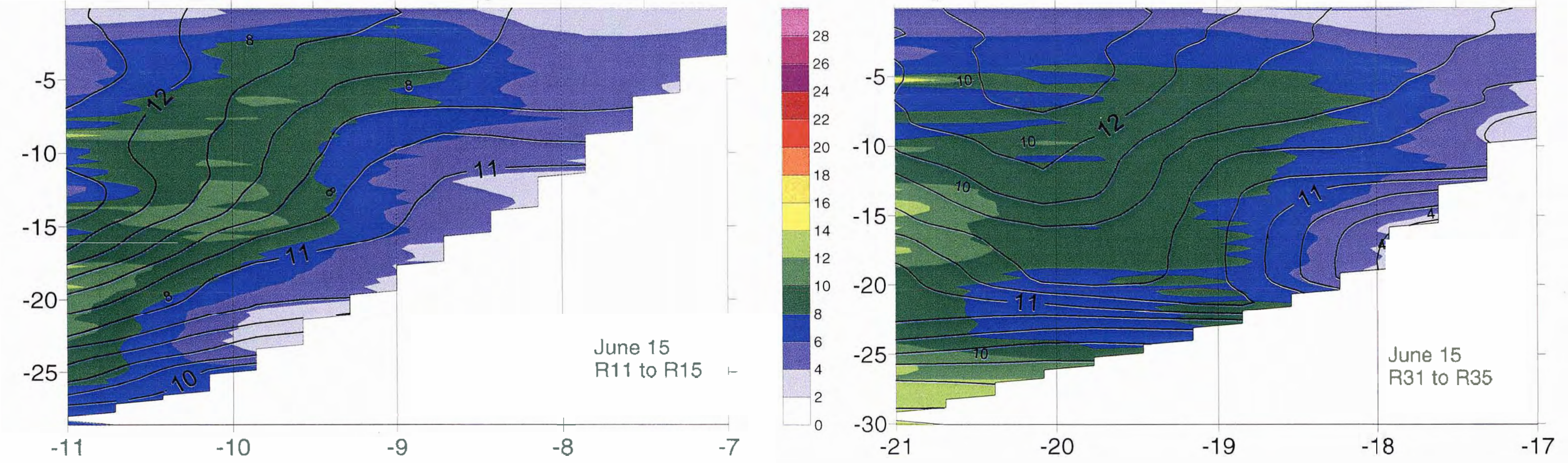
Between July 7 and 15, the 10 °C isotherm shifted from approximately 30 m to between 10 and 15 m with isotherms arching towards the surface at nearshore stations (R11, R12, R21, R22, R32) (Figures 15 & 16). Colder water moving up from deeper depths is also present between July 25 and August 1 as the 11 °C isotherm moved from between 25 and 30 m to between 10 and 15 m (Figures 18 & 19). On July 25 much of the water column (top 20 m) was warmer than 12 °C while on August 1 the 12 °C isotherm was within the top few metres except at the nearshore stations of line R4 (R41 and R42) (Figures 18 &19). This explains the small surface temperature decrease despite an average temperature drop of 1.2 °C (Figure 12). Between August 7 and 20, the water column changed from being quite stratified, with variation in temperature from the surface to the bottom of over 3 °C, to being mixed, with temperature variation as small as 0.6 °C from the surface to the bottom (Figures 20 & 21). Localized upwelling appears to be occurring on August 7 particularly at R34 seen as contours arching towards the surface (Figure 20 c). This period had the largest drop in surface temperature (Figure 12). Although surface temperature increased between August 20 and 30, mean temperature continued to decrease very slightly (11.59 to 11.56 °C) and the contour plots show that stratification has reformed along with colder water moving up along the bottom (Figures 12, 21, 22). These results support the idea that changes in surface and mean water column temperatures coincide with upwelling and mixing events.

Evidence of upwelling, such as doming or arching of isotherms towards the surface and/or water less than 10 °C along the bottom, was also present to a lesser extent or in localized areas on other days. This prevalence of upwelling is consistent with the Pacific Fisheries Environmental Lab's Upwelling Index which shows that the season was dominated by upwelling favourable conditions (Figure 24). Downwelling or upwelling relaxation is shown in the index for only for a few days at a time around June 15, between June 20 and 30, around July 17, between August 4 and 9, between August 24 and 29 and the first few days in September. The timing of upwelling relaxation/downwelling coincides with periods of temperature increases (Figure 12).

Table 1: Station information relevant to vertical section plots: station numbers as shown on vertical section plots (Figures 13 - 23), station name, distance from shore and distance between stations.

Station #	*Station Name*	*Distance from shore (km)*	*Distance from previous station (km)*	*Station #*	*Station Name*	*Distance from shore (km)*	*Distance from previous station (km)*
-7	R11	0.36		-17	R31	0.64	
-8	R12	0.86	0.50	-18	R32	1.20	0.56
-9	R13	1.42	0.56	-19	R33	1.77	0.57
-10	R14	1.94	0.52	-20	R34	2.31	0.54
-11	R15	2.51	0.57	-21	R35	2.89	0.58
-12	R21	0.70		-22	R41	0.37	
-13	R22	1.28	0.58	-23	R42	0.89	0.52
-14	R23	1.85	0.58	-24	R43	1.43	0.54
-15	R24	2.42	0.57	-25	R44	1.96	0.53
-16	R25	2.95	0.53	-26	R45	2.49	0.53

Figure 13 a–d: Section plots of temperature (line contours = 0.2 °C isotherms, large font) and chlorophyll (filled contours = 2 mg/m^3, small font) for stations (x-axis) vs depth (y-axis) on June 15. X-axis indicates stations heading offshore from right to left, as though viewing a slice of the water column along each line of stations. See Table 1 for precise distance from shore and station names.



a: R11, R12, R13, R14, R15 **b:** R21, R22, R23, R24, R25 **c:** R31, R32, R33, R34, R35 **d:** R41, R42, R43, R44, R45

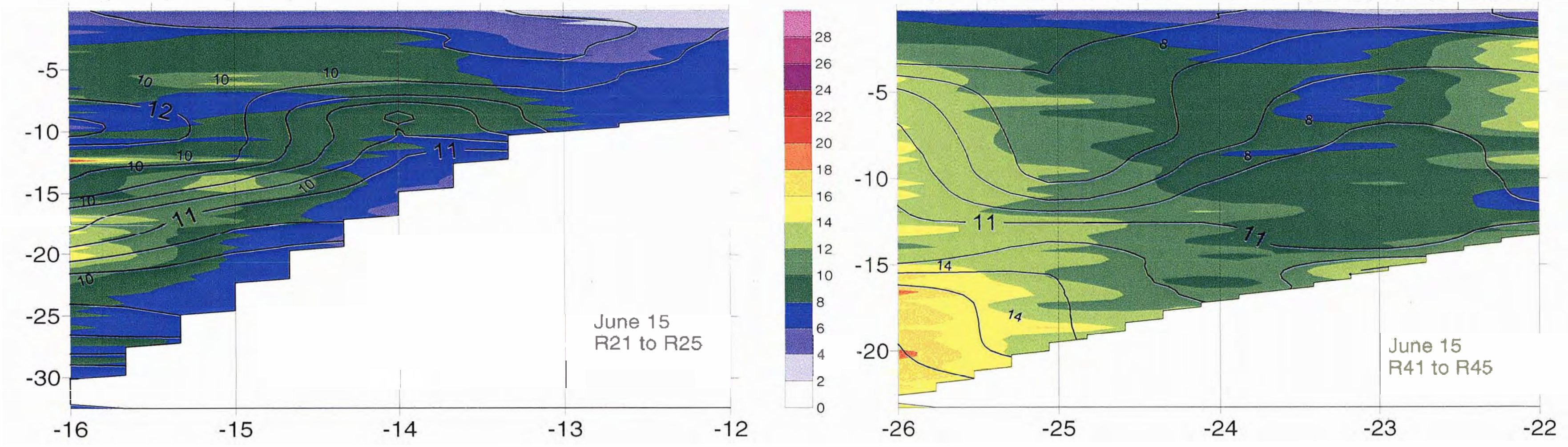
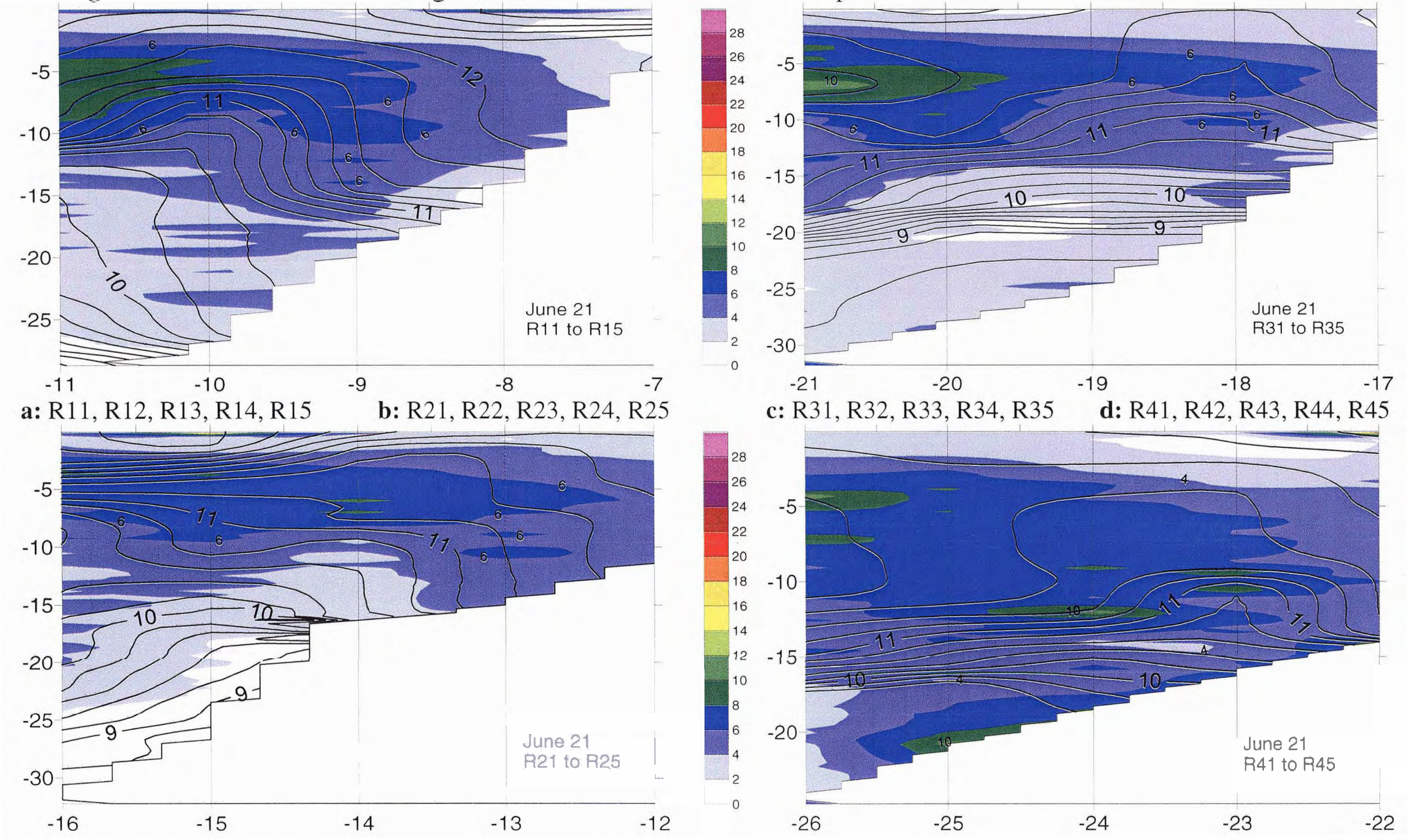


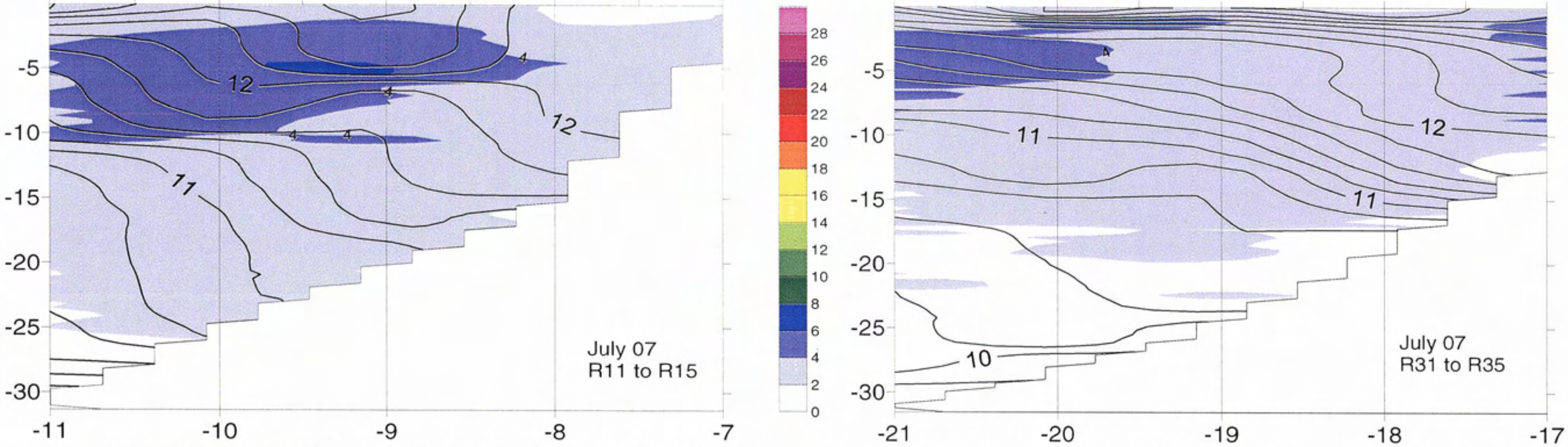
Figure 14 a–d: Section plots of temperature (line contours = 0.2 °C isotherms, large font) and chlorophyll (filled contours = 2 mg/m^3, small font) for stations (x-axis) vs depth (y-axis) on June 21. X-axis indicates stations heading offshore from right to left, as though viewing a slice of the water column along each line of stations. See Table 1 for precise distance from shore and station names.



a: R11, R12, R13, R14, R15 **b:** R21, R22, R23, R24, R25

c: R31, R32, R33, R34, R35 **d:** R41, R42, R43, R44, R45

Figure 15 a–d: Section plots of temperature (line contours = 0.2 °C isotherms, large font) and chlorophyll (filled contours = 2 mg/m^3, small font) for stations (x-axis) vs depth (y-axis) on July 07. X-axis indicates stations heading offshore from right to left, as though viewing a slice of the water column along each line of stations. See Table 1 for precise distance from shore and station names.



a: R11, R12, R13, R14, R15 **b:** R21, R22, R23, R24, R25 **c:** R31, R32, R33, R34, R35 **d:** R41, R42, R43, R44, R45

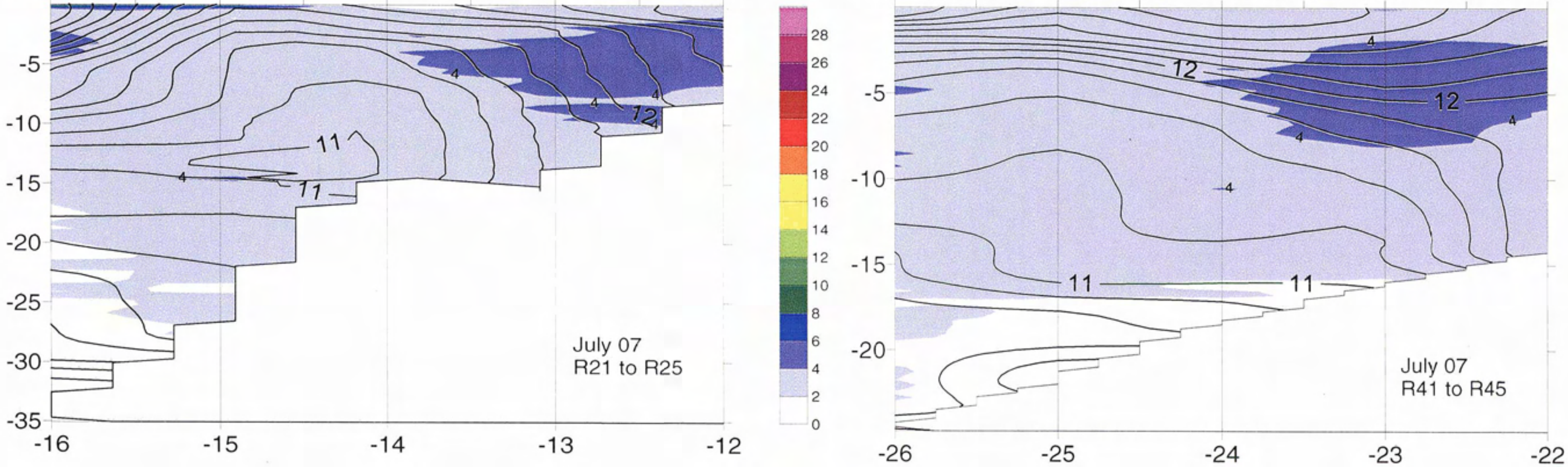
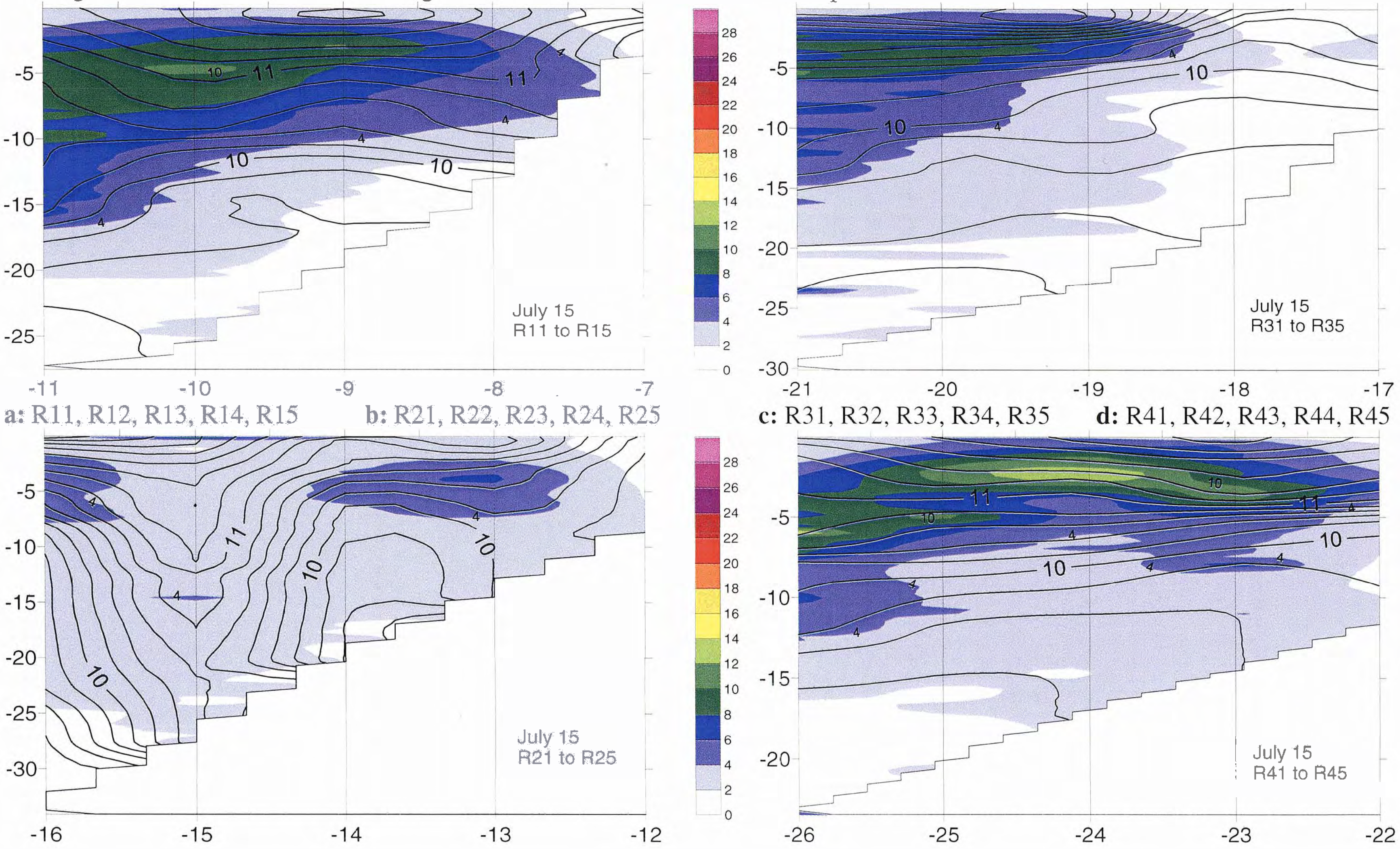
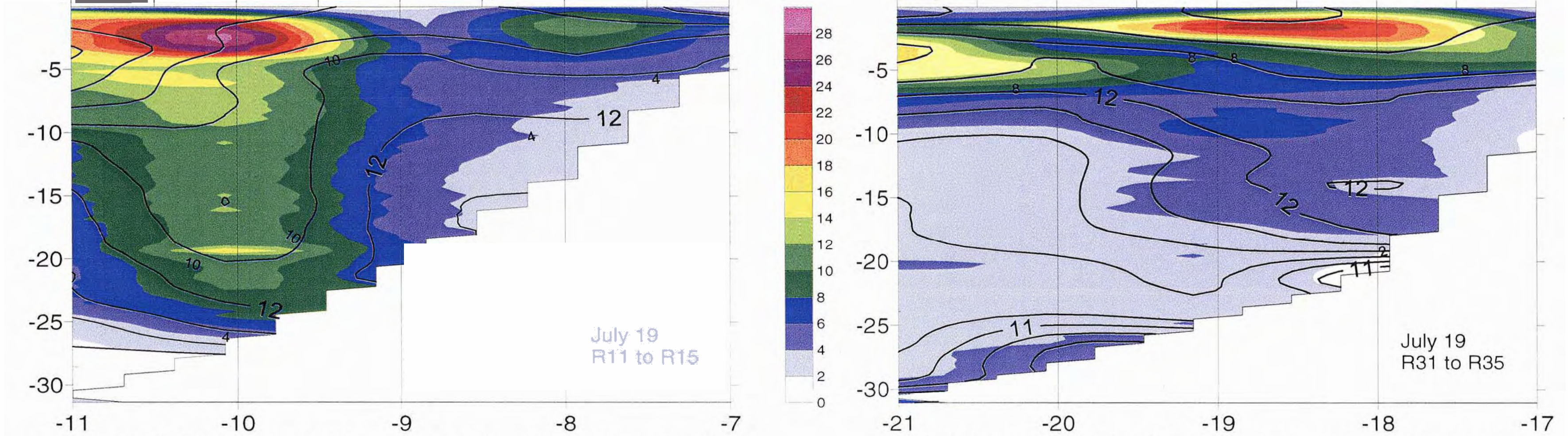


Figure 16 a–d: Section plots of temperature (line contours = 0.2 °C isotherms, large font) and chlorophyll (filled contours = 2 mg/m^3, small font) for stations (x-axis) vs depth (y-axis) on July 15. X-axis indicates stations heading offshore from right to left, as though viewing a slice of the water column along each line of stations. See Table 1 for precise distance from shore and station names.



a: R11, R12, R13, R14, R15 **b:** R21, R22, R23, R24, R25 **c:** R31, R32, R33, R34, R35 **d:** R41, R42, R43, R44, R45

Figure 17 a–d: Section plots of temperature (line contours = 0.2 °C isotherms, large font) and chlorophyll (filled contours = 2 mg/m^3, small font) for stations (x-axis) vs depth (y-axis) on July 19. X-axis indicates stations heading offshore from right to left, as though viewing a slice of the water column along each line of stations. See Table 1 for precise distance from shore and station names.



a: R11, R12, R13, R14, R15 **b:** R21, R22, R23, R24, R25 **c:** R31, R32, R33, R34, R35 **d:** R41, R42, R43, R44, R45

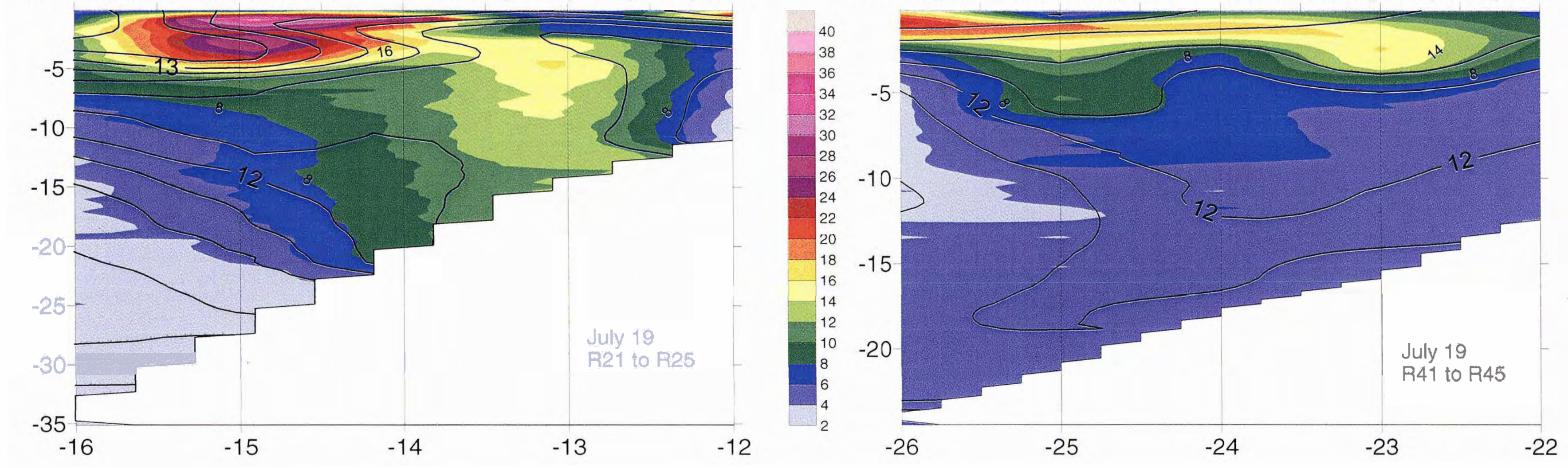
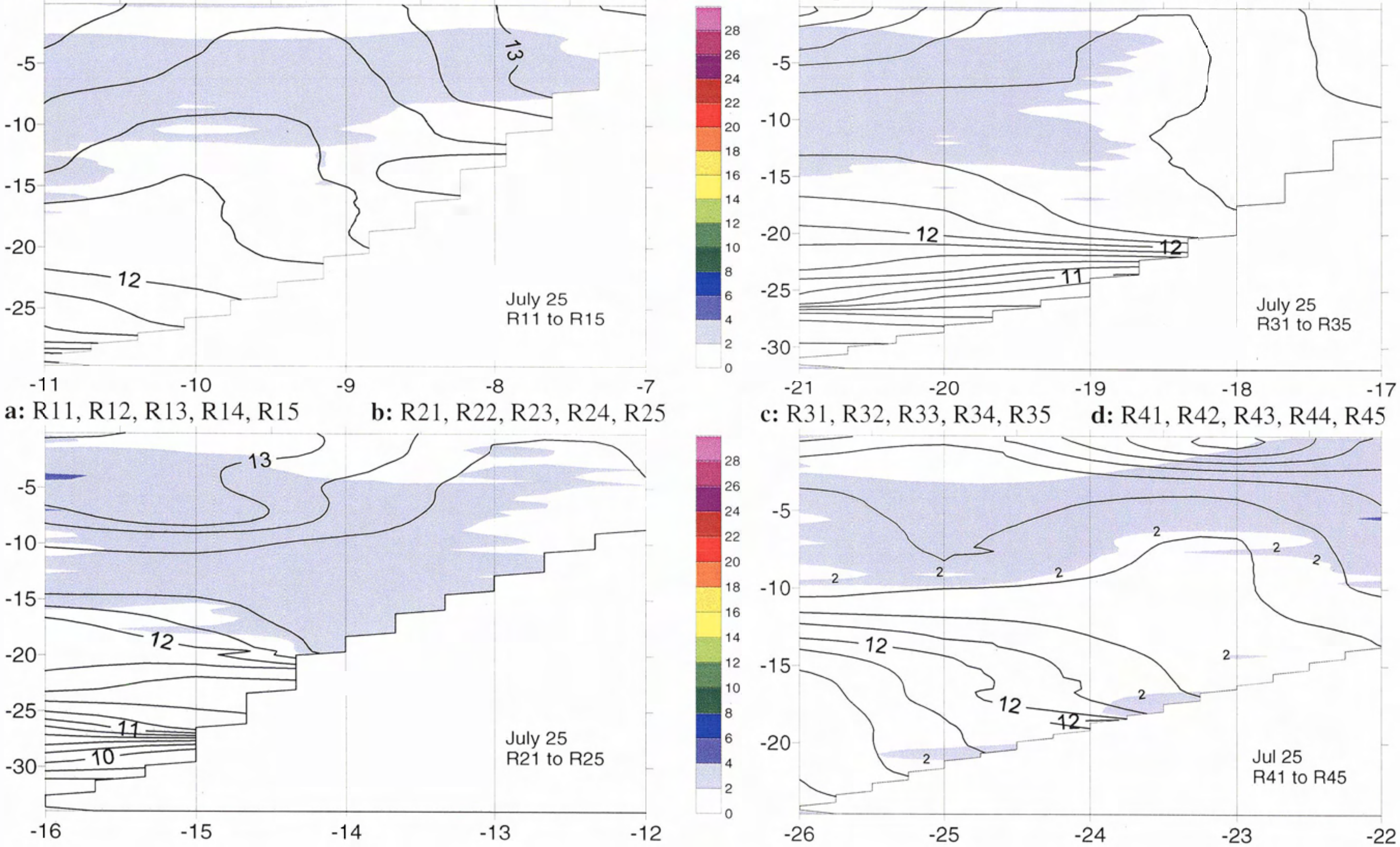


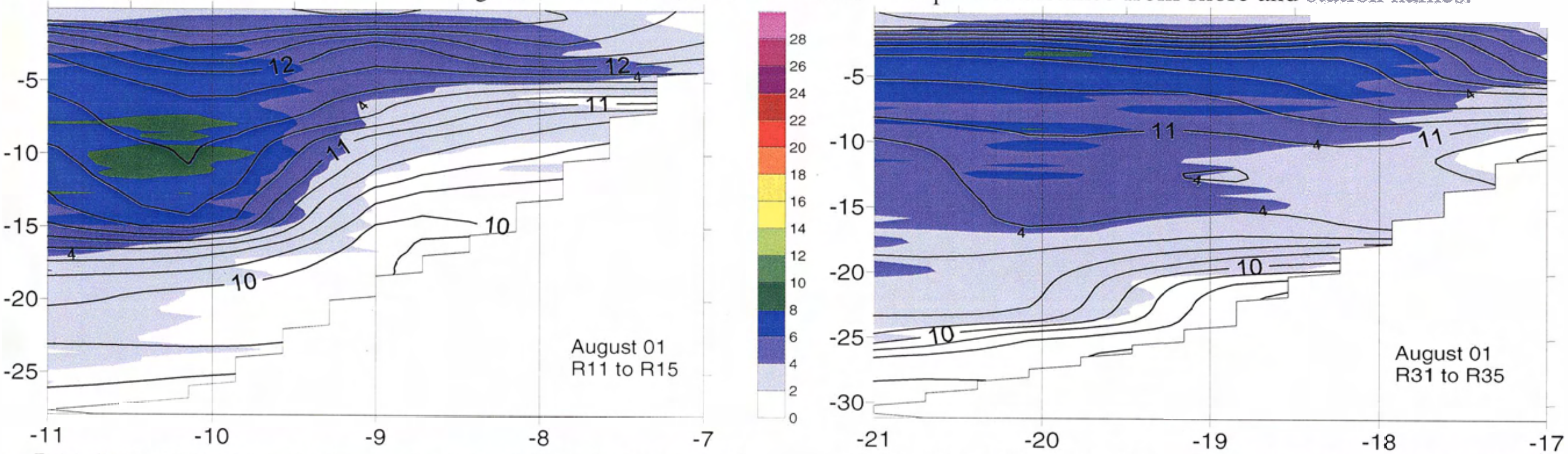
Figure 18 a–d: Section plots of temperature (line contours = 0.2 °C isotherms, large font) and chlorophyll (filled contours = 2 mg/m^3, small font) for stations (x-axis) vs depth (y-axis) on July 25. X-axis indicates stations heading offshore from right to left, as though viewing a slice of the water column along each line of stations. See Table 1 for precise distance from shore and station names.



a: R11, R12, R13, R14, R15 **b:** R21, R22, R23, R24, R25

c: R31, R32, R33, R34, R35 **d:** R41, R42, R43, R44, R45

Figure 19 a-d: Section plots of temperature (line contours = 0.2 °C isotherms, large font) and chlorophyll (filled contours = 2 mg/m^3, small font) for stations (x-axis) vs depth (y-axis) on August 01. X-axis indicates stations heading offshore from right to left, as though viewing a slice of the water column along each line of stations. See Table 1 for precise distance from shore and station names.



a: R11, R12, R13, R14, R15 **b:** R21, R22, R23, R24, R25 **c:** R31, R32, R33, R34, R35 **d:** R41, R42, R43, R44, R45

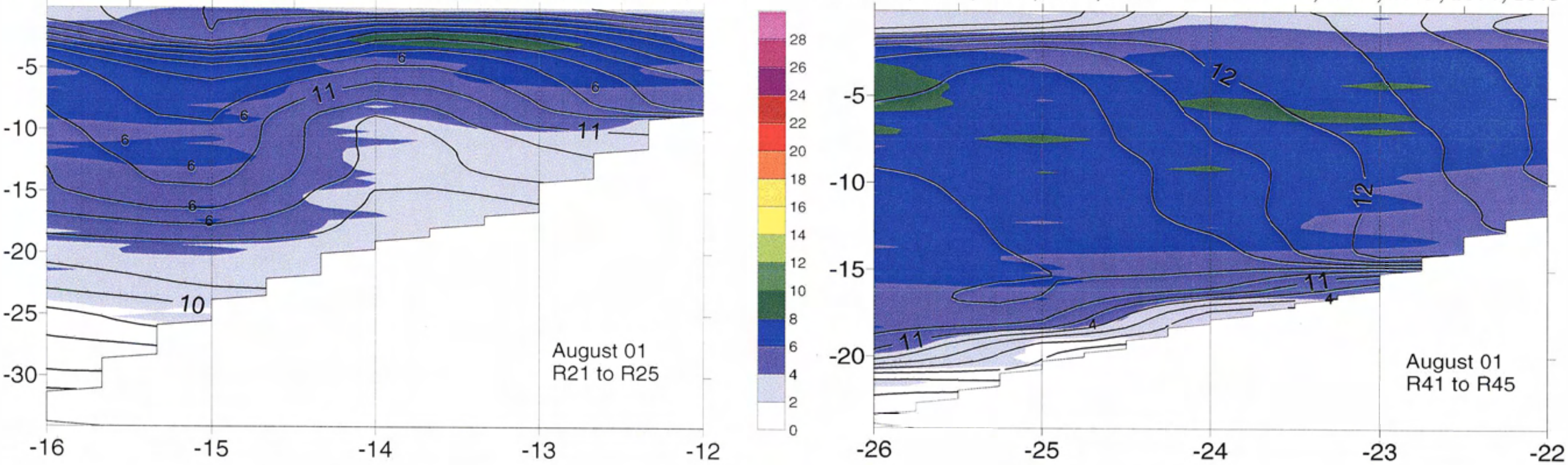
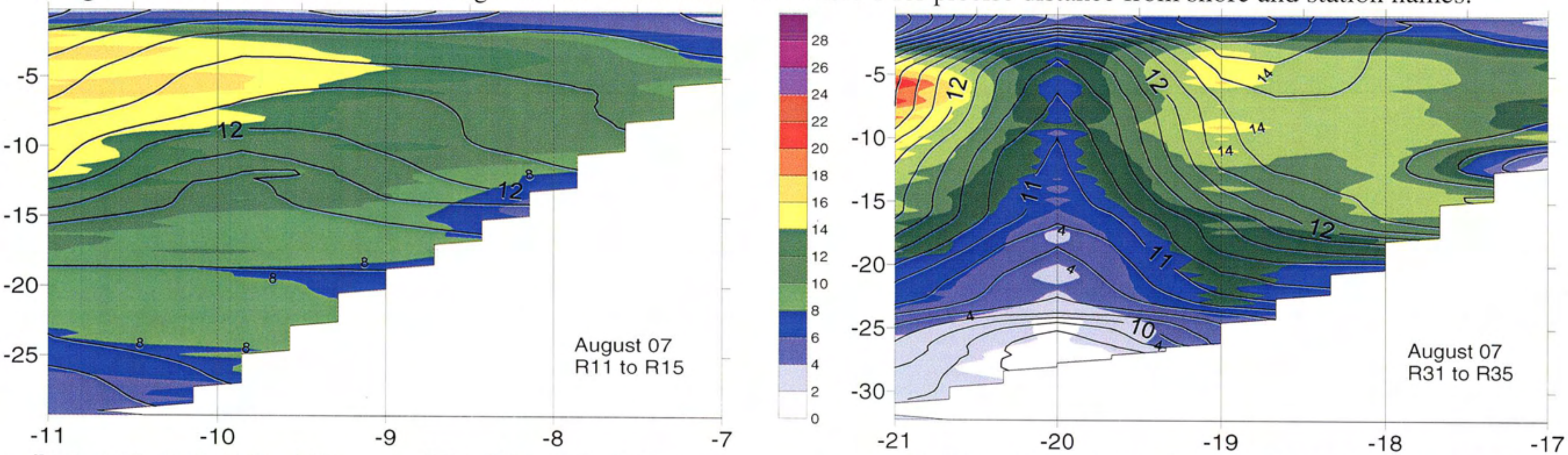


Figure 20 a–d: Section plots of temperature (line contours = 0.2 °C isotherms, large font) and chlorophyll (filled contours = 2 mg/m^3, small font) for stations (x-axis) vs depth (y-axis) on August 07. X-axis indicates stations heading offshore from right to left, as though viewing a slice of the water column along each line of stations. See Table 1 for precise distance from shore and station names.



a: R11, R12, R13, R14, R15 **b:** R21, R22, R23, R24, R25 **c:** R31, R32, R33, R34, R35 **d:** R41, R42, R43, R44, R45

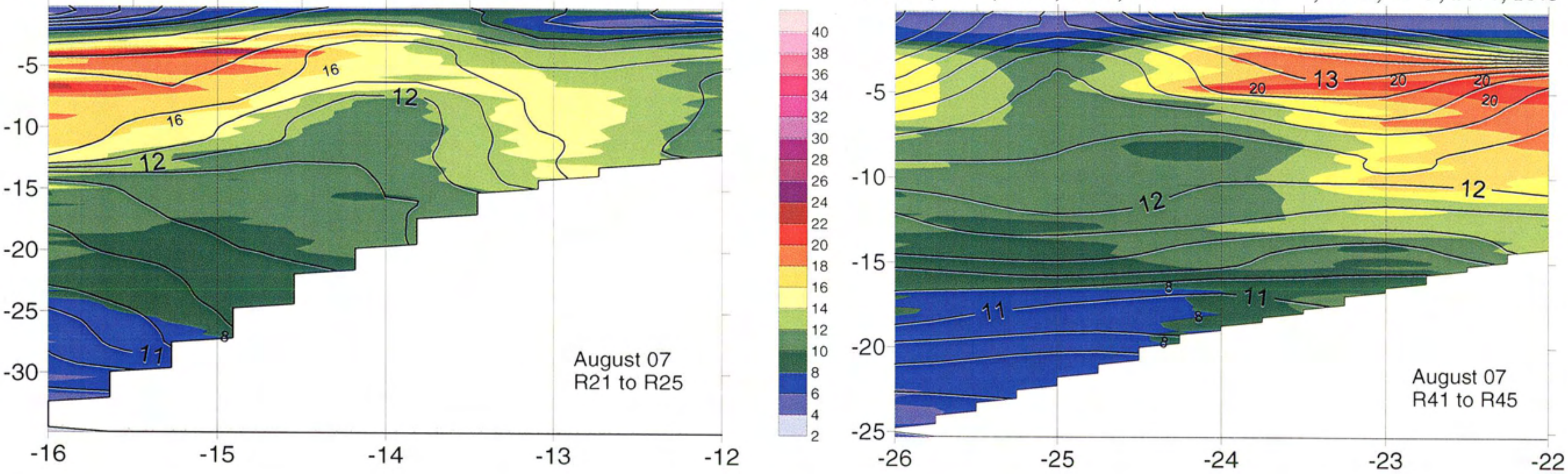
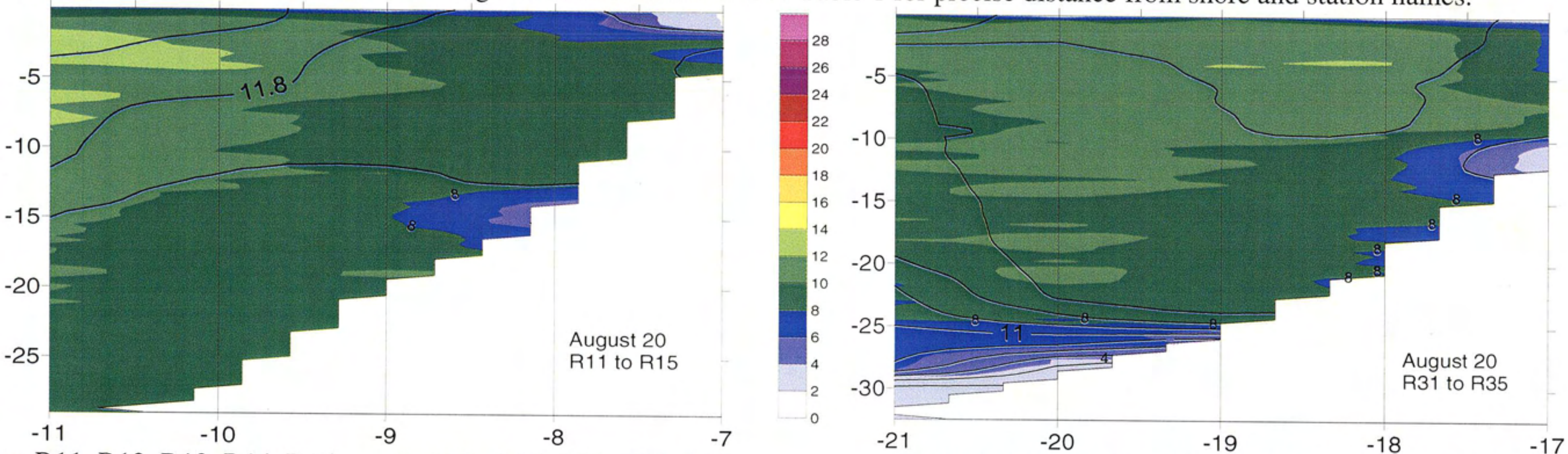


Figure 21 a–d: Section plots of temperature (line contours = 0.2 °C isotherms, large font) and chlorophyll (filled contours = 2 mg/m^3, small font) for stations (x-axis) vs depth (y-axis) on August 20. X-axis indicates stations heading offshore from right to left, as though viewing a slice of the water column along each line of stations. See Table 1 for precise distance from shore and station names.



a: R11, R12, R13, R14, R15 **b:** R21, R22, R23, R24, R25 **c:** R31, R32, R33, R34, R35 **d:** R41, R42, R43, R44, R45

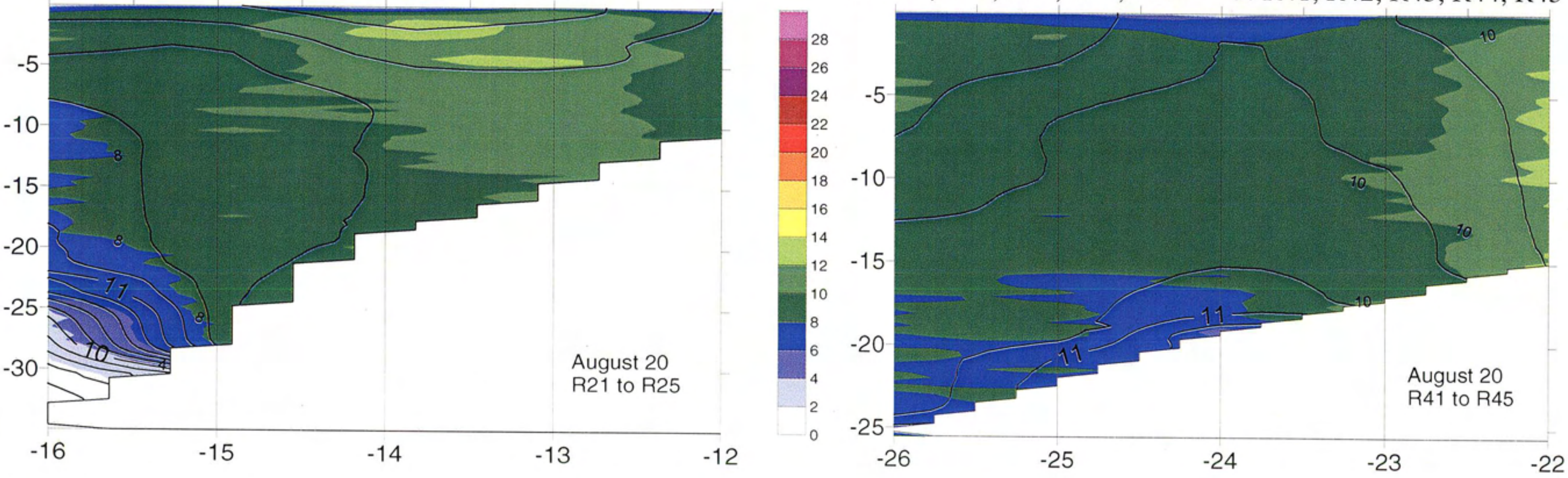
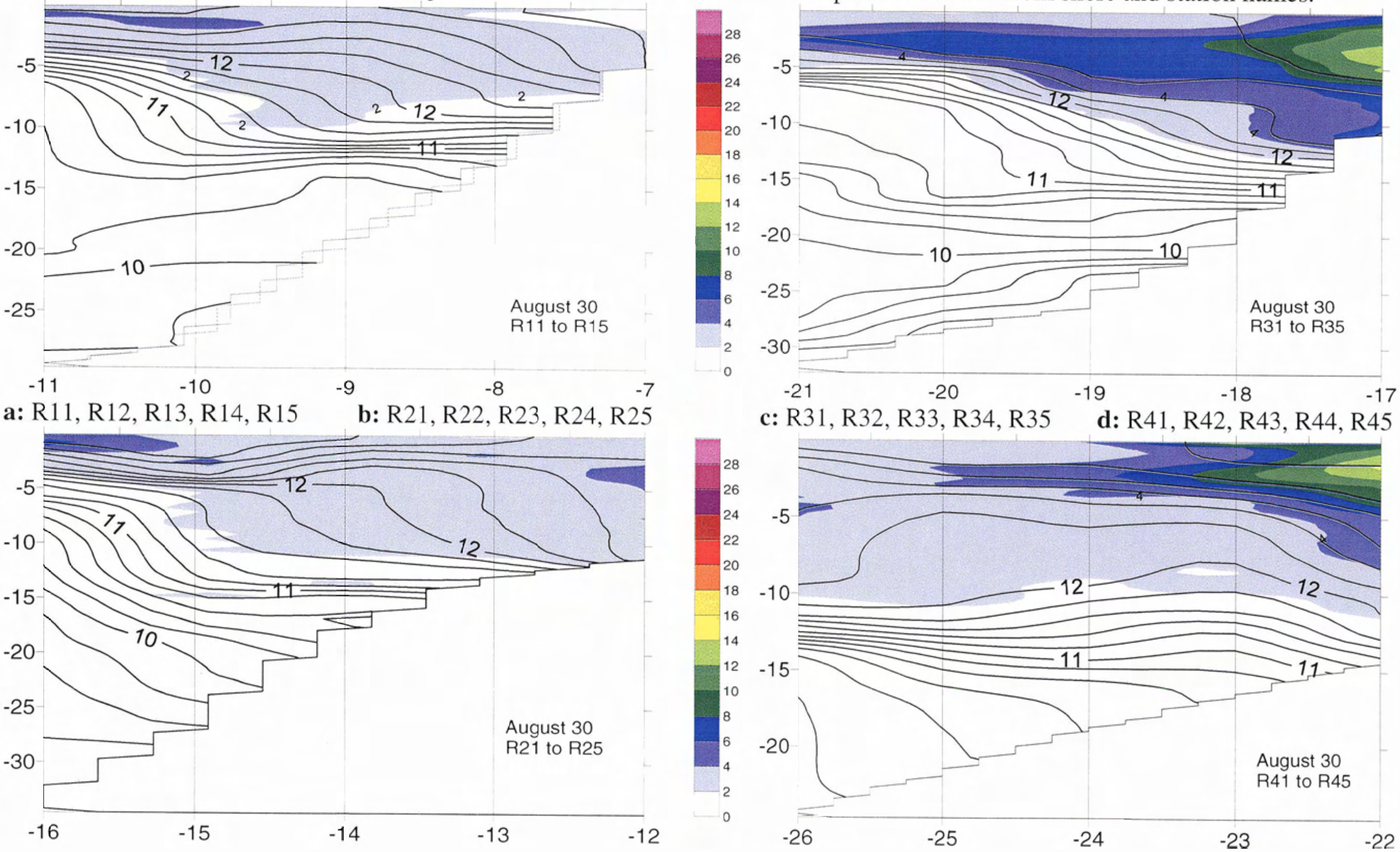


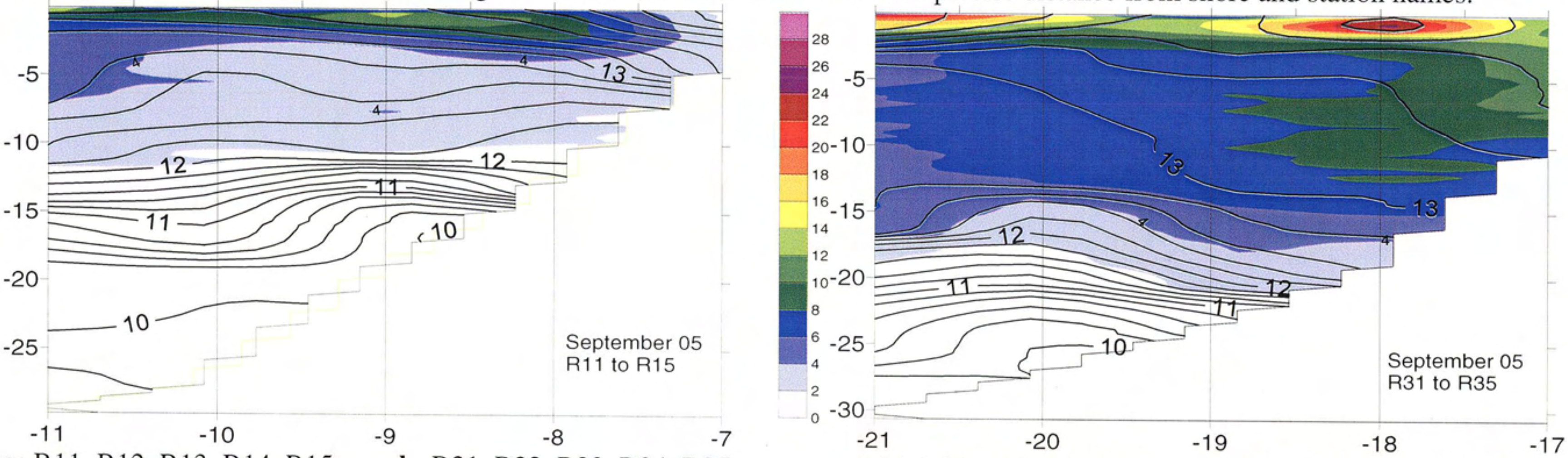
Figure 22 a–d: Section plots of temperature (line contours = 0.2 °C isotherms, large font) and chlorophyll (filled contours = 2 mg/m^3, small font) for stations (x-axis) vs depth (y-axis) on August 30. X-axis indicates stations heading offshore from right to left, as though viewing a slice of the water column along each line of stations. See Table 1 for precise distance from shore and station names.



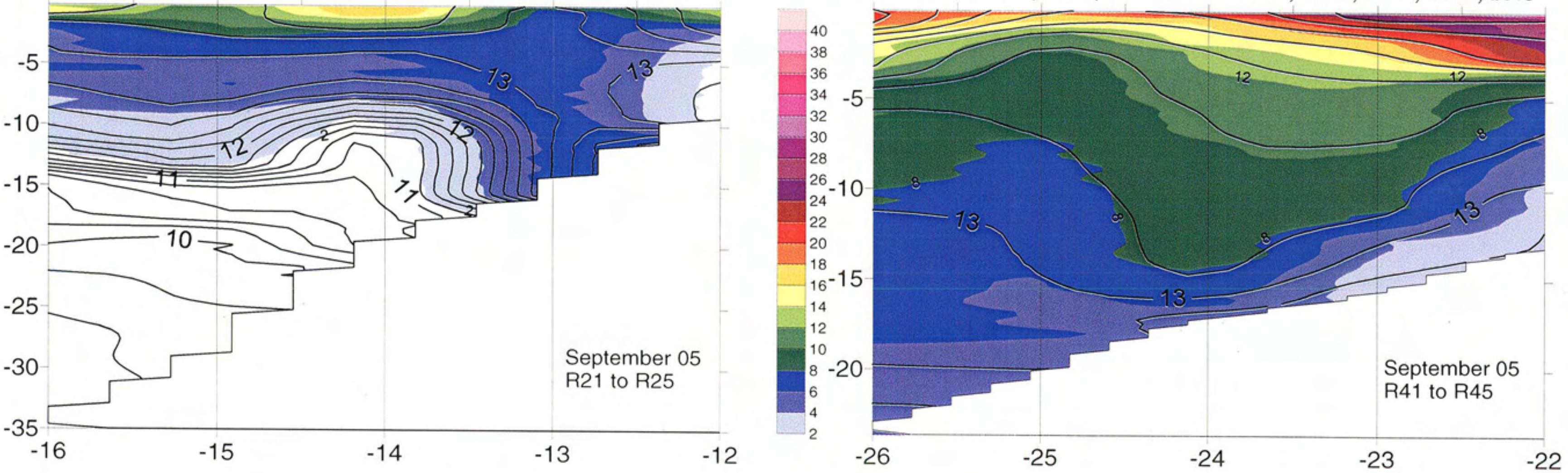
a: R11, R12, R13, R14, R15 **b:** R21, R22, R23, R24, R25

c: R31, R32, R33, R34, R35 **d:** R41, R42, R43, R44, R45

Figure 23 a–d: Section plots of temperature (line contours = 0.2 °C isotherms, large font) and chl (filled contours = 2 mg/m^3, small font) for stations (x-axis) vs depth (y-axis) on September 05. X-axis indicates stations heading offshore from right to left, as though viewing a slice of the water column along each line of stations. See Table 1 for precise distance from shore and station names.



a: R11, R12, R13, R14, R15 **b:** R21, R22, R23, R24, R25 **c:** R31, R32, R33, R34, R35 **d:** R41, R42, R43, R44, R45



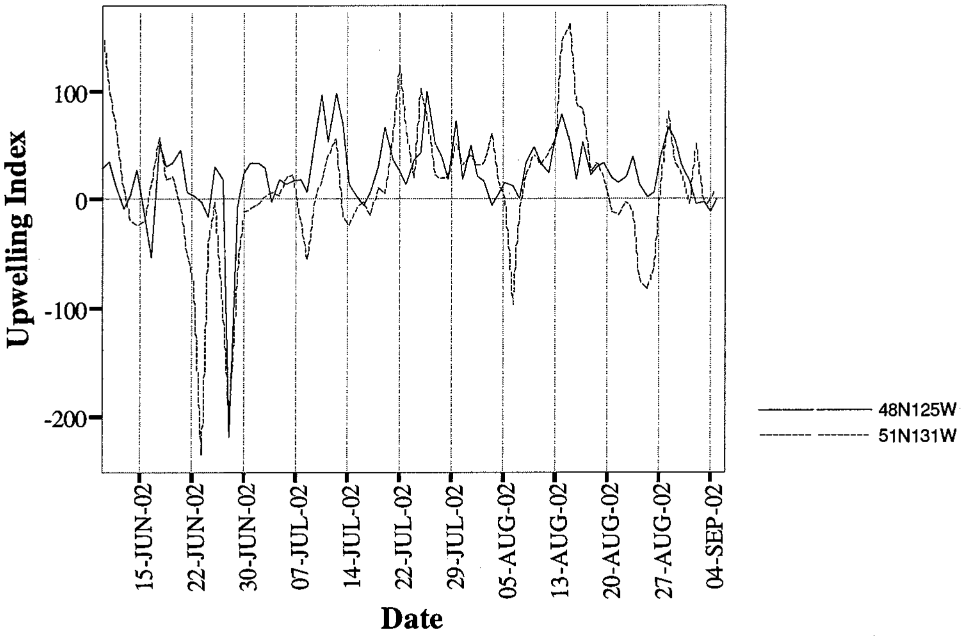


Figure 24: Average upwelling index calculated by Pacific Fisheries Environmental Lab for locations 48°N 125°W and 51°N 131°W between June 10 and September 5, 2002. Positive = upwelling, negative = downwelling favourable conditions.

While mean and surface temperature changes fit well with PFEL's upwelling data, colder water moving to shallower depths along the bottom could also be the result of large amplitude tides. To assess the influence of the lunar tidal cycle on the presence of cold water along the bottom, the spring/neap tidal cycle was compared with water temperature data shown in vertical section plots (Figures 13-23, Table 2). No consistent trend in the presence or extent of water less than 10 °C in relation to tidal cycles is evident (Table 2). However, strong vertical motion evident in the temperature and chlorophyll data is present at R34 on August 7, two days before the largest spring tide of the sampling period and when the upwelling index shows upwelling relaxation (Figures 20 & 24). Upwelling relaxation is also shown in PFEL's index on September 5, two days before the spring tide and doming of isotherms is seen at R23.

In contrast, on June 21, two days after the neap tide, cold water along the bottom is most extensive and doming of isotherms towards the surface is present at R12, R13, R23, R32, R42, R43. According to the upwelling index, upwelling has been occurring but relaxation is beginning (Figures 14 & 24). On August 01, one day after the neap tide, cold water moved up along the bottom since the previous sampling date at all station lines and upwelling is occurring according to PFEL's upwelling index (Figures 19 & 24). August 30 was also one day after the neap tide, upwelling had been occurring and cold water along the bottom increased between August 20 and 30 (Figures 22 & 24).

Table 2: Presence of cold water along the bottom, lunar and semidiurnal tidal state of the four lines of stations around Rafael and Dagger Points. Dates were considered spring (S) or neap (N) if the spring or neap tides occurred within two days of sampling. A star denotes presence of water less than 10 °C and two stars denote presence of water less than 9 °C. Letters under station line headings denote semidiurnal tidal state. L = low, F = flood, H = high and E = ebb.

Date	*Spring/Neap*	*R1*		*R2*		*R3*		*R4*	
Jun-15	S	*	L	*	L	*	F		F
Jun-21	N	**	H	**	H	**	H	*	F
Jul-07			H	*	H	*	E		E
Jul-15		*	F	*	L	*	L	*	L
Jul-19	N		E		E		E		L
Jul-25	S		F	*	F	*	F		F
Aug-01	N	*	E	*	L	*	L	*	F
Aug-07	S		F		H	*	H		H
Aug-20	S		F	*	F	*	H		H
Aug-30	N	*	F	*	F	*	F	*	F
Sep-05	S	*	F	*	F	*	L		L
Total		6		9		10		4	

Doming or arching of isotherms towards the surface and/or water less than 10 °C present along the bottom is evident along at least one line of stations on all sampling days. Water 10 °C or less is seen along the bottom in vertical contour plots of at least one line of stations on all sampling days except July 19 (Table 2). This is most prevalent along station lines R2's and R3's with less than 10 °C water along the bottom at the R3 station line on 10 sampling days. R4's had water less than 10 °C along the bottom during 4 sampling days, each when all four station lines had cold water move shallower than the previous sampling date.

A large whirlpool at the surface was observed at or between stations R22, R23 and R24 on several days. Vertical contour plots show isotherms arch towards or away from the surface at these stations on July 07, 15, 19, August 01, 07 and September 05 (most notable on July 15) (Figures 15, 16, 17, 19, 20 & 23). In addition, surface temperatures drop at or near these stations on these dates (Figure 6). Localized downwelling is apparent in the temperature and chlorophyll contours on June 15 at R34 and R44, at R24 on July 15 (as mentioned above), and on July 19 at R14, R22 and R43/44 (Figures 13, 16 & 17).

2) Temporal and Spatial Variation in the Nearshore Biological Oceanography of Flores Island

Temporal Variation

Daily average chlorophyll *a* concentration varied from a low on July 25 (1.91 mg/m^3, SE = 0.153) to a high on August 7, 2002 (10.03 mg/m^3, SE = 0.427) (Figure 25). Integrated chlorophyll (sum of all chlorophyll values for the top 10 m of each station, expressed as mg/m^2) exhibits the same temporal changes as average chlorophyll concentration. Minimum chlorophyll *a* point measurements within a cast were below 1 mg/m^3 for all sampling days except June 15 when the minimum recorded value was 1.63 mg/m^3. Maximum point measurements within a cast ranged from 10.36 mg/m^{3}on July 7 to 46.72 mg/m^3 on August 1 and 7.

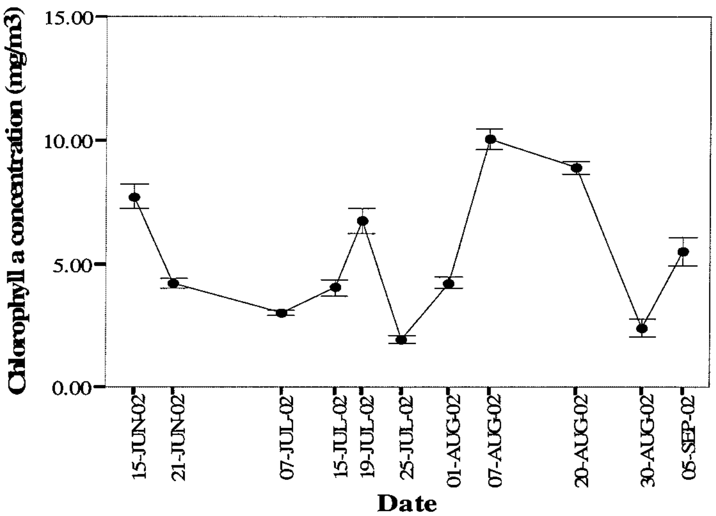


Figure 25: Temporal changes in mean chlorophyll *a* concentration of all stations (error bars represent 1 SE).

Spatial Variation

Mean chlorophyll *a* concentrations for the top 10 m averaged across all dates varied between a minimum of 4.86 mg/m^3 (SE = 0.738) at R12 (Rafael Bay) to a maximum of 7.77 mg/m^3 (SE = 1.335) at R41 (Dagger Point), both nearshore stations (Figure 26, note R11 and SW2 were excluded from this analysis due to station depths of less than 10 m). Integrated chlorophyll values (mg/m^2) show a general trend of increasing chlorophyll towards the Dagger Point end of the study area (Figure 27).

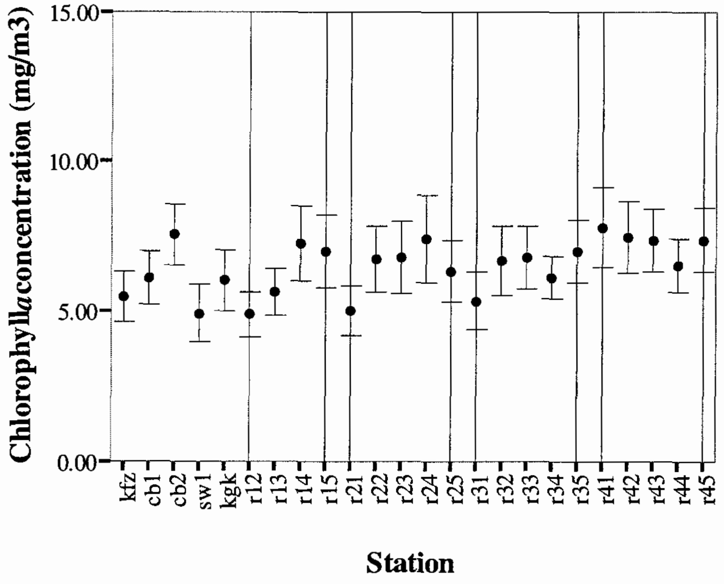


Figure 26: Mean chlorophyll *a* concentration for the top 10 m of each station averaged over all sampling dates (error bars = 1 SE). Stations R11 and SW2 are excluded due to depths of less than 10 m. Reference lines indicate beginning and end of station lines off Rafael and Dagger Points (R12, R15, R21, R25, R31, R35, R41, R45).

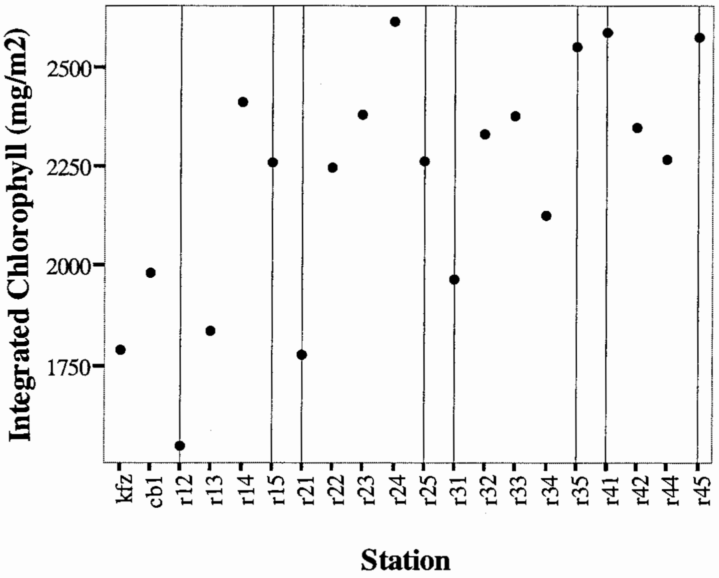
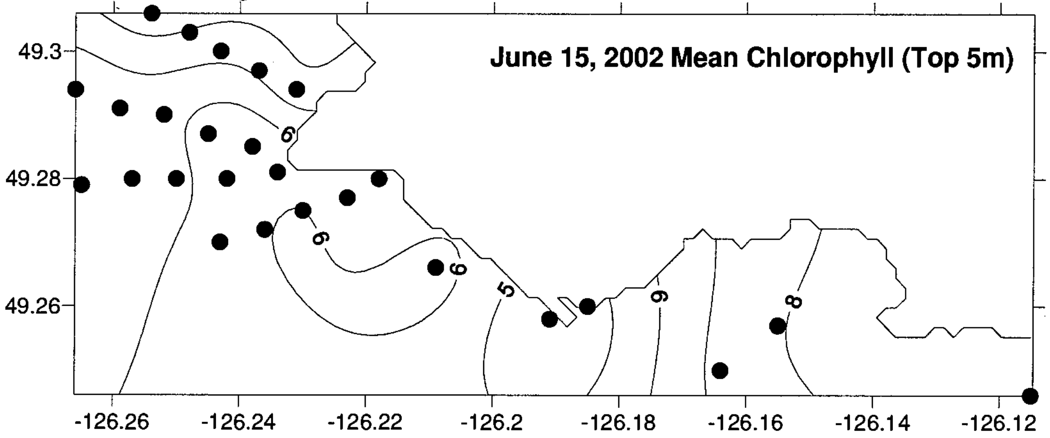


Figure 27: Chlorophyll values integrated over the top 10 m and all sampling dates (mg/m2). Stations less than 10 m deep or not sampled on all 11 sampling dates are excluded. Reference lines indicate R12, R15, R21, R25, R31, R35, R41, R45.

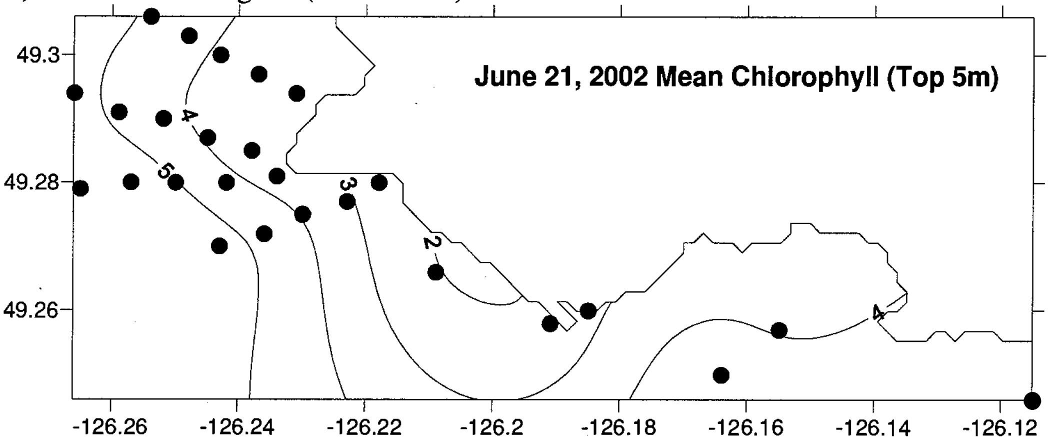
The temporal differences in mean chlorophyll discussed earlier result in variation within a location that masks spatial differences in average chlorophyll concentration. Contour maps of mean chlorophyll *a* concentration over the top 5 m for each date separate temporal changes allowing a clear picture of spatial and temporal variation in chlorophyll (Figure 28 a-k). When chlorophyll levels are low (ex: June 21, July 7 and July 25), spatial variation in chlorophyll is also low (Figure 28 b,c&f). However, chlorophyll *a* concentration is consistently higher around headlands when strong variation occurs. High values of chlorophyll *a* appear to concentrate mainly around Rafael Point (ex: July 19, Aug 07, Sept 05) (Figure 28 e,h,k).

Figure 28 a-k: Contour maps of mean chlorophyll *a* concentration (mg/m^3) of the top 5 m of the water column for each sampling date. Each contour represents 1 mg/m^3 chlorophyll *a*. Circles represent CTD sampling station locations. X-axis = latitude, Y-axis = longitude.

a) mean = 6.38 mg/m^3 (SE = 0.357)



b) mean = 4.09 mg/m^3 (SE = 0.242)



c) mean = 3.64 mg/m^3 (SE = 0.133)

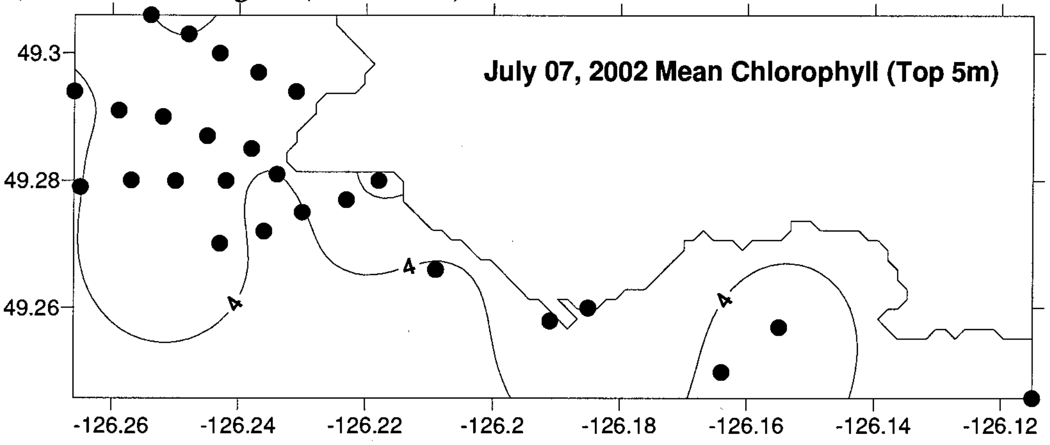
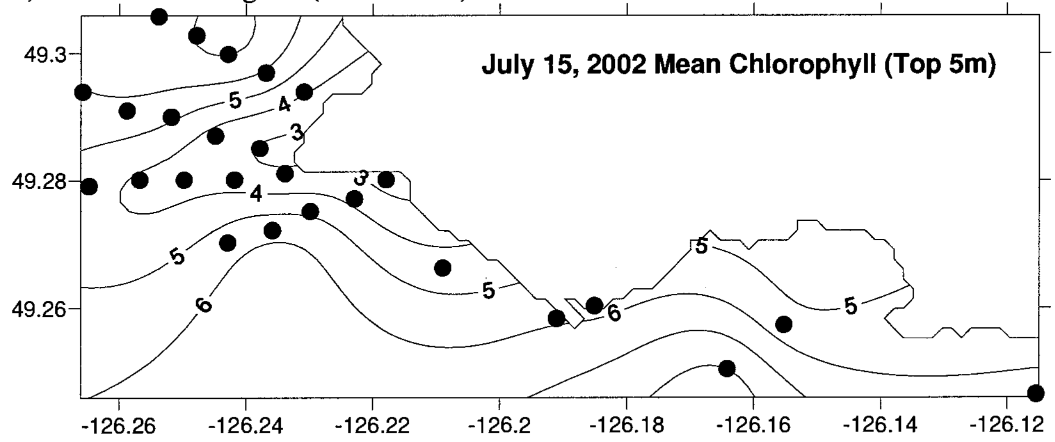
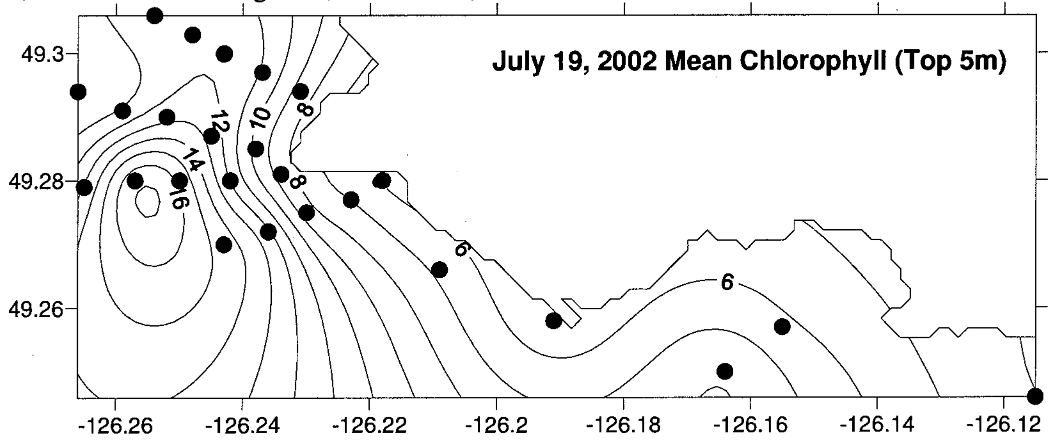


Figure 28 a-k continued: Contour maps of mean chlorophyll *a* of the top 5 m of the water column for each sampling date. Each contour represents 1 mg/m^3 chlorophyll *a*. Circles represent CTD sampling station locations. X-axis = latitude, Y-axis = longitude.

d) mean = 5.05 mg/m^3 (SE = 0.421)



e) mean = 10.22 mg/m^3 (SE = 0.923)



f) mean = 2.13 mg/m^3 (SE = 0.171)

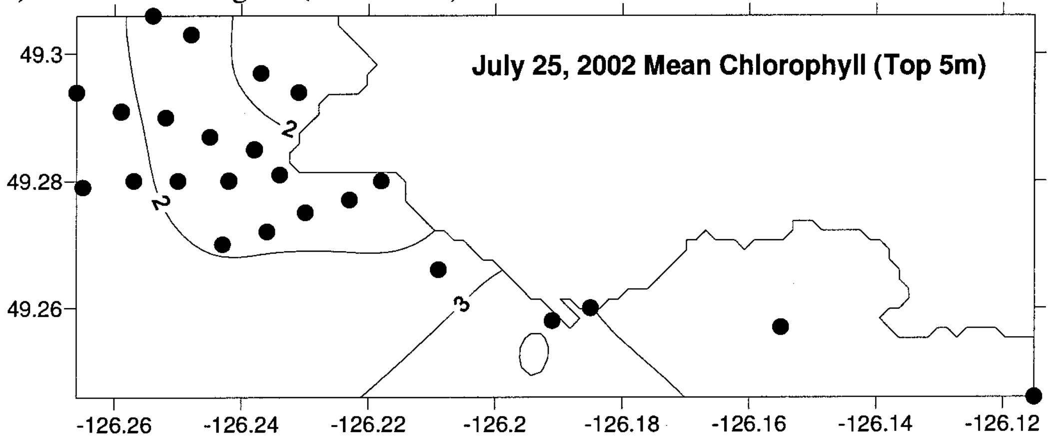
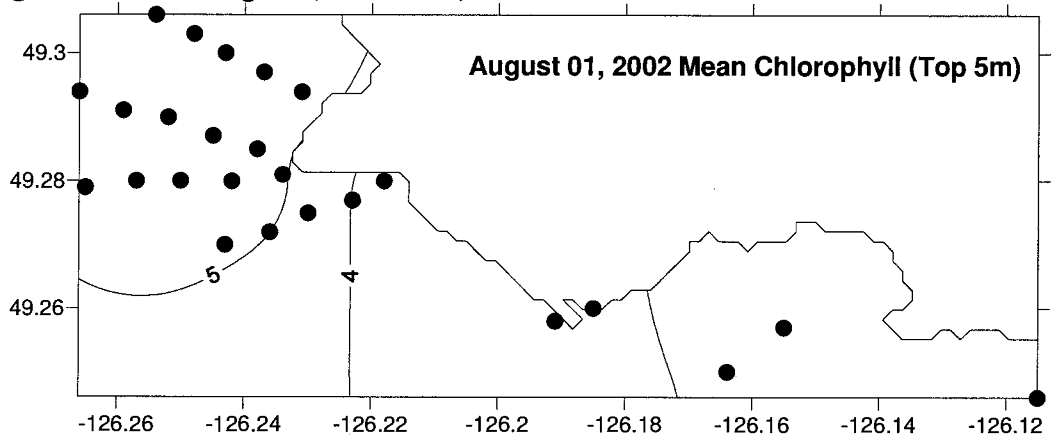
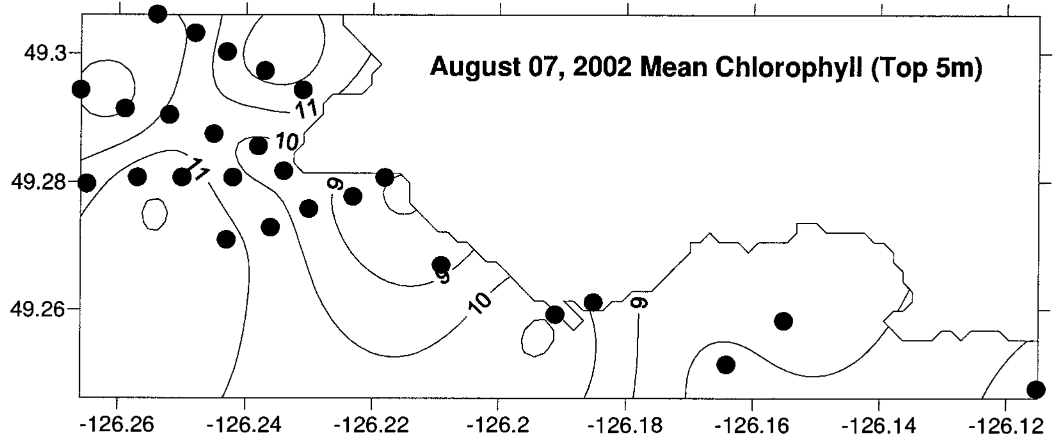


Figure 28 a-k continued: Contour maps of mean chlorophyll *a* of the top 5 m of the water column for each sampling date. Each contour represents 1 mg/m^3 chlorophyll *a*. Circles represent CTD sampling station locations. X-axis = latitude, Y-axis = longitude.

g) mean = 5.02 mg/m^3 (SE = 0.180)



h) mean = 9.94 mg/m^3 (SE = 0.465)



i) mean = 9.29 mg/m^3 (SE = 0.274)

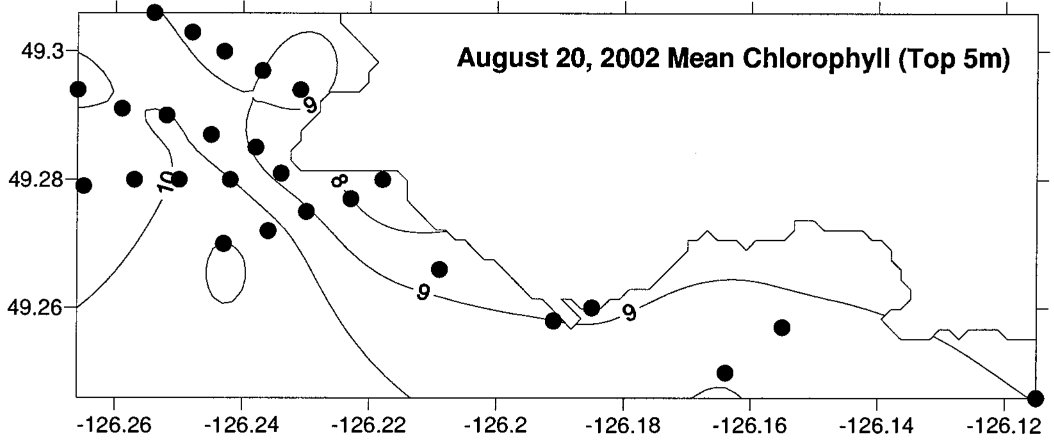
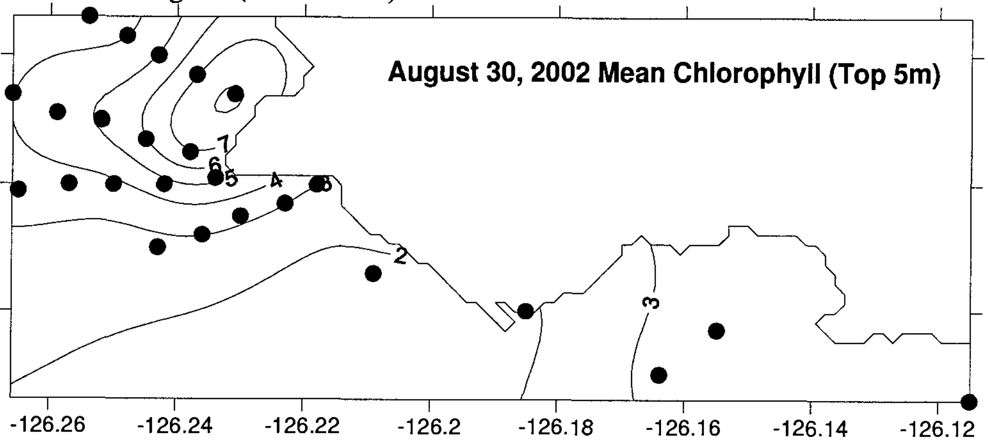
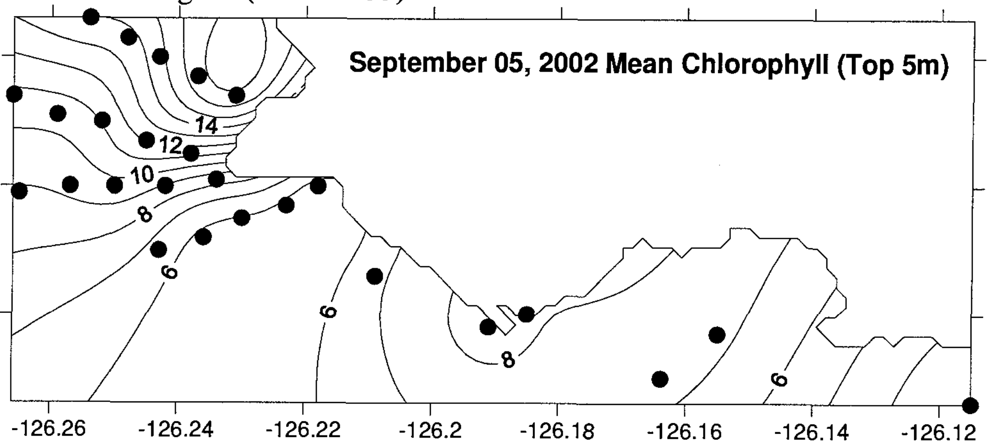


Figure 28 a-k continued: Contour maps of mean chlorophyll *a* of the top 5 m of the water column for each sampling date. Each contour represents 1 mg/m^3 chlorophyll *a*. Circles represent CTD sampling station locations. X-axis = latitude, Y-axis = longitude.

j) mean = 4.14 mg/m^3 (SE = 0.462)



k) mean = 9.51 mg/m^3 (SE = 0.855)



Vertical Variation

The minimum range in chlorophyll *a* concentration within a cast was 0.88 mg/m^3 at KFZ on July 25 and the maximum range was 45.61 mg/m^3 at SW2 on August 1. Maximum chlorophyll point measurements within a cast ranged from 1.67 to 46.72 mg/m^3 (mean = 10.950 mg/m^3, SD = 7.5095). The depth at which the chlorophyll maximum occurred ranged from 0.01 to 26.68 m (mean = 5.08 m, SD = 4.481, Figure 29). The chlorophyll maximum within a cast occurred in the top 2 m in 19% of casts and the top 6 m in 68% of casts (Figure 30). Chlorophyll structure generally followed temperature structure (Figure 31 a-d). The water temperature at which the chlorophyll maximum occurred (mean = 12.149 °C, SD = 0.8927, range 9.251 to 14.670) was significantly higher than the average water temperature per cast (mean = 11.614 °C, paired sample t-test = -11.571, df = 280, $p < 0.001$).

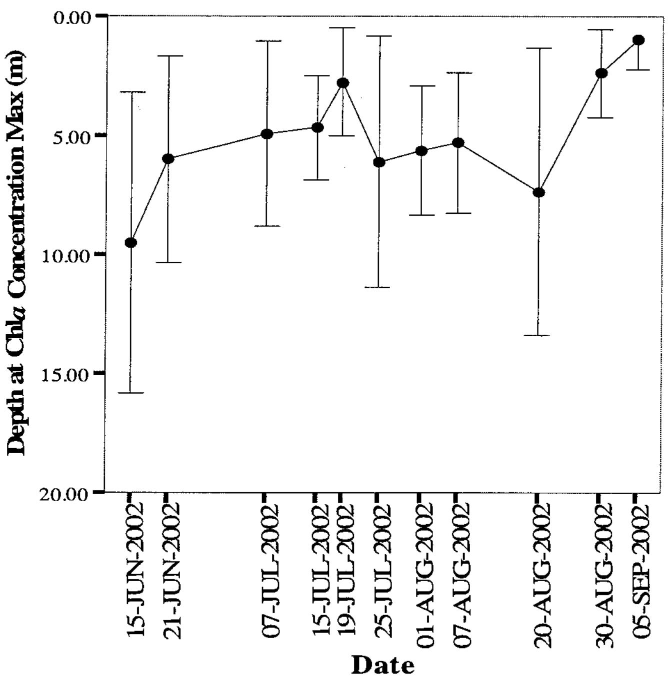


Figure 29: Average depth below the surface (m) (error bars = SD) of the maximum chlorophyll *a* concentration over the course of the field season.

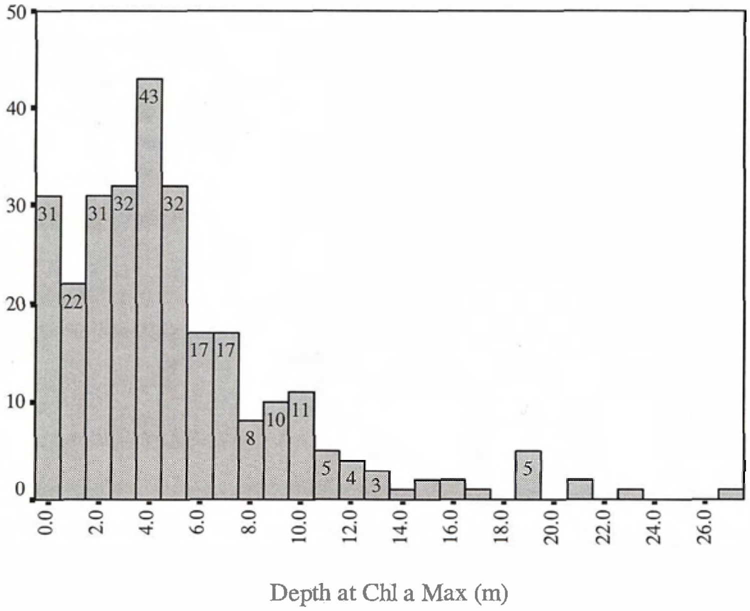


Figure 30: Histogram of the depth of chlorophyll maximum within a cast (N=281).

Vertical section plots show a slice of the water column from a few hundred meters off Rafael Point and Dagger Point to approximately 2.7 km offshore (Table 1, Figures 13 - 23). These plots emphasize that temporal differences are much larger than spatial differences between lines of stations within a day. However, on August 30 and September 05 the R3 and R4 lines of stations have higher concentrations of chlorophyll than the other two lines of stations. On June 21 and July 15 the R2 line has a lower chlorophyll concentration than the other three lines.

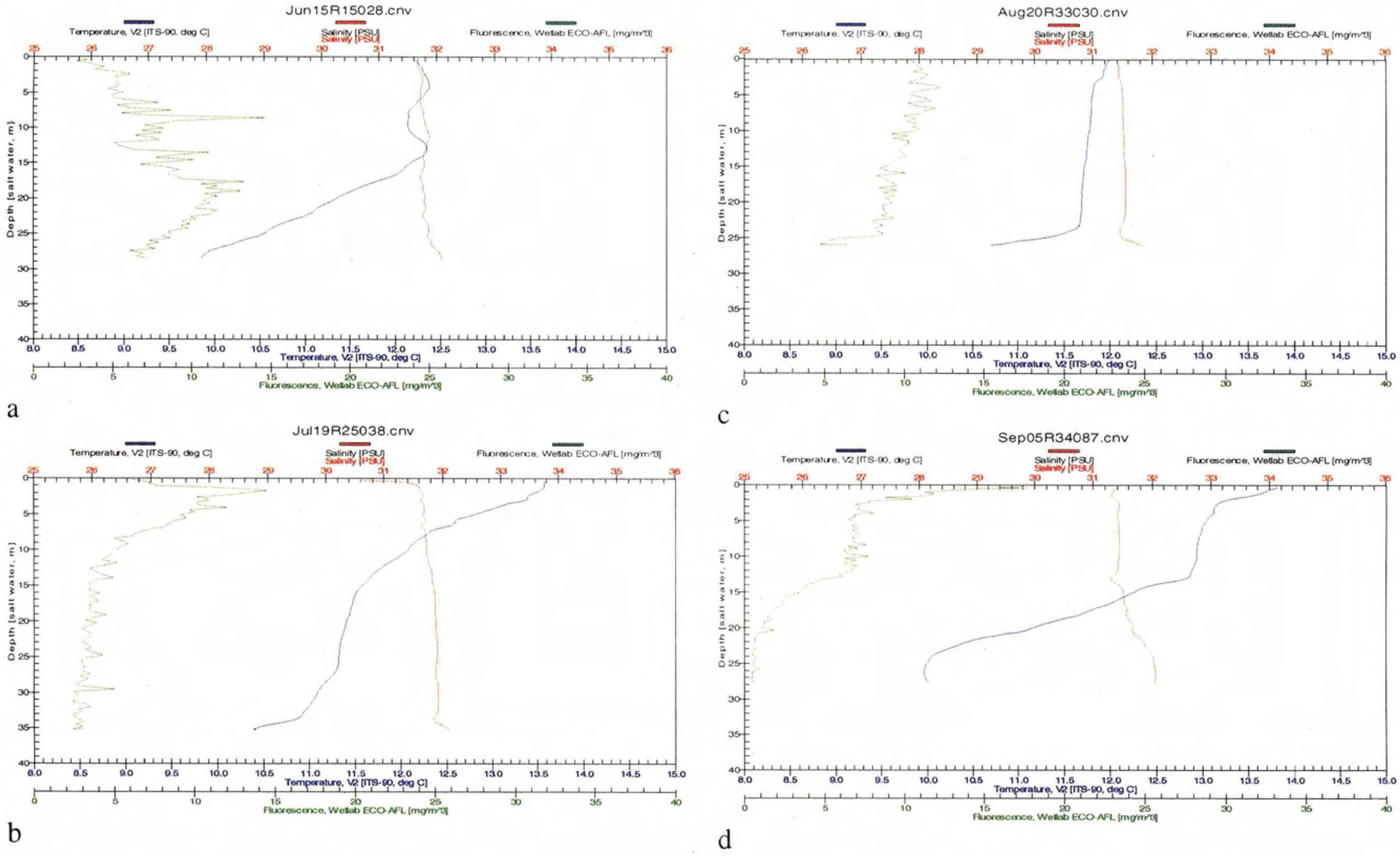


Figure 31 a-d: Vertical profiles of temperature (blue), salinity (red) and chlorophyll *a* concentration (green) showing examples of chlorophyll *a* concentration following temperature structure.

3) RESPONSE IN PHYTOPLANKTON BIOMASS TO VARIATION AND STRUCTURE OF PHYSICAL OCEANOGRAPHY

In addition to showing upwelling and changes in thermocline strength and position, vertical section plots support the results above stating that the structure of chlorophyll in the water column follows that of temperature. Temperature and chlorophyll concentration contours fit together well (Figures 13 -23). Further, the influence of warmer water temperature on phytoplankton biomass is seen. When the 11 °C isotherm is located below 20 m depth, high chlorophyll concentrations are generally observed (June 15, July 19, August 07, August 20, September 05) (Figures 13, 17, 20, 21 & 23). The exception to this is July 25 (Figure 18). Highest concentrations of chlorophyll are often located just above the thermocline (Figure 14, 16, 20, 22, 23). Movement of phytoplankton biomass through localized upwelling and downwelling can be seen on June 15, July 19 and August 07 as higher concentration of chlorophyll is extended downwards towards the bottom or water with very low chlorophyll concentration is pushed towards the surface (Figures 13, 17 & 20).

As mentioned above, high concentrations of chlorophyll were seen on days when warm water extended through much of the water column. This response in phytoplankton biomass to temperature variation is evident in the temporal results as an increase in chlorophyll concentration at the same time as an increase in temperature after there had been a decrease in both average and surface temperatures. The two largest decreases in mean water temperature (between July 7 and 15, -1.10 °C; between July 25 and August 1, -1.27 °C) were followed by increases in water temperature (between July 15 and 19, +1.68 °C; between August 1 and 7, +0.84 °C) and increases in mean chlorophyll *a* concentration (between July 15 and 19, +2.89 mg/m^3; between August 1 and 7, +5.77 mg/m^3) (Figure 32). A third large increase in mean chlorophyll *a* concentration of 3.15 mg/m^3 was observed on September 5 after a smaller decrease in mean water temperature of 0.62 °C over 2 sampling periods (between August 7 and 30) (Figure 32). This period was also largest decrease in mean surface temperature of 1.28 °C between August 7 and 20 followed by an increase in surface temperature of 1.83 °C between August 20 and September 5 (Figure 12).

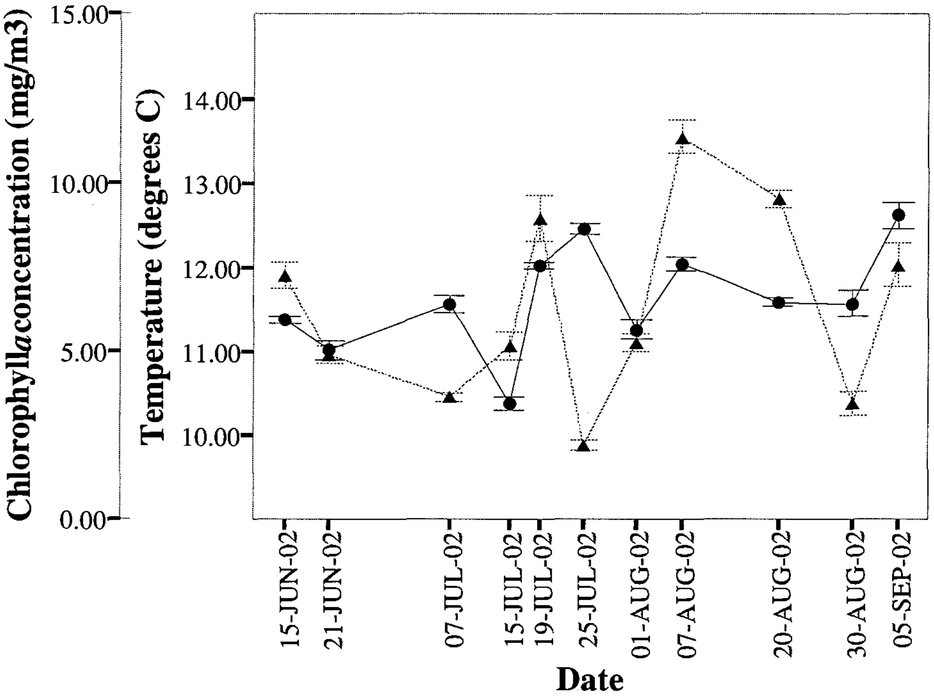


Figure 32: Mean temperature (solid line, circles, error bars = SE) and mean chlorophyll concentration (dotted line, triangles, error bars = SE) across the sampling period.

DISCUSSION

The overall trend of increasing surface temperature over the field season follows the expected trend over the summer months of surface warming due to longer, more intense insolation with less frequent storms (Thomson 1981). Drops in surface and mean water temperature (Figures 3 & 4) could be due to increased precipitation and freshwater runoff or mixing with colder deeper waters via tides or upwelling. Salinity data show that precipitation and runoff are not the cause of temperature changes as all drops in temperature are associated with increases in salinity, except on July 25 when there was an increase in both temperature and salinity (Figures 3 & 5). Increases in salinity at the same time as decreases in temperature indicate intrusions of deeper denser waters.

Colder water intrusions as a result of large amplitude tides are a possibility; however large amplitude tides were not consistently present during average temperature decreases. The only date which showed a mean temperature decrease near a spring tide was August 20, however this was the smallest spring tide of the season with amplitude less than 0.25 m larger than the larger neap tides of the season (Figure 12, Table 2, Fisheries and Oceans Canada 2002). As established in the results section, all major average and surface temperature changes coincide with evidence for upwelling or upwelling relaxation in the surface temperature results, vertical section plots and PFEL's upwelling index. These results are consistent with other studies off western Vancouver Island which found that upwelling largely controlled temperature changes (Crawford & Dewey 1989). As Schumann (1999) found in coastal South Africa, nearshore water temperature off western Vancouver Island may be a good indicator of local upwelling conditions.

Kopach (2004) found water currents around Rafael Point to be controlled primarily by tidal state and bathymetry when winds were less than 15 knots. On the flood tide currents travel to the northwest in the vicinity of station lines R3 and R4 and WSW near station lines R1 and R2 (Kopach 2004). The north flowing flood tide appears to be deflected by the shallow extension off Rafael Point (Kopach 2004). On the south flowing ebb tide, currents flow southward near R3's and R4's and ESE near R2's and R1's (Kopach 2004). While tidal influences may not be the strongest control on temperature changes in this area, there is evidence in the temperature data for effects on water movement and vertical mixing. Despite relatively low wind speeds and upwelling relaxation, doming of isotherms was present at some stations during two spring tides (August 07 and September 05) (Figures 20, 23, 24). The compounding effects of upwelling and the spring/neap cycle make it difficult to determine if there is an effect of the diurnal tidal cycle on water temperature. Upwelling relaxation and neap tides occurred on a couple of sampling days including July 19. However, this was the only date when water less than 10 °C was not present at any of the lines of stations and was also the only date primarily sampled on the ebb tide (Table 2). While upwelling/upwelling relaxation may result in the largest short term temperature changes, the lunar and daily tidal cycles also have effects on water movement and mixing thus influencing temperature variation.

Spatial and temporal differences in the vertical structure of temperature were observed. Water column structure can be influenced by winds, tidal fluctuation and surface warming by the sun. Based on temperature variation within the water column (Figure 8), thermocline categorization (Figure 10) and vertical section plots, August 20 (Figure 21) showed little vertical temperature structure while September 05 was stratified (Figure 23). Tidal amplitude was nearly equal prior to August 20 and September 5 (Fisheries and Oceans Canada 2002), however, high winds from the NW prevented sampling for several days prior to August 20 while several days prior to September 5 were very calm (personal observation). Intense upwelling conditions were recorded prior to August 20 while upwelling relaxation and slight downwelling conditions occurred prior to September 5 (Figure 24). Water column structure in this area appears to be primarily influenced by wind and wind effects such as upwelling. Surface warming by the sun amplifies stratification when winds are relatively calm (Figure 9 a-d).

This observed temporal variation in vertical temperature structure is more intense than seen in other nearshore studies. Other studies have found mixed water columns with less than 0.2 °C change over 20 m depth or seasonal stratification with variation of up to 5 °C over 20 m (Johannes *et al.* 1994, Narváez *et al.* 2004). In Chile, waters were mainly stratified during the summer but some spatial variation in stratification was observed (Narváez *et al.* 2004). The site in Chile where stratification was not as strong had slight temporal variation in stratification (Narváez *et al.* 2004). This relatively consistent stratification compared to what is seen in the current study is likely related to the depth that mixing penetrates. The current study area clearly has periods of thermal stratification but mixing events are common and intense with their influence extending through the majority of the water column. In Chile temperatures below 5 m did not change more than 2 °C over the entire year, while, in this study, the maximum mean temperature in the 20 m depth bin varied by 2.44 °C in only 10 days between July 15 and 25 (Figure 8, 16 & 18). Temperature structure and thermocline stability are considered important for the biology of plankton and larval fish through impacts on growth and vertical distribution which affects community interactions (Gray & Kingsford 2003). The results of this study add to the growing body of literature demonstrating that water column temperature structure of nearshore areas is more complex than has been previously assumed by oceanographers and intertidal ecologists.

Spatial variation in salinity, while small, appears to be related to water movement through the study area. The lowest mean salinity pooled across dates was located at KFZ, the second lowest at CB1 (Figure 7) and the lowest salinity per cast was at SW2. These lower salinities are likely related to their locations relative to the opening of Clayoquot Sound and the direction of overall water movement out of the Sound. Kopach (2004) found that water moved across the opening of Cow Bay in a westerly fashion regardless of tidal state. KFZ is the station located closest to the entrance to Clayoquot Sound and SW2's shallow depth, location nearshore and along the path of water movement could increase the influence of water flow out of the Sound and runoff from Flores Island/Cow Creek. The low average salinity seen at R24 may be associated with localized eddying/downwelling seen near this location on some days.

Chlorophyll results show that this nearshore zone is characterized by relatively high productivity with short term changes in chlorophyll *a* concentration of nearly fivefold magnitude (Figure 25). While the fluorometer was not calibrated with locally collected samples, mean values of extracted chlorophyll samples collected at approximately 1 m depth in the inlets of Clayoquot Sound in the summer of 2001 ranged from 0.5 to 11 μg/L, which are approximately the same range of mean values found in this study (Hahn 2004). The average chlorophyll *a* concentration of 5.37 mg/m^3 (SE = 0.187) is also comparable to interannual average chlorophyll *a* concentration during the summer months of ~6 mg/m^3 for "nearshore" areas of western Vancouver Island (note: nearshore in that study was further offshore than the most offshore stations used in the current study) (Mackas & Galbraith 1992). The three major peaks in mean chlorophyll *a* concentration, July 19, August 7 and September 5, occurred after there had been a decrease and then an increase in mean water temperature (Figure 32). As discussed above, the water temperature decreases are likely due to upwelling which would provide nutrients and vertical mixing of the water column. The subsequent increases in water temperature and chlorophyll *a* concentrations indicate surface warming through solar radiation providing both the energy for photosynthesis and increasing metabolism.

Decreases in chlorophyll fluorescence were of larger magnitude than preceding increases. Particularly striking is the decrease between August 20 and 30. These decreases could be due to grazing pressure by zooplankton and microzooplankton, movement of blooms offshore or intense mixing episodes that break up phytoplankton colonies or aggregations and disperse them (Yin *et al.* 1996, Strom *et al.* 2001, Hickey & Banas 2003). Intense mixing has occurred immediately prior to August 20 as can be seen in the temperature data (Figures 8, 9 a&b, 10 & 21), chlorophyll dispersed throughout the water column (Figure 21) and high upwelling index values (Figure 24). Movement offshore between these dates is supported by the large increase in cold water along the bottom between these dates and high upwelling index values between August 27 and 30 (Figures 21, 22 & 24).

Spatial variation in chlorophyll *a* concentration was evident in the integrated chlorophyll values and when contour maps of the top 5 m are used to separate temporal variation (Figures 27, 28 a-k). Spatial variation in chlorophyll *a* at scales of 10's of kilometers has been found in other studies of nearshore oceanography (Archambault *et al.* 1999, Weiters *et al.* 2003, Shanks & McCulloch 2003, Shanks *et al.* 2003, Menge *et al.* 1997b, Menge *et al.* 2002). Variation in chlorophyll observed in these studies was attributed to differential upwelling, shoreline topography, bottom topography and topographically generated fronts. In this study, the areas where chlorophyll appeared to concentrate were around headlands, particularly Rafael and Dagger Point. Headlands along Flores Island have the strongest mean current velocities and most turbulent flow (Kopach 2004). Strong currents and turbulent flow can increase phytoplankton growth via increased nutrient availability, act to aggregate plankton and may increase encounter rates between zooplankton and their prey (Arin *et al.* 2002, Dower & Denman 2001, Dower *et al.* 1997). In addition, current flow patterns suggest eddying near R41 and as mentioned above, whirlpools were observed at the surface near R24, both locations of high values of integrated chlorophyll (Kopach 2004). Eddying may trap phytoplankton patches and allow for growth of patches in a localized area.

Vertical variation in chlorophyll *a* concentration generally followed the temperature structure of the water column. Additionally the temperature at which the chlorophyll maximum occurred within the water column was significantly higher than the mean water temperature. While other studies have found the highest chlorophyll concentrations within or below the thermocline, the chlorophyll maxima in this study generally occurred just above the thermocline or very near the surface (Figure 20, Dekshenieks *et al.* 2001, Rines *et al.* 2002, Shanks *et al.* 2003).

Factors influencing phytoplankton productivity are light and nutrient availability, temperature, and water column structure and stability (Demers *et al.* 1989, Klausmeier & Litchman 2001, Macedo *et al.* 2001, Moore *et al.* 2003, Reay *et al.* 2001, Weiters *et al.* 2003, Yin *et al.* 1996). Light limitation in this shallow study area may occur due to shading by existing phytoplankton blooms but is unlikely when phytoplankton concentrations are low. Phytoplankton could also be thermally limited and/or limited by nutrients that are supplied by upwelling (Reay *et al.* 2001). In shallow water bodies, temperature can be the dominant factor controlling photosynthesis (Kirk, 1994). Weiters *et al.* (2003) found that major peaks in chlorophyll occurred when the water column showed strong temperature stratification and surface waters had begun to warm after a rapid drop in sea surface temperature. Prior to two of the three major increases in chlorophyll *a* (August 7 and September 5), water temperature had dropped and then warmed and the water column went from being mixed above 20 m (July 25 and August 20) to becoming stratified (Figures 8, 18-20, 21-23). These results and the shape and intensification of the chlorophyll concentration contours between August 1 and 7 and August 30 and September 5 support the idea that upwelling or mixing processes provide nutrients and then surface warming allows increased photosynthesis (Figures 19, 20, 22 & 23).

Seasonal and interannual variations in temperature and water column structure are often cited as important for seasonal and interannual changes in phytoplankton and zooplankton (Bertram *et al.* 2001, McFarlane *et al.* 1997). Short term changes in temperature on the order of seasonal changes are common in the Pacific Northwest and have been observed in surface waters in Chile in as short a period as the diurnal cycle (Hickey & Banas 2003, Kaplan *et al.* 2003). Seasonal variation in mean water temperature off Vancouver Island is generally approximately 4°C, with interannual variation of approximately 1°C (Mackas 1995, Thomson 1981). While short term temperature variation observed in this study was not as large as seasonal changes, variation of over 1°C occurred within the water column on several occasions over periods as short as a few days.

This study adds to the large body of literature documenting the influence of temperature and temperature structure on chlorophyll *a* concentration. Temperature also has a significant effect on growth of invertebrates and larval fish (Huntley & Boyd 1984, Kinne 1970, Moloney *et al.* 1994, Meekan *et al.* 2004). If smaller scale temporal variation, down to the level of diurnal changes, is large enough to influence growth or behaviour of organisms, these short term changes can have important impacts on communities (Narváez *et al.* 2004, Sanford 1999). Although temperature changes associated with upwelling or the diurnal cycle likely do not have a significant effect on all organisms in the nearshore zone, impacts on key species interactions have been found and show that small changes in temperature have the potential to result in ecologically significant changes in communities (Sanford 1999).

FUTURE RESEARCH

The results of this study indicate that short term temporal variation in chlorophyll *a* concentration off Flores Island is primarily controlled by water column properties induced by wind events observed as temperature variation. To more thoroughly understand this process and document the development of these variations, I suggest that wind events are recorded within the study area and temperature fluctuations are tracked daily. The most effective way to do this would be to install an anemometer and a moored temperature logger at Rafael Point. The installation of an anemometer would allow documentation of local winds rather than relying on data from lighthouses or data buoys. A moored thermistor placed a few metres below the surface at Rafael Point would allow consistent temperature data collection even when weather conditions prevent sampling in a small boat. In addition, CTD sampling as soon as possible after a wind event and for several days there after would allow the documentation of changes in the water column that occur during and after mixing events.

Further, documentation of small scale spatial variability of physical and biological oceanography with more inshore-offshore coverage could confirm the existence of phytoplankton blooms consistently occurring around Rafael Point. If present, possible understanding of this could be gained through evidence of spatial variation in upwelling or water column structure. CTD sampling should be conducted along several strategically placed transects perpendicular to the shoreline. Each transect should consist of at least 3 sampling stations to allow production of vertical section plots. My suggestions for placement are from the center of Cow Bay to offshore, Siwash Point to offshore, Grassy Knoll to offshore, Rafael Point to offshore and Dagger Point to offshore. Fewer stations overall with more inshore to offshore coverage would allow better comparisons among different parts of the study area and allow vertical contouring at locations other than just Rafael Point.

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CHAPTER 3: SPATIAL AND TEMPORAL DISTRIBUTION OF PORCELAIN CRAB LARVAE IN CLAYOQUOT SOUND, BRITISH COLUMBIA

INTRODUCTION

Occasional events of intensive feeding by gray whales on porcelain crab zoeae (Family Porcellanidae) in Clayoquot Sound prompted my interest in potential drivers of these events (Dunham & Duffus 2001). Plankton patchiness across scales has been well documented in marine systems but a clear understanding of the causes of patchiness remains elusive (Pinel-Alloul 1995). Potential mechanisms for crab larvae patch formation and maintenance include synchronous spawning events, associative larval behavior and aggregative physical processes (Natunewicz & Epifanio 2001). In addition, parameters which influence development and survival of crab larvae impact the abundance and distribution of larvae in the plankton.

The two main controls on development and survival are thought to be temperature and food availability. Temperature is considered a primary control on growth and length of the larval period in crustaceans (Kinne 1970, Warner 1977). A temperature change from 14 to 10 °C at a salinity concentration of 30 ppt may add 40 days or more to development from zoea I to megalopa in Dungeness crabs (Moloney *et al.* 1994). Salinity also impacts survival at extreme levels and can affect growth rate in conjunction with variation in temperature (Anger 2003). Physical environmental conditions not only directly influence larval ecology but also have an influence on larvae indirectly through impacts on lower trophic levels. Temperature influences chlorophyll *a* concentration by affecting the metabolic rate, photosynthesis and thus growth in phytoplankton (Gessner 1970). In addition, chlorophyll structure within the water column often “follows” temperature structure. Simulations of temperate coastal zooplankton production on the scales considered in the present study (100s of m to 10s kms, days to months) have shown temperature to be more important than food limitation (Daly & Smith 1993).

Concentration of chlorophyll *a* indicates the amount of food available at the base of the food web. At times, development of larvae in coastal waters is also limited by food availability (Anger *et al.* 1981, Paulay *et al.* 1985, Scheltema 1986). Food limitation is particularly detrimental to decapod zoeae during the period immediately following larval release, with starvation for as little as one day during this crucial time resulting in very high mortality (Anger *et al.* 1981). Thus, variability in temperature and chlorophyll *a* concentration, on the scale documented in Chapter 2, can alter larval development time impacting overall survival (Moloney *et al.* 1994).

Knowledge that these factors influence decapod zoeae prompted me to try and link the presence of dense patches of porcelain crab zoeae with oceanographic conditions of the area. If temperature is an important control on growth in porcelain crab larvae, I would expect an increase in the proportion of later stage larvae (zoea II or megalopa) after an increase in temperature. Porcellanid zoeae rely on encounters with suitable prey items rather than exhibiting hunting behaviour as some other crab larvae do, placing their survival particularly dependent upon suitable prey density (Gonor & Gonor 1973a). An increase in primary productivity increases food availability through the food web thus increasing survival. I would expect this to be expressed as a high abundance of porcelain crab larvae, with a time lag, following an increase in chlorophyll *a* fluorescence.

Very little is known about porcelain crab larvae despite the fact that they are highly abundant at times. Apart from the research that prompted this study (Dunham & Duffus 2001, 2002), most of the information available has been the result of researchers capturing larvae for use in laboratory studies or mentions of porcelain crab larvae in field studies concentrating on commercially important species. Gonor & Gonor (1973b) collected larvae of all four porcellanid species (*Pachycheles pubescens* Holmes 1900, *Pachycheles rudis* Stimpson 1858, *Petrolisthes cinctipes* Randall 1839, *Petrolisthes eriomerus* Stimpson 1871) between May and September in Oregon for a laboratory larval description study, however, no further information about larvae in the plankton is given. A survey conducted from Tofino, BC to 185 km offshore of Clayoquot Sound found that *Petrolisthes cinctipes* zoeae were the dominant crab larvae in waters less than 8 km from shore (Jamieson & Phillips 1988). *Petrolisthes cinctipes* larvae are also mentioned in a series of meroplankton studies off California (Wing *et al.* 1995, 1998a,b). In one of these studies, porcelain crab larvae are referred to as "coastal crab larvae" and conclusions include a statement that the poor vertical migration ability of coastal crab larvae contribute to the spatial distribution differences between these and other crab larvae

(Wing *et al.* 1998a). Dunham and Duffus (2001, 2002) found porcellanid zoeae patches of high enough densities to attract foraging gray whales mainly during late July through August of 1996 and 1997 in Clayoquot Sound, BC.

Through this study I aim to document the distribution and abundance of porcellanid larvae in Clayoquot Sound over spatial scales of 0.5 km to tens of kilometers and temporal scales of days to weeks to clarify the findings of Dunham and Duffus (2001, 2002). Specifically, is there a peak period of porcelain crab larvae abundance? How does the study area-scale abundance of porcelain crab larvae vary over the three-month study? Is there an area where porcelain crab larvae are consistently found at higher densities? Is there evidence that the spatial and temporal distribution and abundance of porcelain crab larvae is related to small scale and short term variation in temperature, salinity and chlorophyll *a* concentration? Are gray whales found near high densities of porcelain crab larvae?

METHODS

THE STUDY AREA

This study was conducted along approximately 15 km of the southwest edge of Flores Island (49°17'N, 126°10'W) in Clayoquot Sound, British Columbia between Dagger Point in the north and the Fitzpatrick Islands in the southeast (Figure 1). The depth of the water column in the majority of the study area is less than 30 m. The coastline is characterized by rocky shores and kelp beds interspersed with sandy beaches and cobblestone bays. Most of the study area, excluding the western edge of Cow Bay, is exposed to prevailing summer wind waves and swell from the northwest.

ZOOPLANKTON / OCEANOGRAPHIC SAMPLING AND ANALYSIS

Zooplankton sampling was conducted between June 15 and September 5, 2002 at 26 stations located along the southwest edge of Flores Island (Figure 2). Station locations were chosen to coincide with water circulation transects completed in 2001; the highest concentration of stations were placed off Rafael and Dagger Points where previous studies found the highest concentrations of porcelain crab larvae (Dunham & Duffus 2001, 2002, Kopach 2004). Spacing of stations around Rafael Point was determined based on crab larvae patch studies which found patches to range in diameter from 0.5 to 2.5 km (Nantunewicz & Epifanio 2001).

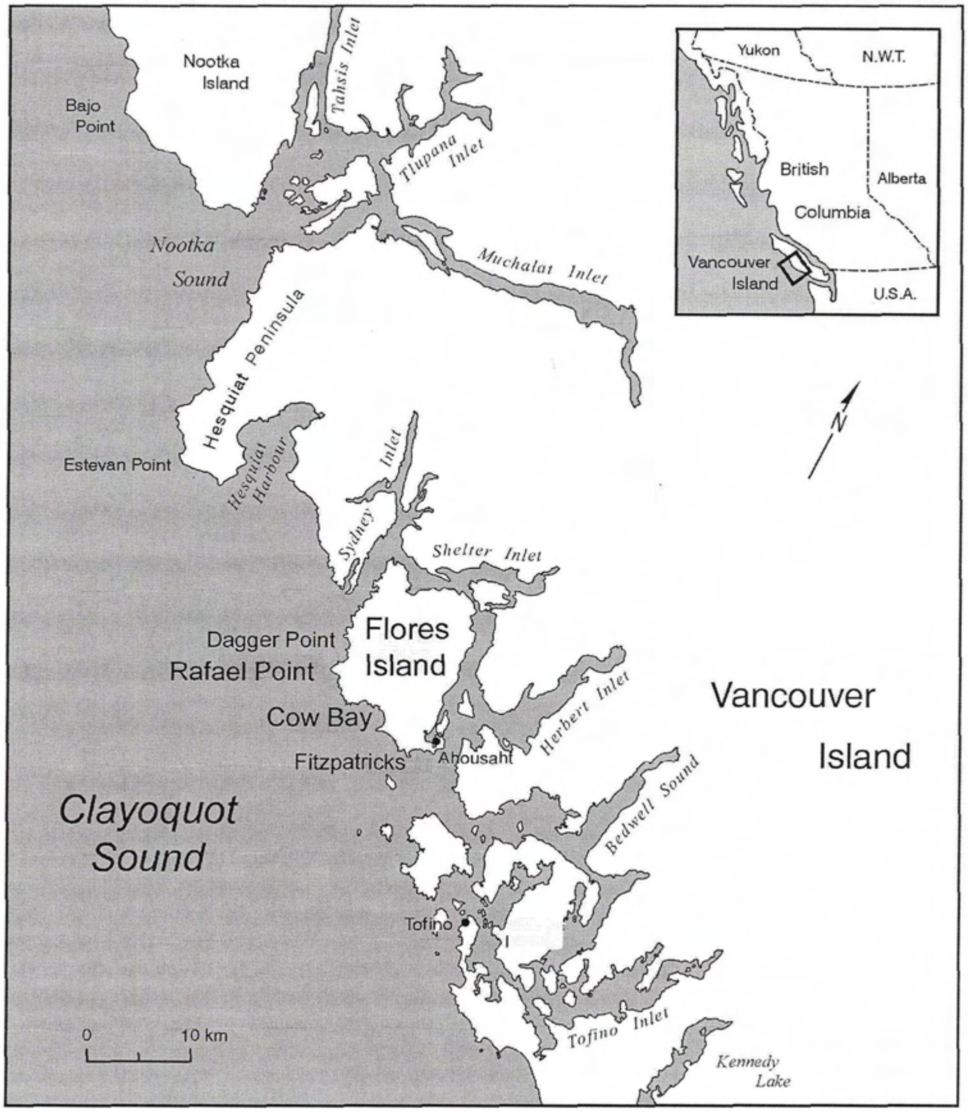


Figure 1: Location of the study area within Clayoquot Sound, BC.

Complete sampling consisted of CTD/fluorometer casts and plankton tows at all stations. Average water depth at the stations is 17 m (SD = 8.0 m). Zooplankton sampling was accomplished via net tows from the seafloor to the surface using a 2X30 cm bongo net with a mesh size of 500 µm. Zooplankton samples were fixed in 7% buffered formalin and then transferred to 95% ethanol which was drained and replenished twice before microscope analysis. Analysed samples were stored in 70% EtOH. Porcellanid larvae were counted and identified to genus (*Pachycheles* or *Petrolisthes*) and developmental stage (zoea I, zoea II, megalopa) based on published descriptions (Gonor & Gonor 1973b, Lough 1975).

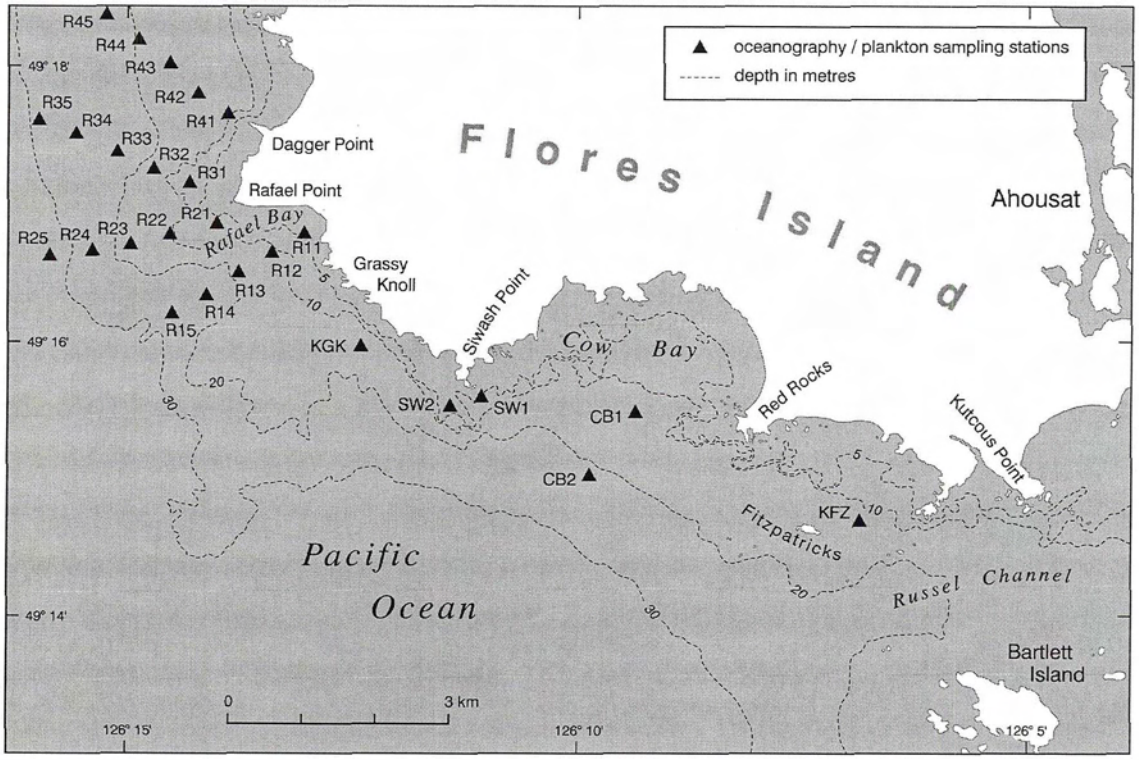


Figure 2: Location of sampling stations within the study area.

Vertical profiles of temperature, salinity and chlorophyll *a* were obtained for the entire water column at each station using a Seabird *SBE 19plus* SEACAT Profiler CTD and attached WetLabs EcoFL Fluorometer. Fluorescence measurements represent relative chlorophyll *a* concentrations as they were not calibrated against extracted chlorophyll *a* samples from the study area. CTD/fluorometer cast files were processed using Seabird's SBE Data Processing software. Standard data processing procedures described in the SBE Data Processing manual were followed. Sampling was conducted, weather permitting, approximately once per week (range = 4 to 13 days), resulting in 11 complete sampling periods.

GRAY WHALE LOCATIONS

To determine the number and prey type of foraging gray whales in the study area I conducted boat-based gray whale surveys a minimum of every three days, weather permitting. A survey consisted of driving at a constant speed of 12-15 km/hr along the 10 m contour line through the study area with 2 to 4 spotters visually scanning in all directions for gray whales. When a gray whale was spotted we approached the whale to obtain its location using a hand-held GPS. When a foraging gray whale was encountered, prey type was determined by a combination of net tows, location within a known prey habitat type, whale behaviour, and presence of sediment plumes (indicative of amphipod feeding). Only survey data collected on days of complete plankton and oceanography sampling are presented here. Locations and number of whales present in the study area were compared to spatial and temporal trends in porcelain crab larvae and oceanographic data to assess the possibility of these factors influencing gray whale abundance and distribution.

DATA ANALYSIS

Porcellanid zoeae density reported here are density approximations calculated using the following equation:

$$\#\ \text{zoeae/m}^3 = \# / 2\ (3.14\ r^2)\ \text{depth} * E$$

\# = number of porcelain crab zoeae per plankton tow
r = radius of the net opening
depth = depth of the water column (approximate distance net was towed using vertical tows)
E = estimated bongo net filtering efficiency of 70%

A density of 40 zoeae/m^3 or greater was assigned to define a patch as this value was found to be substantially higher than overall densities of porcellanid zoeae in this and a previous study (Dunham & Duffus, 2002).

RESULTS

Analysis of 279 plankton samples, 228 of which contained porcelain crab zoeae, showed low overall levels of porcelain crab zoeae throughout the season. Counts of total zoeae per plankton tow (both zoeal stages of *Pachycheles* spp. and *Petrolisthes* spp.) ranged from 0 to 1082 with density approximations ranging from 0 to 311.9 zoeae/m^3 (Table 1). 222 samples contained zoea I while 151 samples contained zoea II. Of the 145 samples (64% of samples with zoeae) that contained both zoeal stages, zoea I larvae were more abundant than zoea II larvae in 117 samples. Counts of zoea I ranged from 0 to 561 with densities ranging from 0 to 270.6 zoeae/m3 (Table 1). Abundance of zoea II per sample ranged from 0 to 789 and densities ranged from 0 to 227.5 (Table 1).

Table 1: Mean and standard deviation of zoeal abundance and density for all zoeae, the two zoeal stages (*Petrolisthe*s and *Pachychele*s combined) and each genus (both zoeal stages combined).

		Mean	*SD*
Zoeae Abundance	Total	24.0	81.51
(# zoeae/net tow)	Zoea I	7.9	48.68
	Zoea II	15.7	41.10
	Petrolisthes	3.3	9.04
	Pachycheles	20.7	76.77
Zoeae Density	Total	10.52	29.898
(# zoeae/m^3)	Zoea I	7.41	21.410
	Zoea II	3.10	15.540
	Petrolisthes	1.50	3.941
	Pachycheles	9.02	27.526

In addition to samples being composed of mixed zoeal stages, both *Pachycheles* spp. and *Petrolisthes* spp. were present in 141 samples (62% of samples with zoea), although *Pachycheles* spp. zoeae made up greater than 50% of the zoeae in 129 samples. Eighty samples contained only *Pachycheles* spp. zoeae and 7 samples contained only *Petrolisthes* spp. The maximum number of *Petrolisthes* zoeae in a sample was 110 on August 1, 2002, substantially lower than the abundances of *Pachycheles* zoeae per sample (maximum = 1061) (Table 1). Maximum density approximation for *Petrolisthes* was 46.1 zoeae/m^3 while the maximum *Pachycheles* density was 305.9 zoeae/m^3 (Table 1).

Mean densities were low throughout the season and temporal variation in density of zoeae was small, however a few high density samples were collected (Figure 3). Major peaks in zoeal density, greater than 200 zoeae/m^3, on July 7 and August 1 indicate the influence of a few large samples rather than a study area-wide increase in larval density (Figure 4). The peak on July 7 is caused by one large sample with a density of 311.93 zoeae/m^3 at R25, while the August 1 peak is due to large samples at R44 (274.95 zoeae/m^3) and R45 (193.07 zoeae/m^3) (Figure 5). The large sample on July 7 was dominated by zoea II while the samples on August 1 were dominated by zoea I (Figure 4). Based on a definition of >40 zoeae/m^3, 11 samples found on June 15, July 7, July 15, August 1, August 20 and September 5 are labelled patches (Figure 5). The temporal trends for the zoeal stages are similar for both *Pachycheles* and *Petrolisthes* spp. (Figures 6&7).

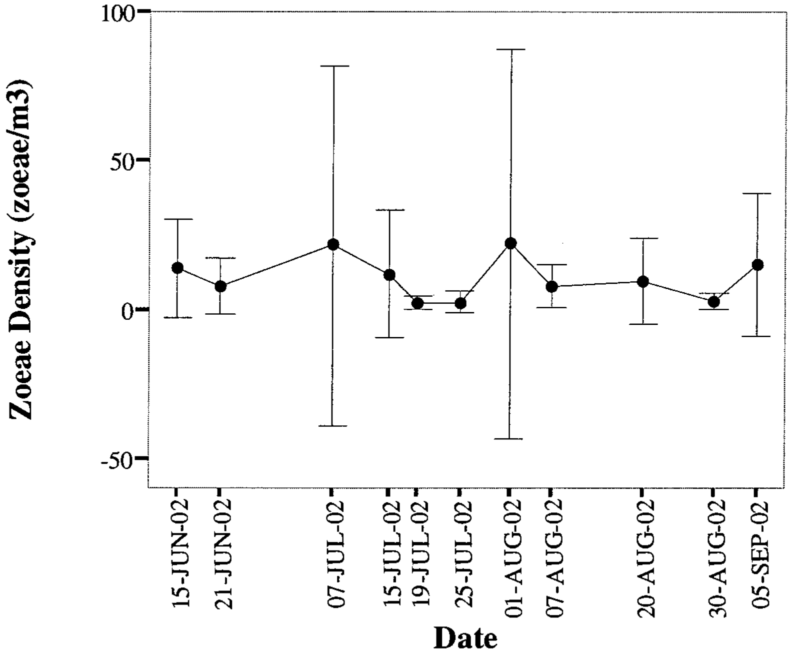


Figure 3: Average density of zoeae (# zoeae/m^3) on each sampling date of the study period (samples from all stations pooled for each date, error bars = SD).

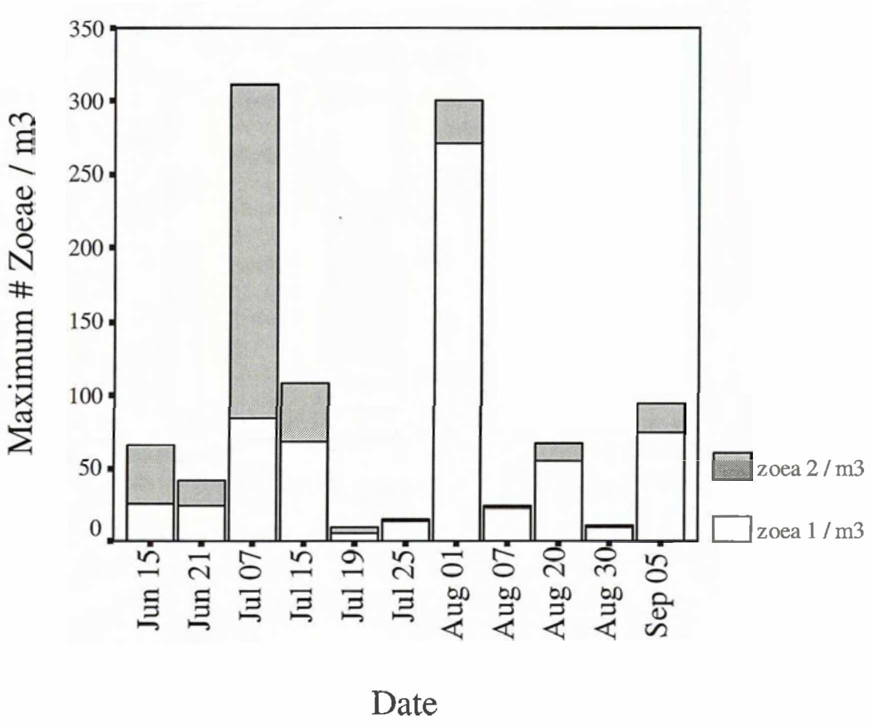


Figure 4: Maximum density of zoea I and zoea II over the study period.

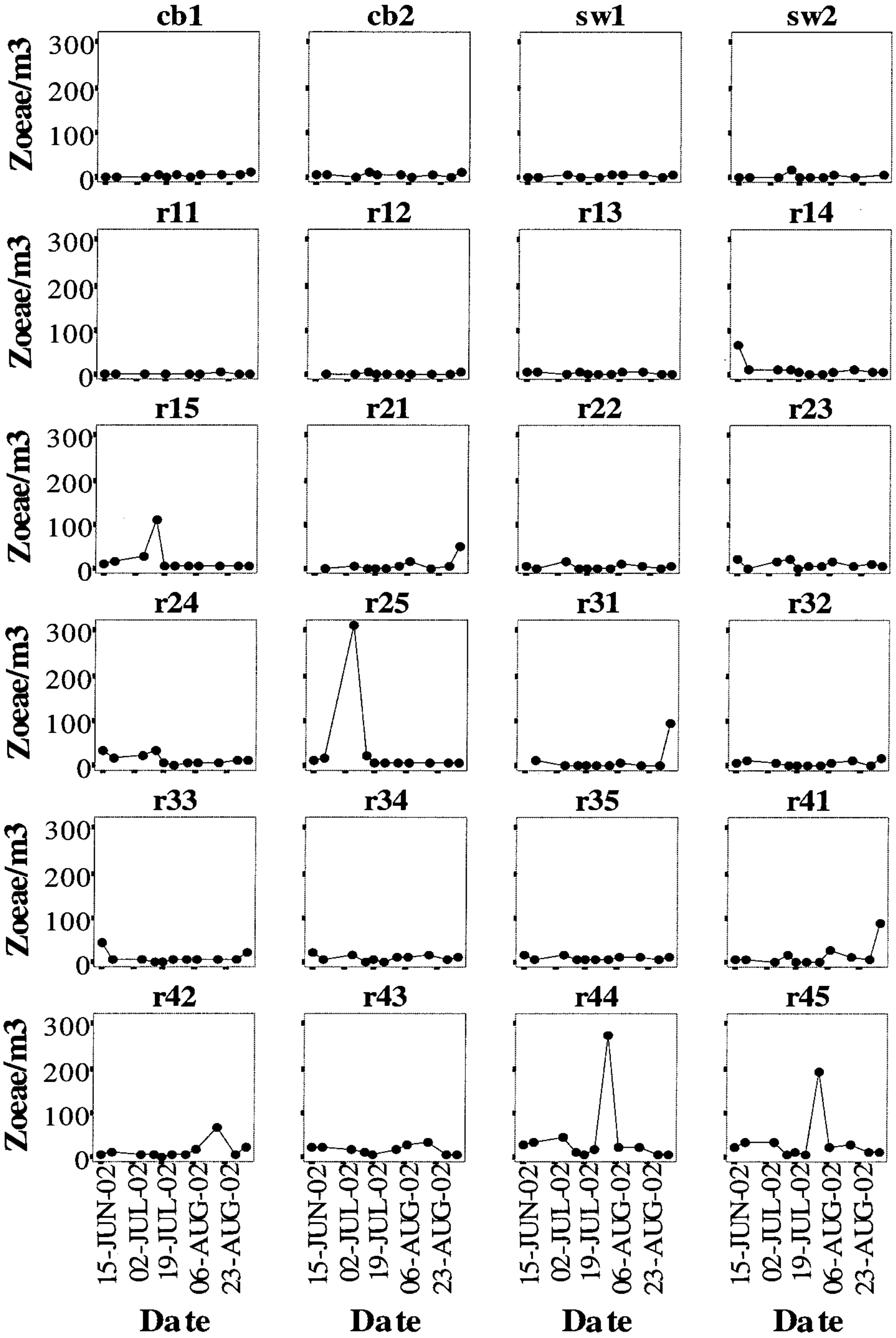


Figure 5: Variation in density of zoeae at each station over the course of the study period. Dates are: Jun 15, Jun 21, Jul 7, Jul 15, Jul 19, Jul 25, Aug 1, Aug 7, Aug 20, Aug 30 and Sep 5. Stations KFZ and KGK had low zoeal densities across the season (max 4.53 for KFZ and 12.25 for KGK) and were excluded for presentation purposes.

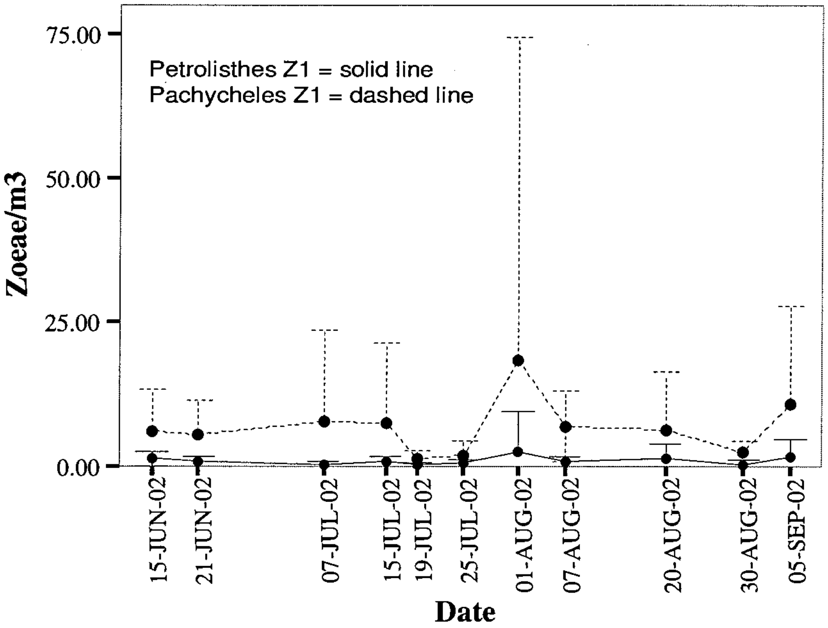


Figure 6: Mean density of Petrolisthes and Pachycheles zoea I over the study period. Samples from all stations pooled. Error bars = SD.

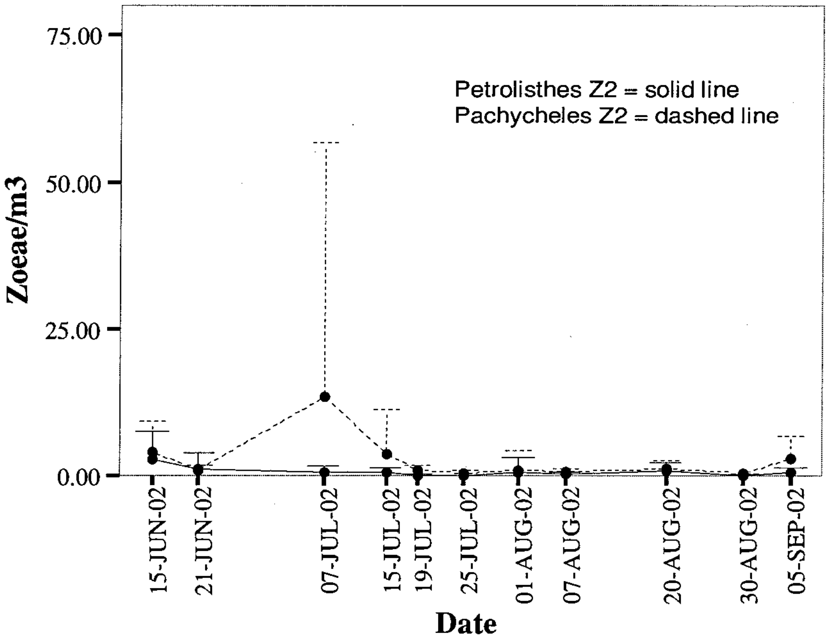


Figure 7: Mean density of *Petrolisthes* and *Pachycheles* zoea II over the study period. Samples from all stations pooled. Error bars = SD.

Porcelain crab larvae were not distributed evenly across the study area. Samples containing high numbers of zoeae (outlier and extreme densities) were obtained at stations around Rafael Point and Dagger Point (Figure 5 and 8). Even when outlier and extreme values were excluded, higher densities were found north of Rafael Point (highest at R44 and R45) (Figure 9). Patches were found exclusively around Rafael and Dagger Point, at stations R14, R15, R21, R25, R31, R33, R41, R42, R44, and R45 (Figure 10). In most cases, patches did not extend across several sampling stations, however on August 1 samples taken at R44 and R45 were defined as a patch and on September 5 a patch appeared to extend around Rafael and Dagger Point, at stations R21, R31 and R41. This patch (R21, R31 and R41) also represents one of two patches found within 1km of shore (the other was at R42 on August 20). Fifty-one samples contained no porcelain crab zoea. All stations had at least one sampling period during which zoeae were found in a sample, but 15 stations, mainly nearshore, had at least one sampling period when zoeae were not captured in the sample (Figure 11).

Megalopae were found in only 8 samples, totalling 12 megalopae. This larval stage was only observed in samples taken from around Rafael Point (R14, R22, R23, R34, R41, R44, R45). Temporally, megalopae were observed in all months except August (June 21, July 7, July 15 and September 5).

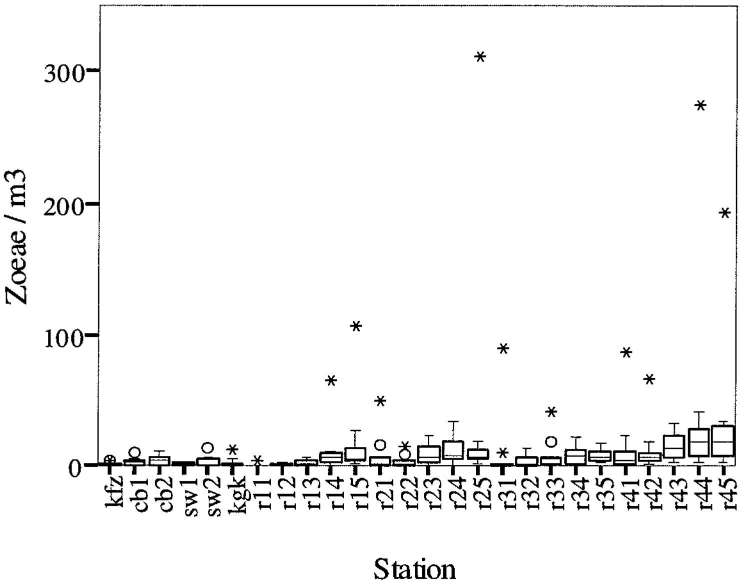


Figure 8: Boxplots of density of zoeae at each station. Circles represent outlier values (values 1.5 to 3 times the interquartile range length, or box length, from the edge of the box or interquartile range) and stars represent extreme values (values greater than 3 times the interquartile range length from the edge of the interquartile range).

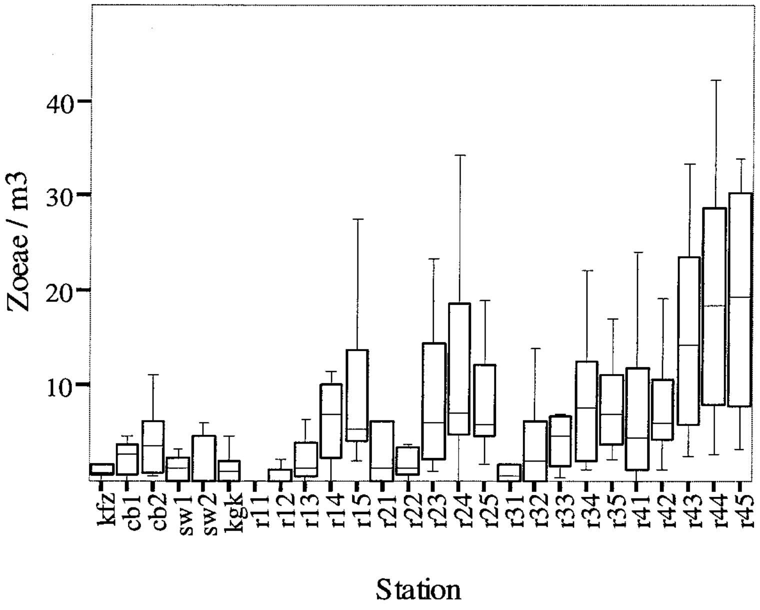


Figure 9: Boxplots of density of zoeae at each station with outlier and extreme values excluded. Box represents the interquartile range and line in the box represents the median value.

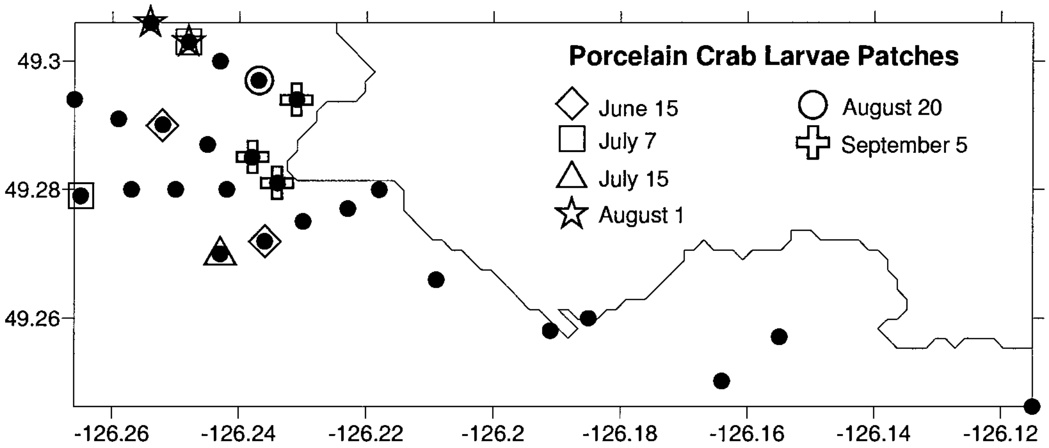


Figure 10: Locations across the season of patches (> 40 zoeae/m^3) of porcelain crab larvae. Legend indicates date that the patch was sampled. Patches were not found on June 21, July 19, 25, August 7 and 30.

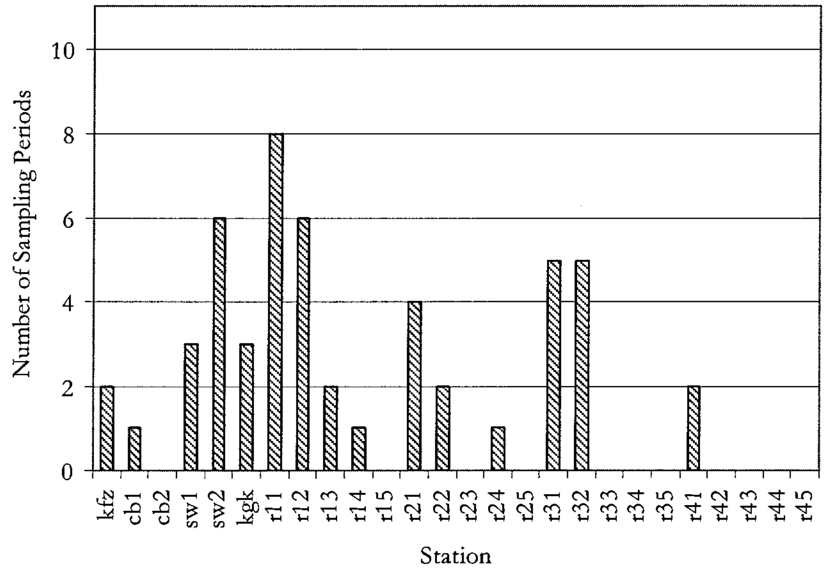


Figure 11: Number of samples at each station which contained zero porcelain crab zoea.

To determine if the spatial and temporal variation of porcelain crab larvae is related to environmental variability, trends in crab larvae density were compared with temperature and chlorophyll fluorescence. Patches of zoeae do not appear to be correlated with temperature or chlorophyll levels. Despite spatial and temporal differences in temperature and chlorophyll *a* fluorescence (reported in Chapter 2), no related trends in density of zoeae were observed. At the patch level, there was no trend in the average temperature or chlorophyll *a* concentration for a cast at a location where a patch of zoeae was found relative to study area wide average conditions. In addition, no temporal trend in temperature or chlorophyll *a* concentration prior to the date when the patch was sampled was seen. However, the oceanographic conditions measured on July 15, the first sampling period after larval release of *Petrolisthes cinctipes* (Chapter 4), were the lowest average water temperature of the season, 10.37 °C (SE = 0.090), and a mean chlorophyll *a* concentration of 4.03 mg/m^3 (SE = 0.350) which is below the season average of 5.37 mg/m^3 (SE = 0.187) (Figures 12 and 13).

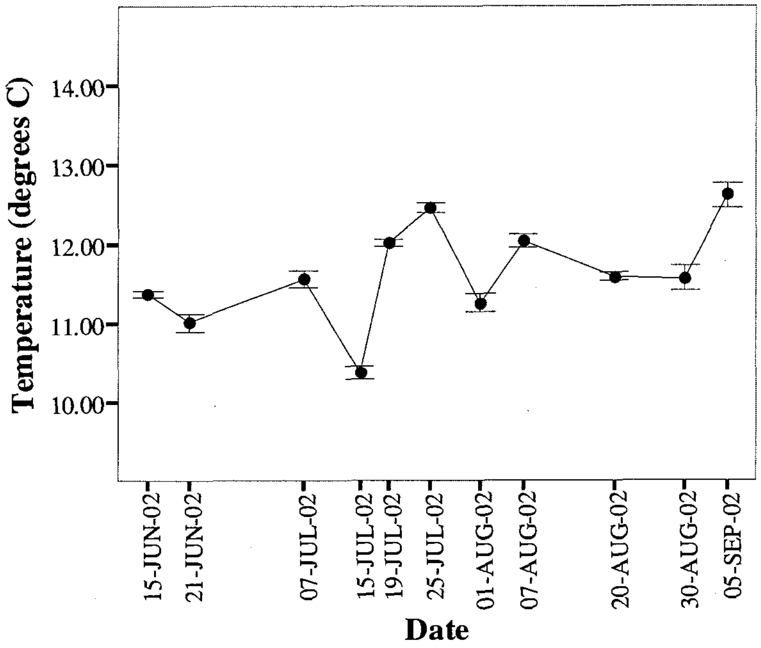


Figure 12: Mean water temperature (error bars = 1 SE) across the sampling period.

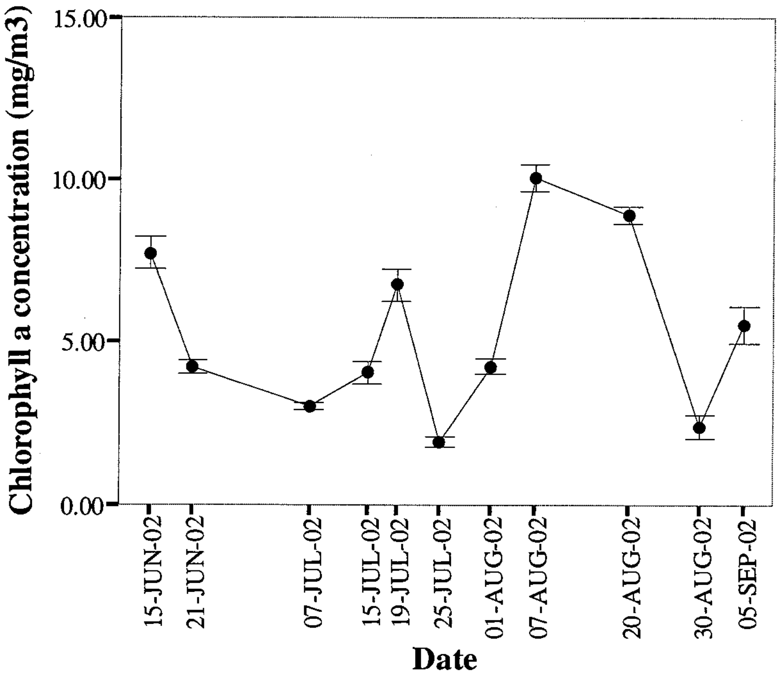


Figure 13: Temporal changes in mean chlorophyll *a* concentration (error bars = 1 SE).

Gray whales were present within the study area throughout the study period but were not observed feeding on porcelain crab larvae. A total of 170 whales in 104 sightings were observed during the 11 days of complete station sampling. The number of whales observed in the study area peaked at 33 whales on July 7, 2002 (Figure 14). Although gray whale abundance peaked on the same day as one of the peaks in porcelain crab larvae density (Figure 3), gray whale distribution and abundance was not related to porcelain crab larvae distribution and abundance (Figure 15a).

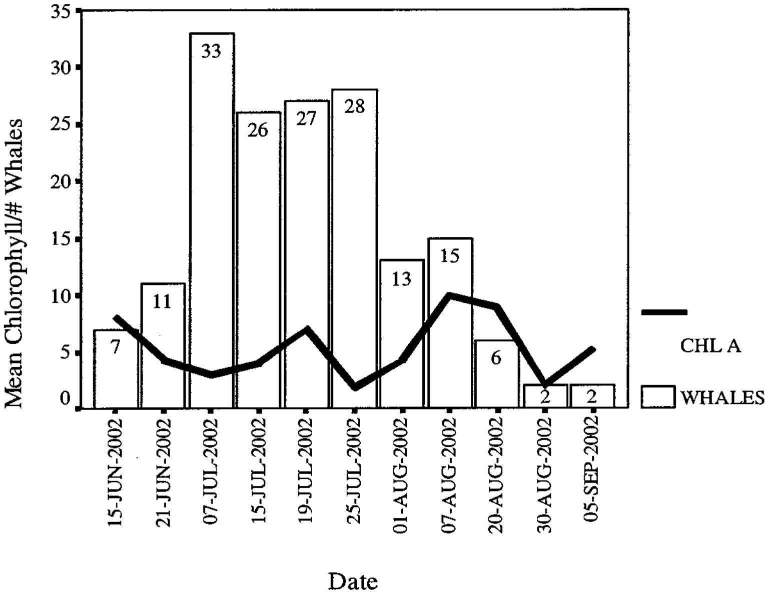
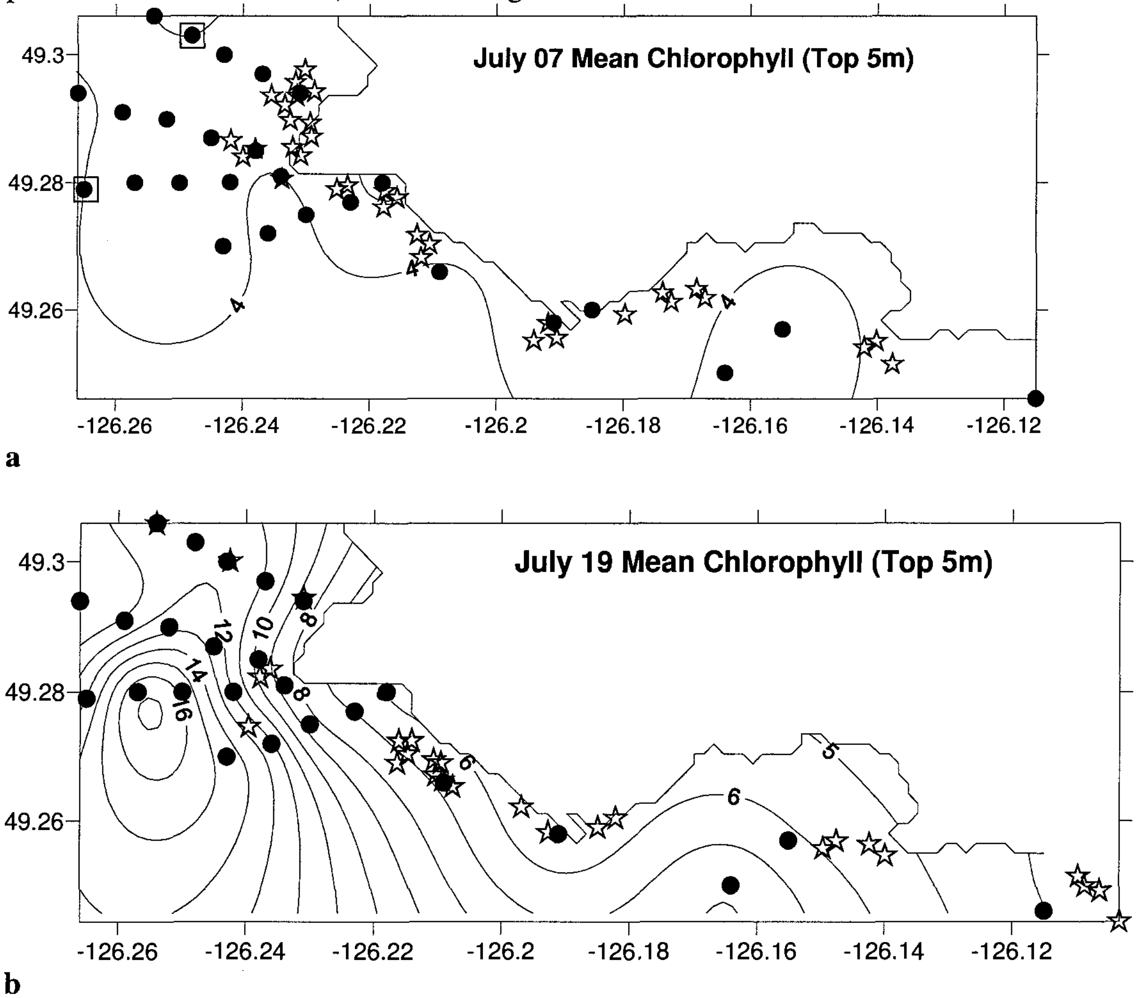


Figure 14: Mean chlorophyll *a* concentration (mg/m3) and the number of whales present in the study area over the course of the field season.

Mysids, one of the major prey groups for gray whales in Clayoquot Sound, are filter feeders utilizing phytoplankton in the water column as one of the components of their diet. Based on prey sampling near feeding gray whales and behavioural observations, gray whales fed primarily on mysids throughout this study. To investigate the possibility that whale distribution and abundance was dependent on chlorophyll concentration indirectly through their prey, number of whales sighted per sampling date and locations of whales on each sampling day were compared to spatial and temporal trends in chlorophyll *a* concentration. Whales show no response to variations in chlorophyll *a* concentration, spatially or temporally. The temporal trend in the number of whales in the study area did not follow trends in chlorophyll *a* concentration (Figure 14). Whales did not locate themselves at areas of high chlorophyll levels during or after phytoplankton blooms (Figure 15 a&b – July 07, the peak in whale abundance, and July 19, a date with both high levels of chlorophyll concentration and whale numbers are shown).

Figure 15 a-b: Whale locations (stars) and contour maps of mean chlorophyll *a* concentration (contours = 1 mg/m^3) of the top 5 m of the water column. Circles represent CTD sampling stations and squares on July 07 are locations of porcelain crab larvae patches. X-axis = latitude, Y-axis = longitude.



DISCUSSION

Average zoeae density in the current study is comparable to that found in 1997 in areas where whales were not feeding on porcelain crab larvae (Table 2). The maximum density found in 2002 is comparable to the maximum density for areas where whales were not feeding on porcelain crab larvae in 1996 (Table 2). In contrast to previous findings, zoea I were present in a larger number of samples and were more abundant than zoea II in the majority of samples that contained both stages (Dunham & Duffus 2001, 2002). The numerical dominance of *Pachycheles* spp. zoeae over *Petrolisthes* spp. zoeae in most samples is consistent with previous results (Dunham & Duffus 2002). The most striking difference between this study and Dunham & Duffus (2002) is the absence of dense patches of porcelain crab larvae in the 2002 field season. During 2002, dense patches of porcelain crab larvae, such as those observed near feeding gray whales in 1996 and 1997 (Table 2), were not documented and gray whales did not feed on porcelain crab larvae. These results support the hypothesis that the conditions which cause dense aggregations of porcelain crab larvae off Rafael Point documented in 1996 and 1997 are rare and of short duration (Dunham & Duffus 2001).

Table 2: A comparison of density (zoeae/m3) parameters (with and without foraging whales nearby) between the current study conducted in 2002 and results of the Dunham & Duffus (2002) study in 1996 and 1997.

	Foraging whales nearby?	*Mean Density (zoeae/m3)*	*Density SD (zoeae/m3)*	*Max Density (zoeae/m3)*
Current Study	No	10.52	29.898	311.9
D&D – 1996	No	72	70	334
D&D – 1997	No	11	13	56
D&D – 1996	Yes	3006	3718	10520
D&D – 1997	Yes	4726	4598	13198

Although a strong peak in the proportion of adult *Petrolisthes cinctipes* carrying prehatch eggs occurred on July 6, indicating a release of larvae between July 6 and July 13, an increase in the number of zoea in the plankton was not observed on the next plankton sampling date, July 15 (Chapter 4 & Figure 3). However, the largest numbers of *Petrolisthes* spp. and *Pachycheles* spp. zoea I were found on August 1 at R44 and R45 (Figure 4, 5 & 6). The length of the zoea I stage is approximately two weeks (MacMillan 1972, Knight 1966) so it is possible that zoea I sampled on August 1 are the result of larval release events in mid-July. The timing of peaks of zoea II in early July (Figure 7) and zoea I in early August (Figure 6) are consistent with 1996 and 1997 results and information on timing of hatching of subsequent broods of larvae in porcelain crab species (Chapter 4, Dunham & Duffus 2001, Knudsen 1964).

Petrolisthes cinctipes and *Petrolisthes eriomerus* settle gregariously (Jensen 1991). Megalopae that find conspecific adults settle within a few days, while megalopae that do not find suitable settlement conditions will delay settlement for up to three weeks (Jensen 1991). The small number of megalopae found in this and previous studies in

Clayoquot Sound (Dunham & Duffus 2001) are likely a reflection of the large amount of suitable habitat for settlement in the study area. Mussel beds densely populated by adult *Petrolisthes cinctipes* found on exposed coastline along some portions of the study area are ideal habitat for *P. cinctipes* and boulder substrate off Rafael Point, Dagger Point and in Dagger Bay is suitable habitat for all four species of porcelain crabs. Thus megalopae in this area would find suitable habitat and settle quickly rather than remaining in the plankton for long periods of time.

The spatial distribution of patches found in this study supports previous observations of higher densities of porcelain crab zoeae around Rafael Point in waters >1 km from shore (Dunham & Duffus 2002). Shoreline morphology is known to alter retention/dispersal patterns through alteration of flow regimes (Archambault 1998, 1999, Wing *et al.* 1998 a&b). A boulder pile off Rafael Point extends the 10 m depth contour to over 1 km from shore, more than double the average distance along the coast between Siwash Point and Dagger Point. A larger scale look at the bathymetry of the study area and surrounding region shows an offshore curve of the 20 and 30 m depth contours at Rafael Point and at another location approximately halfway between Rafael Point and Siwash Point ("Grassy Knoll"). These extensions of shallow water away from shore make the area between this part of the study area and Hesquiat Peninsula to the northwest act as a large embayment. The results of this study, dense porcelain crab larvae patches off Rafael Point in other years and results of a current velocity study indicate the interaction of water currents and bathymetry cause temporary accumulation of zooplankton off Rafael and Dagger Points (Dunham & Duffus 2001, 2002, Kopach 2004). The spatially discrete distribution of higher densities of zoeae on a particular sampling day, rather than several samples in an area having large numbers of zoeae, indicates that patches were generally smaller than 0.5 km in diameter (exceptions are August 1 at R44/R45 and September 5 at R21/R31/R41).

Links between physical and biological oceanography and porcelain crab larvae were not clear in this study. While laboratory studies have shown the influence of temperature, salinity and food availability on growth and survival of decapod larvae, few studies have been able to show these links in the field on a patch or population level. One of the major reasons for this is our current inability to track larvae over significant periods of time (such as the entire period of the larval stages). Additionally, the lack of knowledge of the larval biology of many species, including porcelain crabs, leaves researchers without important information (for example diet of porcelain crab larvae) that would aid in study design. Without good tracking ability, transport of larvae by currents prevents researchers from knowing the conditions the larvae were experiencing prior to sampling. Larval transport and dispersal remains a central question in marine ecology (Largier 2003).

The highly variable nature of the nearshore zone means that organisms have little chance of "matching reproductive events with oceanographic conditions conducive to spawning, larval development and recruitment" (Wing *et al.* 1998b, pg 119). An interesting observation of this system comes from the combined results of the plankton, oceanography (Chapter 2) and larval release (Chapter 4) portions of this study. The release of larvae by *Petrolisthes cinctipes* timed with the new moon and nocturnal large amplitude ebbing tides, between July 7 and 13 (Chapter 4), coincided with the lowest average water temperature of the study and low average chlorophyll fluorescence (Figures 12 & 13). No significant peak in porcelain crab zoeae was observed within the study area following the peak in larval release. While the timing of larval release indicates that hatching is influenced more strongly by diurnal, tidal and lunar cycles than other environmental factors, environmental factors such as temperature and salinity are good indicators of water column conditions that will influence larval transport, growth and survival. In this study area, where estuarine outflow is not an important factor, crab larvae patch movement would be mainly controlled by upwelling wind strength (Nantuenwicz *et al.* 2001). Release during upwelling conditions, as occurred during this study (Chapter 2), combined with the lack of vertical migration behaviour of porcelain crab larvae (found in surface and upper water column during both day and night) (Wing *et al.* 1998a), could lead to strong transport out of the nearshore zone. In addition, larval release at a time when food availability and/or temperature are low could result in slow development and high mortality. On the other hand, aggregative processes during the time of release or shortly after combined with relatively high water temperatures and food availability would result in high abundance and high density patches of larvae that whales can occasionally exploit.

An expanded study which included documentation of timing of larval release for all four porcelain crab species, monitoring of wind and current speed and direction, and year to year comparisons of upwelling conditions, water temperature and chlorophyll *a* concentrations would allow testing of these hypotheses. While important gaps in knowledge of the biology of porcelain crab larvae exist, the ease of identification of porcelain crab zoeae to the family level, potential for synchronous release of large numbers of larvae and relatively short larval period could make this group ideal for further study of the influence of environmental variability on larval dispersal.

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CHAPTER 4: TIMING OF LARVAL RELEASE IN THE PORCELAIN CRAB, *PETROLISTHES CINCTIPES*, IN CLAYOQUOT SOUND, BC

INTRODUCTION

Gray whales in Clayoquot Sound feed predominantly on mysids (Order Mysidacea) and amphipods (Suborder Gammaridea) but have been observed exploiting dense patches of porcelain crab larvae (Infraorder Anomura, Family Porcellanidae) during several summer feeding seasons (Dunham & Duffus 2001, 2002). The irregular timing of these events prompted interest in the factors controlling porcelain crab larvae patch formation. Plankton patch formation is a highly complex interaction of physical and biological factors acting on multiple scales. The most obvious factor in the timing of the presence of dense patches of larvae is the timing of larval release. To determine when larvae are being released in the region I monitored the presence of egg-carrying females at three sites between May 23 and September 6, 2002 in conjunction with a study of coastal oceanography, porcelain crab larvae and foraging gray whales.

Four species of porcelain crabs, *Pachycheles pubescens, Pachycheles rudis, Petrolisthes cinctipes, Petrolisthes eriomerus*, are known to inhabit the west coast of Vancouver Island (Hart 1982, Kozloff 1993). Few studies have been conducted on porcelain crab reproductive ecology and much remains unknown. Knudsen (1964) examined the reproductive cycles of many of the common brachyuran and anomuran crabs in Puget Sound, Washington. The porcelain crabs studied, *Petrolisthes eriomerus* and *Pachycheles rudis*, were both found to produce two, sometimes three, broods of eggs in a year. Hatching of the first brood for *Petrolisthes eriomerus* occurred between early May and early August while the second brood began to hatch in early August and continued into October. The peak of hatching for the first brood of *Pachycheles rudis* occurred in April and May while the second brood appeared to be hatching in August. No information on the reproduction of *Petrolisthes cinctipes* or *Pachycheles pubescens* was provided. Gonor and Gonor (1973a) collected gravid females of all four species of porcelain crabs in May and June to supply larvae for laboratory studies and they comment that gravid females were observed during other months of the year in agreement with Knudsen (1964). Zitten (1979) reported females carrying eggs in Barkley Sound, BC during transplant experiments between April and September 1976 with most of his 18 experimental females carrying eggs in April and May and the majority of these same animals no longer carrying eggs between the end of July and September. While the timing of the hatch for *P. cinctipes* and proportion of multiple broods are not known (Jensen 1990), Boolootian *et al.* (1959) found ovigerous *P. cinctipes* in all months except October and November at Monterey, CA and the proportion of females with eggs showed three peaks throughout the year; January to March, May and August. However, sample sizes were small; approximately 10 females sampled per month with a total N over 12 months of 156 (Boolootian *et al.* 1959). Sporadic sampling in the summer months (June to September) over several years in Washington showed most females were not carrying eggs past late July (Jensen, unpublished data). No references to timing of hatching in relation to tidal, lunar, diurnal cycles or oceanographic conditions were found for any of the four species.

P. cinctipes was chosen for this study because of the lack of information available on the timing of larval release in this species and the relative ease of sampling large numbers of individuals due to its abundance in mussel beds which are located at a tidal height regularly exposed during low tide. This study was designed to determine when female *Petrolisthes cinctipes* were carrying eggs in Clayoquot Sound, BC and approximate the timing of larval release. Potential influences on the timing of hatching such as tidal cycle and oceanographic conditions are discussed.

METHODS

Adult *Petrolisthes cinctipes* are found in abundance in well-developed beds of the mussel, *Mytilus californianus*, in the upper to mid intertidal zone of rocky exposed coasts (Jensen & Armstrong 1991). Three locations within mussel beds on the southwest coast of Flores Island, Clayoquot Sound (Figure 1) were sampled 9 times, a minimum of once every two weeks between May 23 and September 6, 2002. Crabs were collected by lifting a cluster of mussels, approximately 20 X 20 cm, off the rocks and placing the mussels in a bucket. As many crabs as possible were captured from underneath the mussel cluster and crabs remaining within the mussel cluster were carefully extracted from between mussels. Crabs were maintained in a bucket of seawater equipped with empty mussel shells for shelter and kept out of direct sunlight during handling. A minimum of twenty-five crabs at each sampling location were measured (carapace width), sexed and the presence and stage of developing eggs noted. As *Petrolisthes cinctipes* eggs develop and near hatching they change from a deep maroon colour to nearly translucent with the eyes of the developing crabs clearly visible (Gonor & Gonor 1973a). Eggs at this translucent and "eyed" stage are referred to here as "prehatch". All crabs and mussels were returned to their original location following data collection.

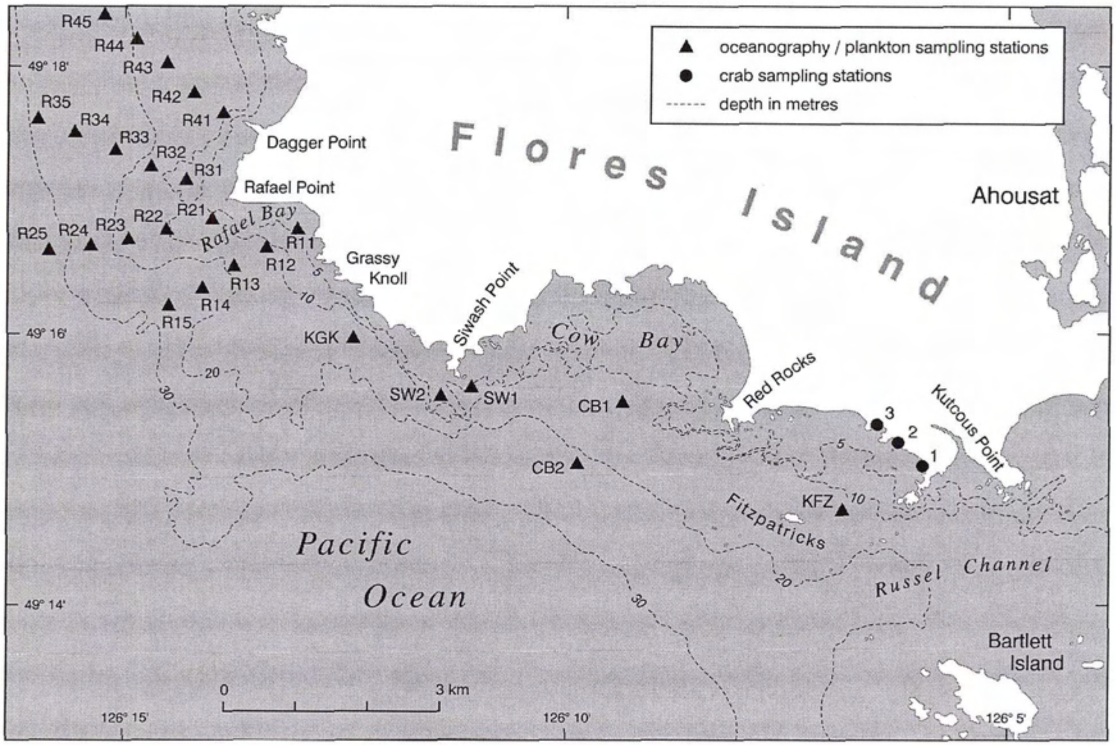

Figure 1: Study area on the southwest coast of Flores Island in Clayoquot Sound, British Columbia. Circles represent locations of crab sampling sites and triangles represent oceanographic sampling stations.

Oceanographic sampling was conducted between June 15 and September 5, 2002 at 26 stations located on the front side of Flores Island (Figure 1). Vertical profiles of temperature, salinity and chlorophyll *a* were obtained using a Seabird *SBE 19plus* SEACAT Profiler CTD and attached WetLabs EcoAFL Fluorometer. Complete sampling was conducted approximately once per week, weather permitting, resulting in 11 sampling occasions.

RESULTS

Data from 1552 porcelain crabs were recorded with sample size per site ranging from 25 to 227 (Table 1). Crabs ranged in size from less than 1 mm to 13 mm with egg-carrying females measuring 3 mm to 12 mm. Female crabs represented between 50 and 60% of crabs sampled throughout the field season. Egg-carrying females were present during all sampling dates but the proportion of crabs with eggs dropped off steeply after July 6 (Figure 2). There was also a strong peak in the proportion of crabs with prehatch eggs on July 6, right before the proportion of egg-carrying crabs declines (Figure 2). This peak in the proportion of crabs with prehatch eggs and subsequent drop in the proportion of egg-carrying crabs indicates a peak in larval release shortly after July 6.

Water conditions during 281 CTD/Fluorometer casts obtained between June 15 and September 5 were examined to determine if environmental conditions may have influenced the timing of larval release. A drop in mean water temperature of 1.1 °C occurred between July 7 and 15, the period during which the majority of larvae were likely released (Figure 3). Chlorophyll *a* concentration during this period was among the lowest recorded during the season (Figure 4).

Table 1: Number of porcelain crabs sampled at each of the three sites across the field season. Note that Site 1 could not be sampled on August 17 due to tide height.

Date	*N (Total)*	*Site 1*	*Site 2*	*Site 3*
23-May-02	329	42	60	227
7-Jun-02	152	43	58	51
22-Jun-02	192	66	57	69
6-Jul-02	179	93	54	32
13-Jul-02	185	87	61	37
24-Jul-02	161	49	44	68
10-Aug-02	143	25	46	72
17-Aug-02	68	0	37	31
6-Sep-02	143	41	44	58
Season Total	1552	446	461	645

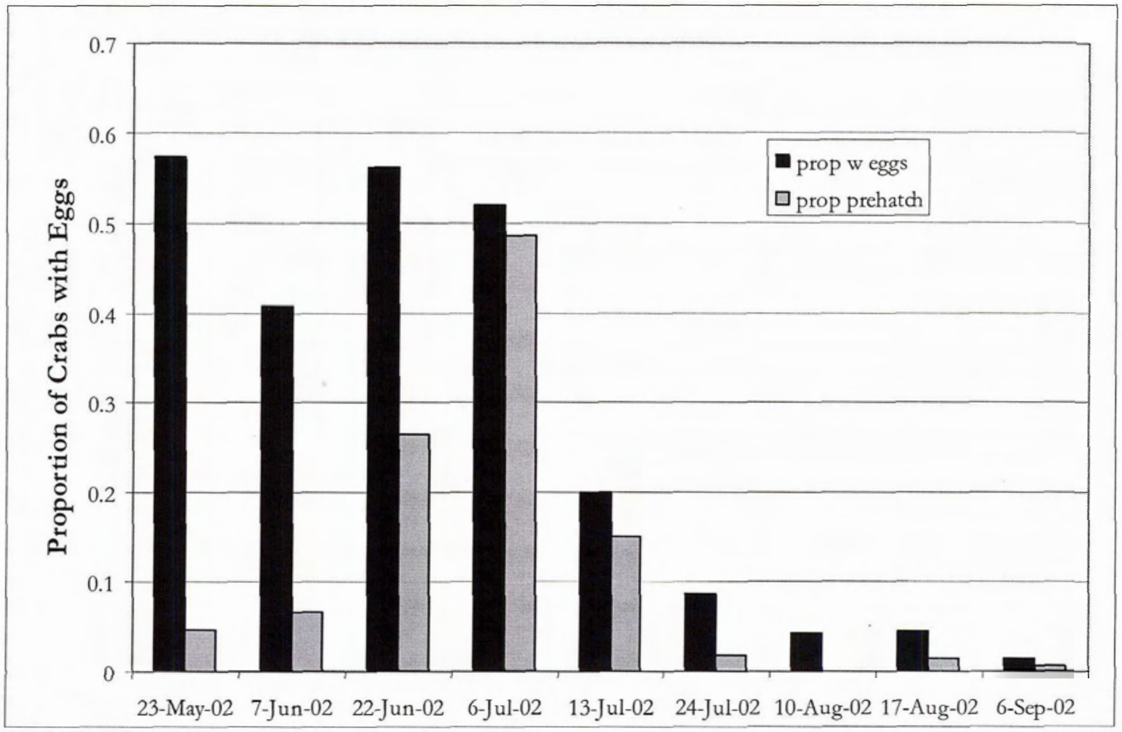

Figure 2: Proportion of crabs carrying eggs (total including prehatch) and prehatch eggs between May 23 and September 6, 2002 on Flores Island, Clayoquot Sound, BC.

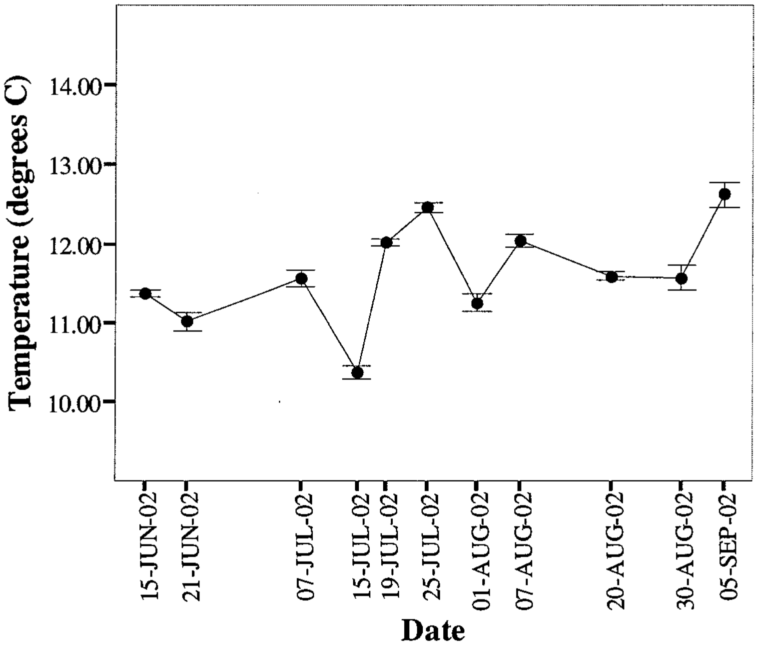

Figure 3: Mean water temperature (error bars = 1 SE) of casts pooled across all stations for each date over the sampling period.

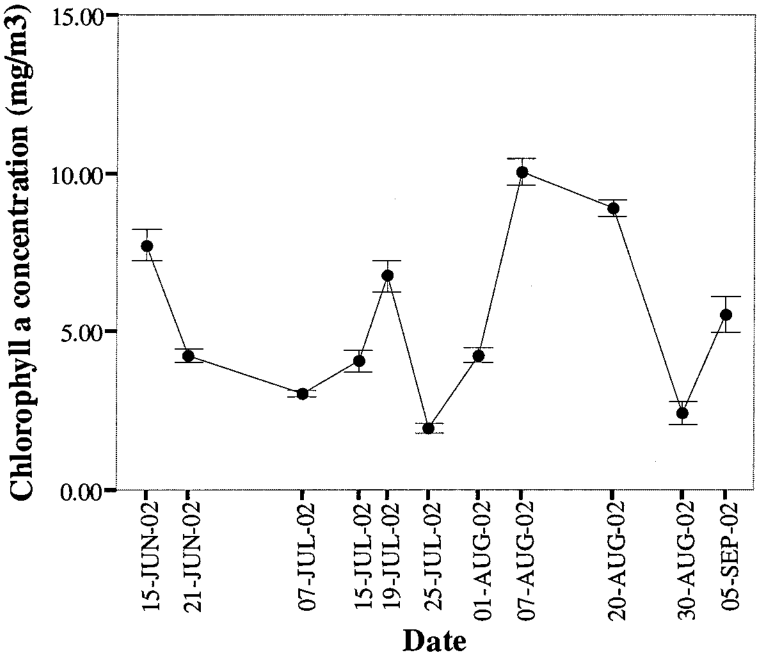

Figure 4: Temporal changes in mean chlorophyll *a* for all stations (error bars = 1 SE).

DISCUSSION

If *Petrolisthes cinctipes* has a similarly timed reproductive pattern to *Petrolisthes eriomerus* and *Pachycheles rudis* as described in Knudsen (1964), then the hatching described in this study likely represents the second brood of eggs of the year. The small proportion of crabs carrying eggs during the rest of the season indicates that another, possibly the third, brood of eggs was not being produced by the majority of crabs in this study.

Coincident with the 0.52 to 0.20 drop in the proportion of crabs carrying eggs between July 6 and 13, the new moon occurred on July 10 and nocturnal, large amplitude, ebbing tides of 3.5 m occurred on July 11 and 12 between high tide at 1:25 and 2:10 PDT low tide at 8:20 and 9:02 PDT (Fisheries and Oceans Canada 2002). These tides were among the largest amplitude tides during the season and were the largest amplitude tides of July. Many crab species in temperate semidiurnal environments release larvae during nocturnal, large amplitude, high tides so that the strong ebbing tide will sweep larvae out of the intertidal and nearshore zone where predation pressure is high during a time when visual predators are not feeding (Forward 1987, Morgan 1995, 1996, Morgan & Christy 1995).

The release of larvae in a coordinated fashion occurs in many animal species (Ims 1990 a&b). Porcelain crab larvae released in synchrony may serve to increase the survivorship of larvae in the more dangerous predation environment of the nearshore zone (Morgan 1996, Morgan & Christy 1994). The two main theories for the adaptive significance of coordinated larval release are the swamping hypothesis and the avoidance hypothesis (Morgan & Christy 1997). The swamping hypothesis states that coordinated release increases overall survivorship by overwhelming predators either through confusion or satiation (Ims 1990b). The avoidance hypothesis states that organisms release their larvae at a time when predators are least likely to be foraging (Morgan & Christy 1997). Research on the timing of crab larvae release indicates that for many species the avoidance hypothesis is more likely (Christy 1986, Morgan & Christy 1994, Morgan & Christy 1997). Most small fish that would feed on crab larvae are visual predators requiring light to find food. Thus larvae released at night will avoid visual predators better than those released during the day. Delay in larval release has been shown for crabs kept under lighted conditions in the lab (De Vries & Forward 1991).

Water temperature data from this study (Figure 3) and upwelling indices calculated by the Pacific Fisheries Environmental Lab for 48°N 125°W, 51°N 131°W (http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/NA/upwell_menu_NA.html) indicate that upwelling was also occurring at the time of larval release. Amend and Shanks (1999) found that wave height and oceanographic conditions influenced larval release in the mole crab, *Emerita talpoida*. Porcelain crab prezoeae are considered slightly photopositive and zoeal stages are strong swimmers indicating they have some control over their position in the water column. While the behaviour of zoeal stages is poorly understood, zoeae have been found in surface and upper water column during both day and night (Wing *et al.* 1998). If larvae remain near the surface, upwelling conditions are likely to increase transport out of the intertidal and nearshore zone. The combined timing of nocturnal, large amplitude ebbing tides during a new moon and potentially upwelling, represent ideal conditions for larvae to escape the intertidal and very nearshore zone during a period when fish predators are not feeding.

Large numbers of porcellanid zoeae were not observed in the plankton at any time during the 2002 season (Chapter 3). The lack of dense patches of porcelain crab larvae or gray whales feeding on porcelain crab larvae in 2002 despite synchronous release of larvae indicate that dense patches of porcelain crab larvae such as those observed in 1996 and 1997 near feeding gray whales appear to be driven by factors other than the timing of hatching (Dunham & Duffus 2002). It is possible that the conditions observed during the peak in larval release in 2002 result in dispersal and transport of larvae away from the coast while less ideal release conditions could result in aggregation of larvae nearshore as was observed in other years (Dunham & Duffus 2002).

Another factor that could influence the abundance of larvae found in the study area after release is food availability. Porcelain crab zoeae are contact predators leaving them dependent on prey density for survival (Gonor & Gonor 1973b). Some species of invertebrates such as barnacles, mussels and urchins are known to time spawning when plankton densities are high (Bosch *et al.* 1987, Pulfrich 1997, Smith & Strehlow 1983, Starr *et al.* 1990, Starr *et al.* 1991). During 2002, chlorophyll *a* concentrations were relatively low during the time of larval release (Figure 4), indicating that prey for porcelain crab larvae, such as smaller zooplankton directly dependent on phytoplankton for food, may also have been low in density. The timing of larval release coincident with factors conducive to larval export rather than phytoplankton concentrations suggests that export out of the nearshore zone is more important than plankton densities. Further study which includes sampling of densities of potential prey of porcelain crab larvae in addition to chlorophyll fluorescence and more precise documentation of when larvae are released relative to nocturnal large amplitude tides and lunar phases would allow better investigation of this assertion.

New findings resulting from this small study emphasize the lack of information available on this group of animals. The four 3 mm females carrying eggs in this study are the smallest egg-carrying *Petrolisthes* reported (Boolootian *et al.* 1959, Greenwood 1965, Jensen 1990, Zitten 1979). Larger females carry larger numbers of eggs (Greenwood 1965). The small females with eggs in this study carried very few eggs and the eggs were not visible without opening the abdomen of the crab.

The presence of densities of *P. cinctipes* in mussel beds of up to 3933 m^{-2} indicates that they are important in nutrient cycling in intertidal communities (Jensen, 1990). Such large numbers of adults producing several broods of larvae per year also place the larvae as an important part of the plankton community as food for fish, birds and whales and as predators on small zooplankton and microzooplankton (McConaugha 1992). Further knowledge of the reproductive ecology, timing of reproductive events and larval dispersal of porcelain crabs would benefit the understanding of intertidal ecology and coastal marine ecology.

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CHAPTER 5: PRESENCE OF PHYTOPLANKTON THIN LAYERS IN A SHALLOW, WAVE-EXPOSED COASTAL ENVIRONMENT

INTRODUCTION

Over the last fifteen years, advances in technology have enabled sampling of biological and chemical properties of seawater on scales equivalent to sampling of physical oceanographic properties such as temperature and salinity (Cowles & Donaghay 1998, Hanson & Donaghay 1998, Holliday *et al.* 2003). These advances in technology and an increased interest in small-scale variability have resulted in observations that physical, biological and chemical properties regularly exhibit significant variation on the spatial scale of centimetres (Cowles *et al.* 1998). Often this variation is distributed as thin layers of high concentrations of biomass or nutrients, centimetres to a few metres in vertical thickness and up to kilometres wide (Dekshenieks *et al.* 2001, Hanson & Donaghay 1998, McManus *et al.* 2003). These layers are generally correlated with physical properties, particularly the pycnocline (Hanson & Donaghay 1998, McManus *et al.* 2003). Thin layers can persist for hours or even days, indicating that their presence could be a significant source of concentrated food for many organisms (Cowles *et al.* 1998, McManus *et al.* 2003). The potential ecological significance of thin layers of biomass is drawing attention to this area of research and experimental studies of the behaviour of grazers/predators in response to these layers are becoming more common (Clay *et al.* 2004, Leising 2001, Metaxas & Young 1998, Bochdansky & Bollens 2004). Thin layers of phytoplankton, bacteria, marine snow and/or zooplankton have been found in bays, estuaries, fjords, continental shelf margin, and offshore but have not been documented in the nearshore open coast environment (Alldredge *et al.* 2002, Bjørnsen & Nielsen 1991, Carpenter *et al.* 1995, Cowles & Desiderio 1993, Mitchel & Fuhrman 1989, McManus *et al.* 2003).

The nearshore zone of shallow wave-exposed environments has long been ignored by oceanographers and is often referred to as homogeneous due to mixing processes. This may be true for some locations and/or periods of time but recent nearshore studies have shown that stratification does exist and persist, resulting in vertical variation in physical properties that could have important implications for organisms living in this environment (Chapter 2 of this manuscript, Narvaez *et al.* 2004, Weiters *et al.* 2003). During a recent study of small-scale oceanography off Flores Island, Clayoquot Sound, BC (Figure 1), I discovered thin layers of chlorophyll fluorescence within vertical profiles. In this chapter I document the presence and characteristics of thin layers in Clayoquot Sound in 2002 and discuss the physical properties with which they are associated.

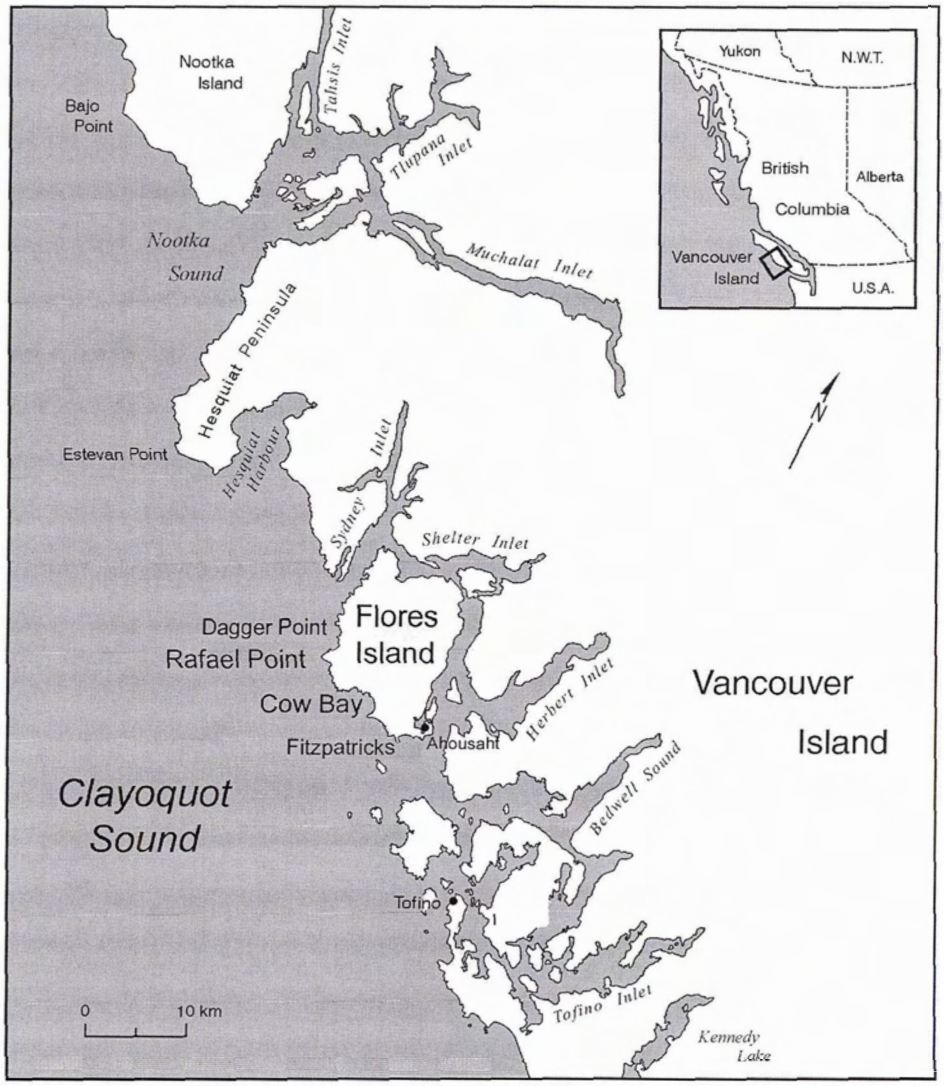


Figure 1: Map of Clayoquot Sound, on the west coast of Vancouver Island. The study area is located along the southwest coast of Flores Island in Clayoquot Sound.

METHODS

THE STUDY AREA

This study was conducted along 12 km (~20 km along the coastline) of the southwest edge of Flores Island (49°17'N, 126°10'W) in Clayoquot Sound, British Columbia between Dagger Point in the north and the Fitzpatrick Islands in the southeast (Figure 2). The majority of the study area is less than 30 m deep. The coastline is characterized by rocky shores and kelp beds interspersed with sandy beaches and cobblestone bays. Most of the study area, excluding the western edge of Cow Bay, is exposed to prevailing summer wind waves and swell from the northwest.

OCEANOGRAPHIC SAMPLING

Oceanographic sampling was conducted between June 15 and September 5, 2002 at 26 stations located along the southwest edge of Flores Island (Figure 2). Average water depth at the stations is 17 m (SD = 8.0 m). Vertical profiles of temperature, salinity and chlorophyll *a* were obtained for the entire water column at each station using a Seabird *SBE 19plus* SEACAT Profiler CTD and attached WetLabs EcoFL Fluorometer. At the beginning of each cast the CTD was raised to allow the sensors to sample within approximately the upper 20 cm of the water column. Sampling was conducted approximately once per week, weather permitting, 11 times between June 15 and September 5, 2002. Periods between sampling occasions ranged from 4 to 13 days.

DATA PROCESSING AND ANALYSIS

Fluorescence is presented both as volts as recorded by the fluorometer before being converted to chlorophyll concentration by data processing software as well as converted chlorophyll concentration. The fluorometer was calibrated before the field season at Seabird Labs in Washington but was not calibrated with water samples collected in the study area.

Contour maps of average chlorophyll *a* concentration for the top 5 m of the water column were created in Surfer 8 using the Radial Basis Function gridding option with no smoothing.

THIN LAYER IDENTIFICATION CRITERIA

The following criteria, defined by Dekshenieks *et al.* (2001), were used to assess whether a CTD/fluorometer cast showed the presence of a thin layer of chlorophyll fluorescence:

1) Thickness of the layer, measured at half intensity, must be less than 5 m.
2) Signal must contain 6 or more datapoints.
3) Maximum intensity must be at least 3 times the background intensity.
4) Present in two or more side by side profiles. Due to the spatial distribution of sampling stations in this study (Figure 2) this criterion was expanded from that in Dekshenieks *et al.* (2001) of 2 or more subsequent profiles to include profiles spatially located side by side.

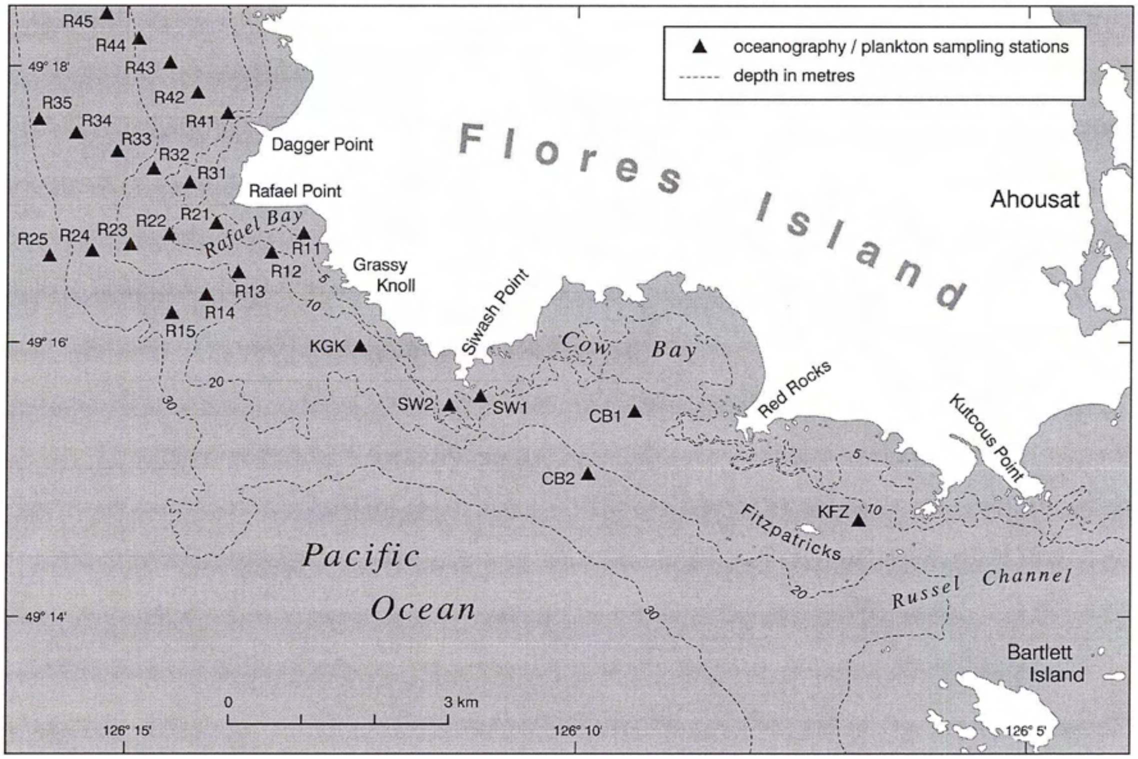


Figure 2: Sampling station locations along the southwest coast of Flores Island, Clayoquot Sound.

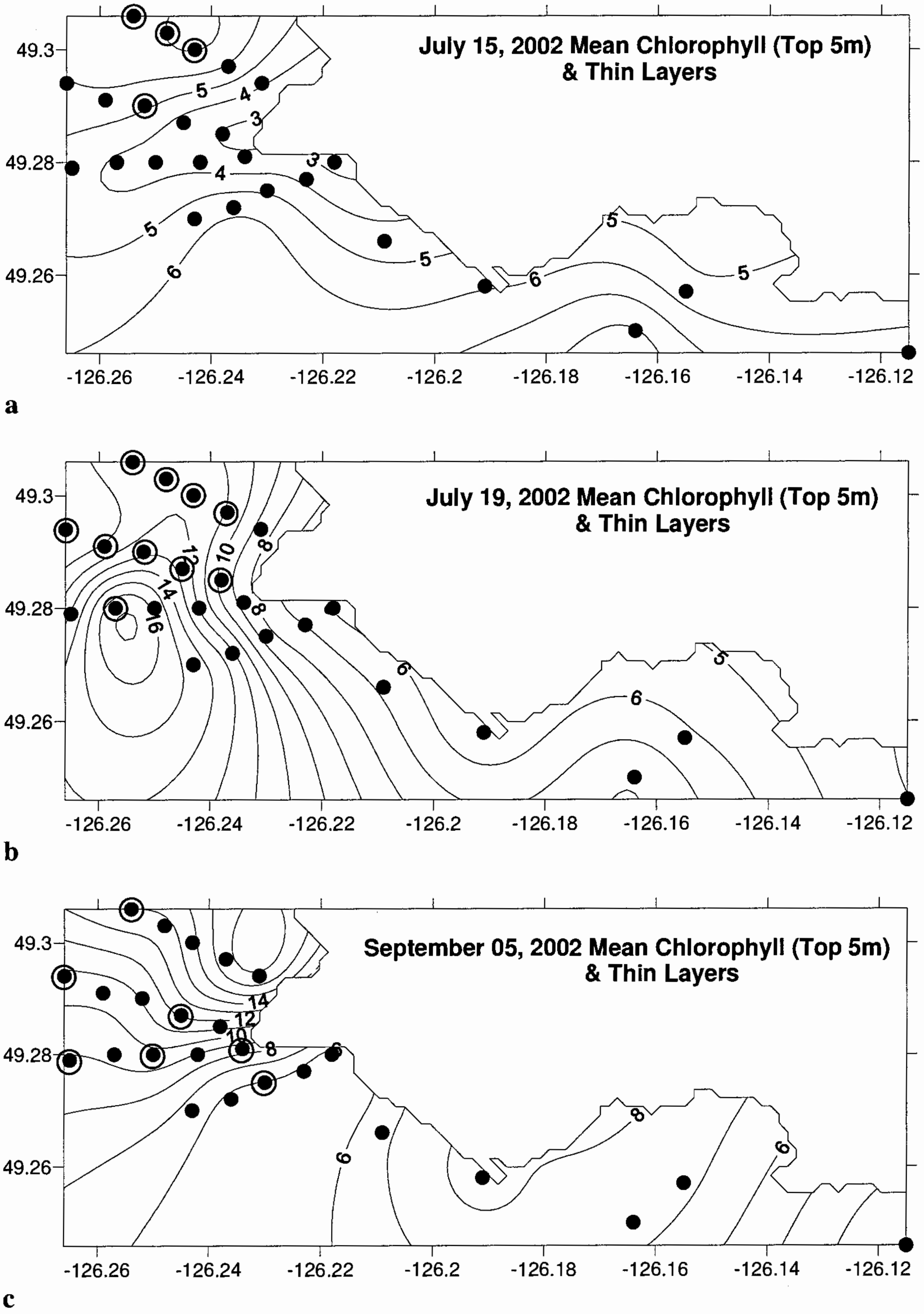
RESULTS

Thin layers of chlorophyll fluorescence were observed in 21 vertical profiles on 3 sampling days; 4 on July 15, 10 on July 19 and 7 on September 5 (Table 1). All thin layers occurred around Rafael and Dagger Point (Figure 3 a-c). The average depth of the peak intensity of the layer was 1.8 m (SD = 1.72). 95% of the layers occurred in the top 5 m of the water column. The average width of the layer was 2.7 m (SD = 1.27). Temperature and fluorescence were significantly correlated, as were change in temperature and change in fluorescence ($r = 0.588$, $p<0.001$; $r = 0.194$, $p<0.001$), indicating that chlorophyll fluorescence and temperature structure of the water column were tightly coupled. Thin layers occurred just above the surface thermocline (Figure 4). Sampling periods when thin layers were found coincided with periods of relatively low wind speeds at offshore data buoys (Figure 5). In addition, these periods coincided with periods of upwelling and subsequent upwelling relaxation (Figure 6). Upwelling and upwelling relaxation were expressed in temperature data off Flores Island as a decrease in water temperature followed by an increase seen by July 19 and September 5 (Figure 7). While the same stations were not repeatedly sampled on the same day, the maximum time that elapsed between the first and the last station sampled with a thin layer within a day was just over 2 hours. Thin layers present on July 15 may have persisted and expanded by July 19 as all stations that had thin layers on July 15 also had thin layers on July 19 (Figure 3 a&b). In addition, layers present on July 19 were of higher intensity and were thinner than those on July 15 (Figure 8 a-h, Table 1). In three of the four comparisons, the thermocline was not as strong on July 19 as on July 15 but overall water temperatures had increased by nearly 2°C between July 15 and 19. Differences in intensity of the layers between dates is also evidenced by the differences in mean chlorophyll *a* values for the top 5 m of the water column (Figure 3 a-c: contour levels).

Table 1: Characteristics of thin layers observed on July 15, 19 and September 5, 2002. Width of the thin layer was measured at half the maximum fluorescence and number of datapoints refers to the number of recorded measurements within the feature between the upper and lower half maximum intensity values.

Date	Station	Maximum Fluorescence		Depth at Max Fluorescence (m)	Width of layer (m)	Background Fluorescence		Number of datapoints
		(mg/m3)	(volts)			(mg/m3)	(volts)	
15-Jul-02	R33	11.13	1.362	2.2	2.8	2	0.43	10
	R43	14.61	1.718	2.2	2.2	4	0.64	7
	R44	11.92	1.443	4.9	5.0	3	0.54	14
	R45	14.90	1.748	6.0	3.9	3	0.54	12
19-Jul-02	R24	42.52	4.570	0.7	3.5	6	0.84	14
	R31	11.99	1.450	3.9	4.0	3	0.53	12
	R32	21.44	2.417	1.4	3.6	5	0.74	14
	R33	22.35	2.509	1.7	1.8	6	0.84	6
	R34	16.40	1.901	4.5	3.4	4	0.64	10
	R35	17.46	2.010	3.2	4.9	4	0.64	14
	R42	16.43	1.904	2.5	4.1	5	0.74	15
	R43	18.78	2.144	1.1	1.1	6	0.84	8
	R44	21.93	2.467	1.0	2.7	6	0.84	10
	R45	23.69	2.646	0.9	1.2	5	0.74	8
5-Sep-02	R13	13.58	1.613	0.4	1.6	2	0.43	6
	R21	13.88	1.644	0.2	1.4	2	0.43	8
	R23	19.03	2.170	0.2	1.8	3	0.54	11
	R25	15.46	1.805	0.8	1.2	3	0.54	7
	R32	25.16	2.796	0.6	1.5	7	0.95	10
	R35	26.17	2.900	0.1	1.3	5	0.74	8
	R45	20.33	2.303	0.2	3.6	6	0.84	16

Figure 3: Locations of vertical profiles with thin layers on (a) July 15, (b) July 19, and (c) September 5. Locations of all stations are shown as solid circles; stations with thin layers are denoted by an open circle around a solid circle. Contours represent 1 mg/m^3 chlorophyll *a* concentration increments. X-axis = latitude, Y-axis = longitude.



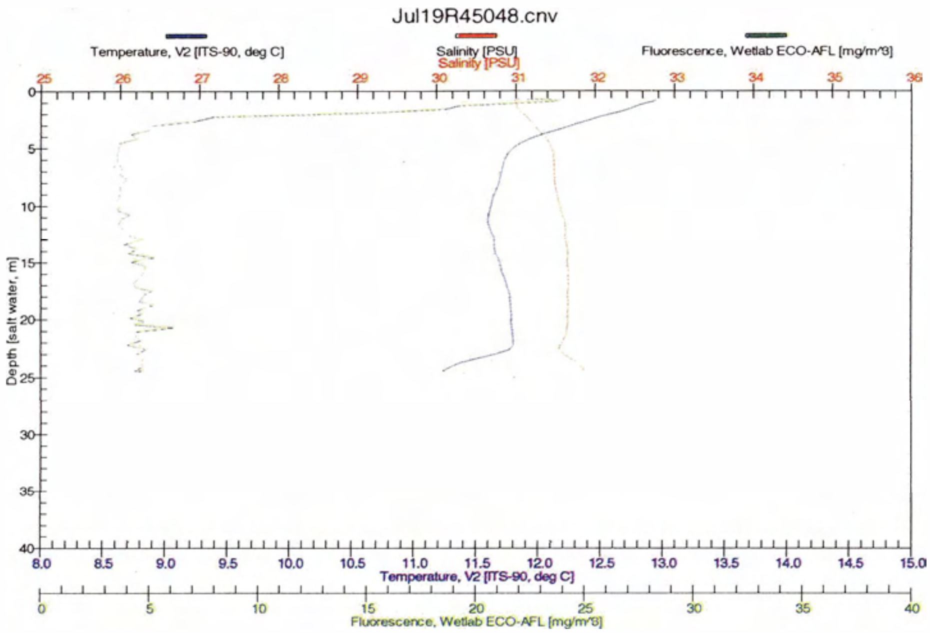


Figure 4: An example of a vertical profile showing the location of a thin layer relative to the thermocline near the surface (July 19 R45). Green = fluorescence (mg/m^3), blue = temperature (° C), red = salinity (psu).

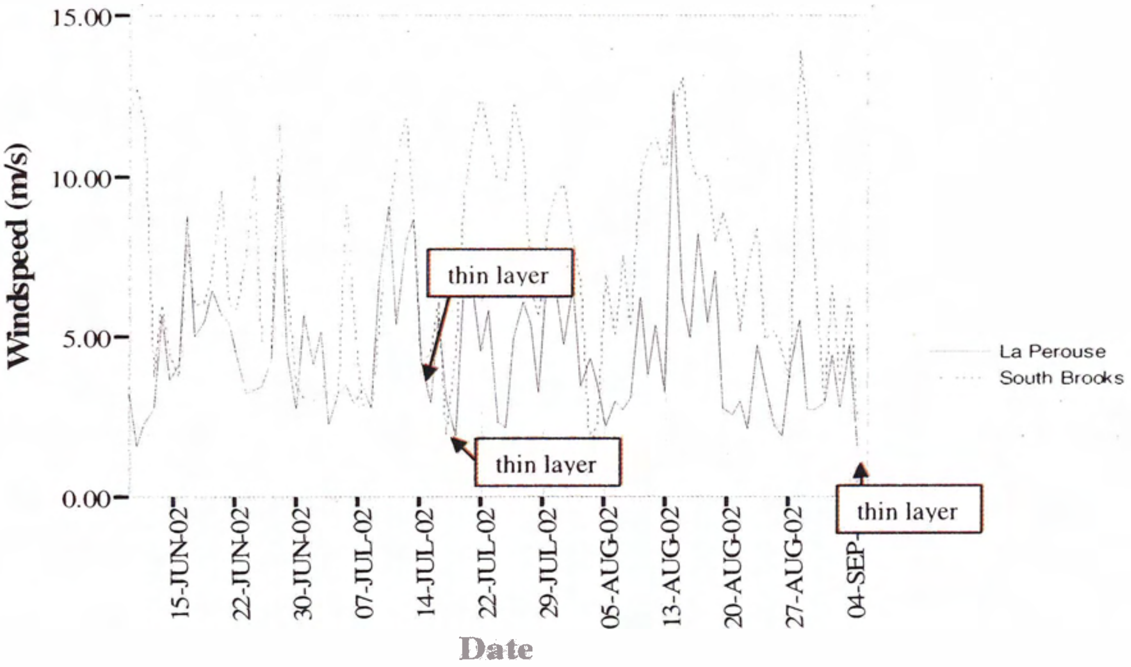


Figure 5: Average wind speed at South Brooks (49.73°N 127.92°W) and La Perouse Bank (48.84°N 126.00°W) data buoys (data recorded and made available by Department of Fisheries and Oceans, Marine Environmental Data Service). "Thin layer" labels indicate the times when thin layers were observed off Flores Island.

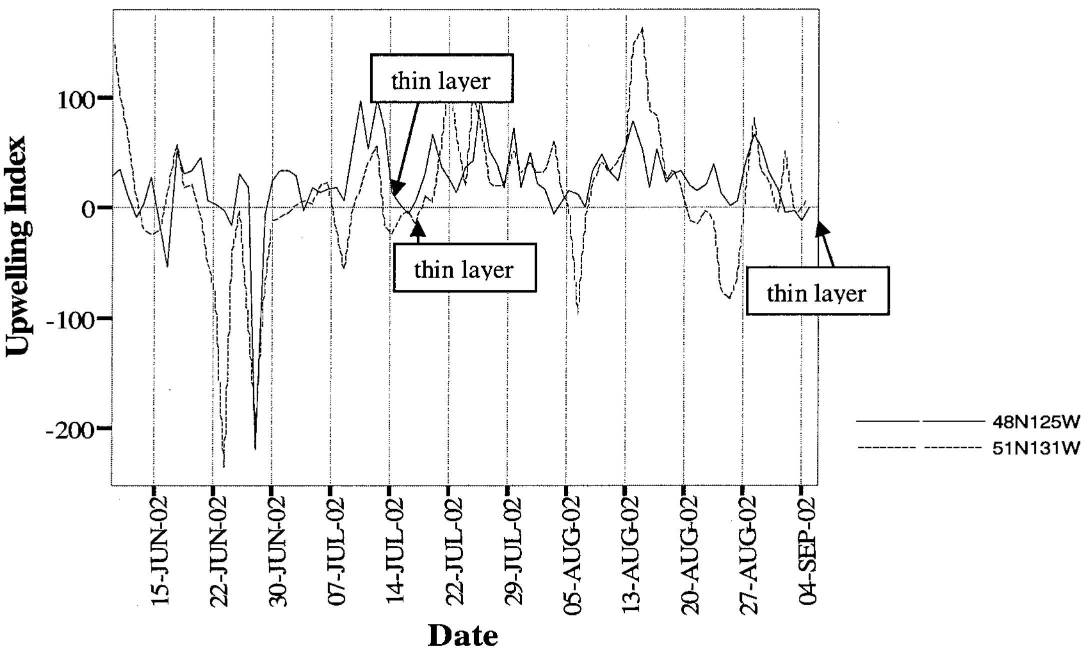


Figure 6: Average upwelling index calculated by Pacific Fisheries Environmental Lab for 48°N 125°W and 51°N 131°W between June 10 and September 5, 2002. "Thin layer" labels indicate the times when thin layers were observed off Flores Island.

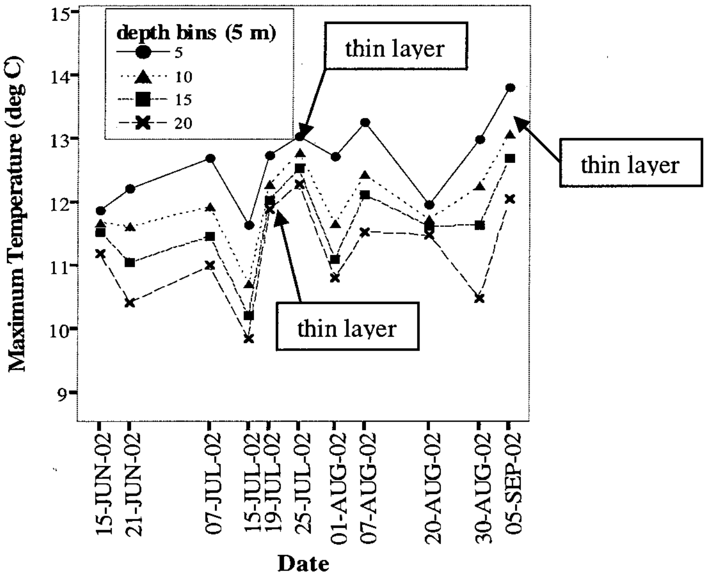


Figure 7: Average maximum temperature within a 5 m depth bin for the top 20 m (N = 14- 26). Depths over 20 have been excluded due to small sample size.

Figure 8 a-h: Comparison of stations that had thin layers on July 15 with the same 4 stations on July 19 (date and sampling location at the top of the profile – ignore last three numbers and ".cnv"). Note increase in water temperature and thin layer intensity and changes in thermocline structure between the two dates. Green = chlorophyll concentration, blue = temperature, red = salinity.

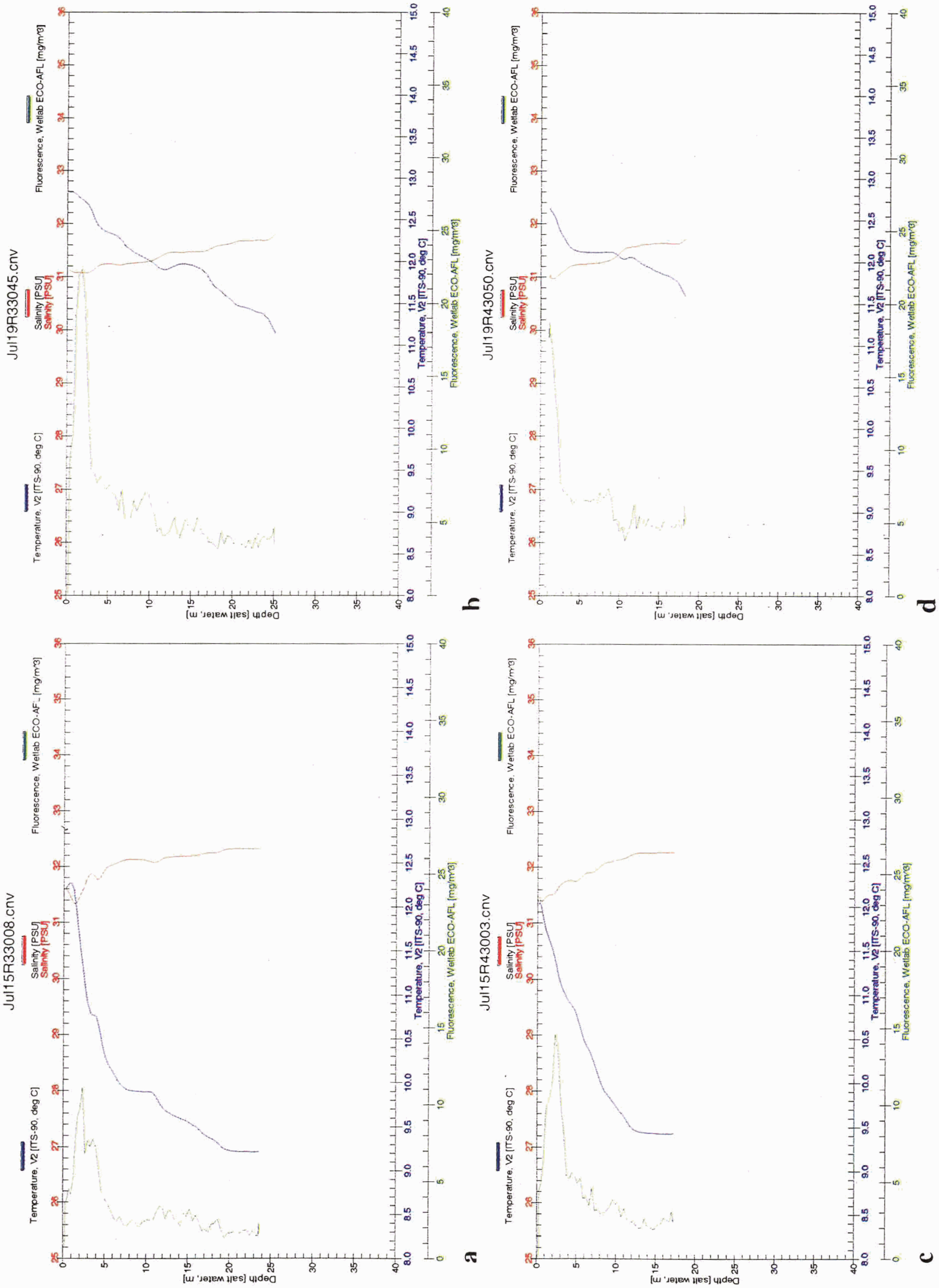
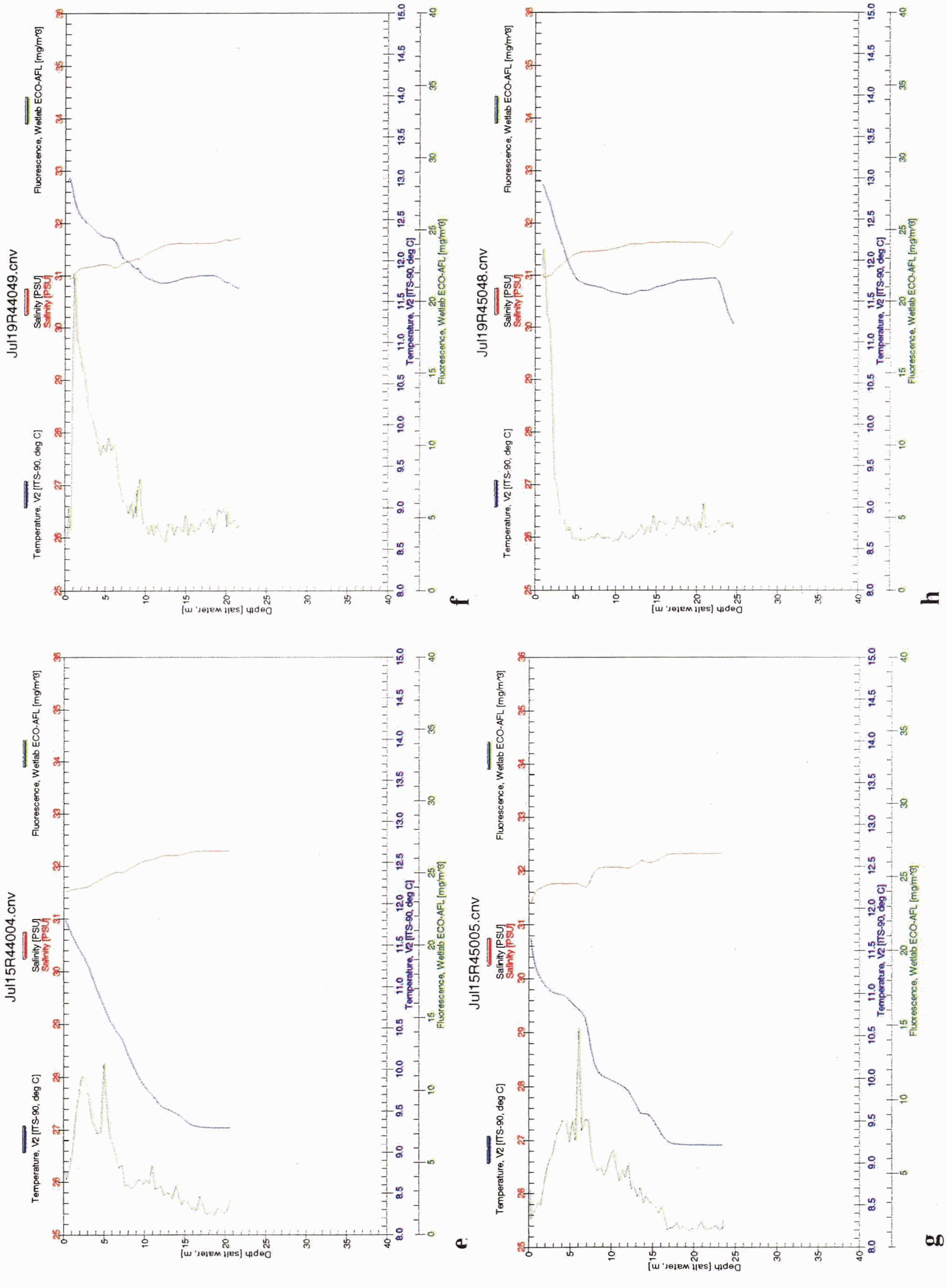


Figure 8 a-h continued: Comparison of stations that had thin layers on July 15 with the same 4 stations on July 19 (date and sampling location at the top of the profile – ignore last three numbers and ".cnv"). Note increase in water temperature and thin layer intensity and changes in thermocline structure between the two dates. Green = chlorophyll concentration, blue = temperature, red = salinity.



DISCUSSION

The results of this study show that thin layers of chlorophyll fluorescence with characteristics similar to those found in other marine environments, exist and persist in this shallow, wave-exposed area. Layers in this study are thicker than many of those found in more sheltered areas (Dekshenieks *et al.* 2001). The profiling system used in this study recorded measurements on average every 30 cm (SD = 10 cm), while other studies have sampled at small enough scales to show layers as thin as 10 cm (Cowles *et al.* 1998). Thus, smaller scale structure in phytoplankton concentration than was reported here could be present within the layers (Osborn 1998). Visual examination of the temperature and fluorescence profiles and the statistical correlation between fluorescence and temperature indicates that, as found by other researchers, thin layers form at the pycnocline (Cowles *et al.* 1998, Dekshenieks *et al.* 2001, McManus *et al.* 2003).

The timing of the presence of thin layers suggests that layer formation occurs after upwelling has provided nutrients to the water column and upwelling relaxation has allowed stratification to occur via surface warming (Figure 5 & 7). Increased temperature speeds metabolism which likely resulted in the stronger intensity layers on July 19 and September 5 compared to July 15 (Table 1, Figure 6, Kinne 1970).

Laboratory studies examining the response of zooplankton and ichthyoplankton to thin layers of phytoplankton and zooplankton have found significant but smaller than expected responses to experimentally generated thin layers (Bochdansky & Bollens 2004, Clay *et al.* 2004, Metaxas & Young 1998). However, the setup of these experiments, while good early examinations, are not ideal for relating results to the natural environment. Tanks used in these experiments are 2 m high, smaller than the thickness of many thin layers, and in one instance the organisms used to test a response of copepods to a food resource were diatoms that the copepods do not likely eat (Bochdansky & Bollens 2004, Clay *et al.* 2004). Further study of the response of organisms to patches of food distributed as thin layers is required. Model simulations of responses of copepods to varying types of thin layers found that even the patchiness of a thin layer can impact foraging efficiency, with more concentrated patchy layers resulting in higher efficiencies and thus increased survival and reproduction (Leising 2001).

Survival and development of larvae that require food nearly immediately after hatching, such as most decapod zoeae, may be dependent on the presence of high quality patches that can be found at predictable places within the water column using physical cues (Anger *et al.* 1981). The presence of layers of nutrients, marine snow, bacteria, phytoplankton and zooplankton all near the pycnocline (McManus *et al.* 2003) suggests that larvae aggregated by physical processes to the pycnocline, or able to migrate to the pycnocline, are much more likely to find food than during periods when the water column is mixed and food is diffusely dispersed over a much wider area. The spatial extent of the thin layers, with a possible maximum length of 2.5 km on July 19 (Figure 3b), and persistence for four days between July 15 and 19, emphasizes the potential importance of these features for zooplankton foraging efficiency, aggregation, development, survival and reproduction. Thus if starvation for a day or two immediately following hatching results in a "point of no return" in terms of survival for decapod zoeae, and possibly other larvae, the presence of thin layers at the time of larval release could result in high survival and growth rates, possibly explaining some of the year to year variation in recruitment success of many species.

The discovery of thin layers in this study area during multiple sampling periods provides further evidence that oceanography of the nearshore oceans is much more complex than has been previously assumed. Further understanding of ecology of these environments will be dependent upon advances in the knowledge of nearshore oceanographic variation and impacts on the biology of the organisms that live there.

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CHAPTER 6: GENERAL CONCLUSIONS

The impetus for this study, the interaction between foraging gray whales and patches of porcelain crab larvae, was not observed during the summer of 2002. Despite the absence of this interaction, this study provides new information specific to the study area and adds to the general literature in topics of nearshore oceanography, thin layers of phytoplankton in the nearshore zone and the timing of larval release in *Petrolisthes cinctipes*.

Gray whales were abundant in the study area during 2002 but did not feed on porcelain crab larvae. This can be explained by the lack of dense patches of porcelain crab larvae documented in other years when gray whales did feed on porcelain crab larvae (Dunham & Duffus 2002). Porcelain crab larvae densities during this study were generally low but some samples contained densities up to 30 times higher than the average density (Chapter 3). However, the maximum densities documented in this study are still an order of magnitude lower than densities known to be sufficient to attract foraging gray whales (Dunham & Duffus 2002). The location of the highest density samples off Rafael and Dagger Points is consistent with the findings of previous research (Dunham & Duffus 2002). A trend relating the distribution and abundance of porcelain crab larvae and oceanographic conditions was not detected.

A sharp decline in the number of egg-carrying *Petrolisthes cinctipes* indicates a peak in larval release between July 6 and 13 (Chapter 4). This period of time coincided with large amplitude nocturnal ebbing tides which are known to be good conditions for release of crab larvae in other species (Forward 1987). The peak in larval release did not translate to an increase in porcelain crab larvae in the study area (Chapter 3). Some possibilities for this are that upwelling conditions swept the larvae out of the study area shortly after larval release (Farrell *et al.* 1991) or that low chlorophyll *a* concentrations prior to larval release resulted in low levels of food available to the newly released larvae compromising their survival (Anger *et al.* 1981).

Short term changes in temperature and salinity appear to be driven primarily by upwelling processes (Chapter 2). The magnitude of these changes is that of interannual variability (Mackas 1995). Changes in chlorophyll *a* concentration generally follow one sampling period behind temperature and salinity changes with decreases in temperature followed by increases in temperature and chlorophyll concentration. This study could not discern if these changes were due to replenishment of nutrients, the temperature changes themselves or movement of patches in and out of the area with upwelling transport. The pattern of short term phytoplankton blooms documented in this study is common for the continental shelf waters of western Vancouver Island during summer however sampling periods in previous studies were much further apart (usually once per month) (Mackas 1992).

Temperature changes associated with upwelling have been shown to have a significant effect on the behaviour of seastars (*Pisaster ochraceus*) in Oregon (Sanford 1999). Seastars are considered keystone predators in rocky intertidal zones, feeding primarily on mussels (*Mytilus californianus* and *M. trossulus*). In the field, Sanford (1999) found that seastars remained inactive in channels and subtidal waters during temperature decreases as small as 2.6 °C resulting in low seastar densities in the mussel zone and low per capita mussel consumption. While temperature changes associated with upwelling likely do not have such a significant effect on all organisms in the nearshore zone, such impacts on key species interactions mean that small changes in temperature have the potential to result in ecologically significant changes in communities.

Spatial variation in salinity with low salinities at the entrance to Clayoquot Sound (KFZ) and at Siwash Point (SW2) indicate the consistent flow of water out of the Sound and across the mouth of Cow Bay (over both flooding and ebbing tides) (Kopach 2004).

Spatially discrete phytoplankton blooms were evident on July 19, August 7, August 30 and September 5 around Rafael and Dagger Points in the spatial examination of chlorophyll *a* concentration data. With the exception of July 19 these blooms coincide with relatively high surface temperatures and vertical stratification of the water column. In addition, two of the three dates, July 19 and September 5, found to contain thin layers of phytoplankton (Chapter 5) also exhibited spatially discrete blooms.

Vertical water column structure, stratification, was present during several sampling days demonstrating that this nearshore zone is not consistently mixed.

However, mixing does occur regularly and vertical mixing penetrates through the majority of this shallow water column emphasizing the dynamic nature of the water column structure in the study area. Localized upwelling/downwelling and possibly tidal mixing were also observed.

As mentioned above, thin layers of phytoplankton were documented on three of eleven sampling days (Chapter 5). These layers were only present around Rafael and Dagger Points and may have extended up to 2.5 km on July 19. Further, the presence of these layers on July 15 and July 19 brings up the possibility that the layers persisted for at least 5 days. Thin layers of phytoplankton that persist for days and extend for hundreds of metres could play an important role in the trophic interactions of the plankton community.

This study provides a greater understanding of the variability of oceanographic conditions in the nearshore, wave-exposed environment of southwest Flores Island, Clayoquot Sound. This work will contribute to a foundation of information on the marine ecology of Clayoquot Sound with the long term goal of understanding the dynamics of gray whale feeding ecology as one of the major apex predators of the area.

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