SEASONAL AND INTERANNUAL VARIABILITY OF PRIMARY AND SECONDARY PRODUCTIVITY IN A COASTAL FJORD

by

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ABSTRACT

The phytoplankton and zooplankton dynamics in a coastal fjord in British Columbia were monitored in spring and early summer 2006 and 2007 to assess the annual variability in primary and secondary productivity and some characteristics of subsequent production. Phytoplankton biomass increased dramatically in early spring (spring bloom), declined abruptly, and then increased to a smaller peak two weeks after the spring bloom. Mesozooplankton biomass peaked one month after the spring bloom. The timing of the spring bloom was 20 days later in 2007. It is hypothesized that higher freshwater discharge and more frequent wind events in early spring 2007 were the driving factors behind the observed shift in bloom timing. The delay of the phytoplankton bloom resulted in a later and lower zooplankton biomass peak, and in a shift in zooplankton species composition. The implications of these changes for the survival of juvenile sockeye salmon are also discussed.

Keywords: Phytoplankton; Spring bloom; Primary productivity; Zooplankton; Zooplankton species composition; Secondary productivity; Seasonality; Trophic dynamics; Biophysical linkages; Environmental forcing variables; Interannual variability; Freshwater discharge; Sockeye salmon; Rivers Inlet; fjord; British Columbia; North Pacific.

Subject Terms: Marine Ecology; Marine Plankton; Marine Productivity; Food Chains (Ecology).

DEDICATION

Per la mia cara nonna, che con fiori, gatti e cani fu la prima a farmi apprezzare tutte le meraviglie del mondo naturale. To my grandma, who was the first to teach me to appreciate and marvel at all the natural wonders of the world.

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Introduction

A new perspective in fisheries science has gained acceptance in the last decade. It is that the carrying capacity of aquatic environments changes over time, and that to set sustainable harvest strategies, fisheries managers have to account for variation in fish stock productivity (e.g. natural mortality rates, Parsons and Harrison 2000) as a consequence of changing climate cycles. Three major changes have been observed in the last century in the climate of the Northeastern Pacific Ocean (Ware 1995) and these regimes were found to relate to changes in the total production of fish stocks. Beamish et al. (1999) show how fluctuations in the total catch of Pacific salmon (*Oncorhyncus* sp.) follow oscillations between different climate regimes. The productivity of Pacific herring (*Clupea pallasi*), Pacific halibut (*Hippoglossus stenolepis*), Pacific sardine (*Sardinops sagax*), northern anchovy (*Engraulis mordax*), and Pacific hake (*Merluccius productus*) has also been observed to respond to climate variation (Clark et al. 1999, Beamish 1995, Ware and Thomson 1991, McFarlane et al. 2000). The direction of these trends appears to change spatially over the North Pacific and has been linked to changes in the strength of the Aleutian Low (Beamish et al. 1999), the Pacific Decadal Oscillation (PDO) (Mantua 1997), the intensity of upwelling (Ware and Thomson 1991), a composite climate index

(Beamish et al. 1999, McFarlane et al. 2000), sea surface temperatures (Yatsu et al. 2005) and surface salinity (Morita 2001).

There is evidence that variation in primary productivity can ultimately affect fish production, although the actual trophic links have not been elucidated. Apparent instances of bottom-up control have been reported for the Pacific and Atlantic oceans (Iverson 1990, Richardson 2004, Ware and Thomson 2005). Diatom abundance has been found to be positively correlated with sardine year-class strength in the California Current system (Ware 2000).

Phytoplankton growth rates are largely controlled by the amount of nutrients, temperature and light available for photosynthesis (Reynolds 2006). In temperate seas, phytoplankton dynamics follow a strong seasonal cycle, characterized by a spring bloom (Longhurst 1995), i.e., a sudden burst in the biomass of phytoplankton. The mechanism describing the development of the spring bloom was first proposed by Sverdrup (1953), and this has remained a widely acknowledged explanation (Mann and Lazier 2006). He hypothesized that during winter, strong storms mix phytoplankton cells below their critical depth, the depth where integrated production equals respiration, and the phytoplankton population is unable to grow even in the presence of abundant nutrients mixed into the surface by strong winds. As the season progresses, the days become longer and the incident radiation stronger, deepening the critical depth. Thermal heating also increases and wind mixing is reduced, shoaling the mixed layer depth. In the spring, a phytoplankton bloom occurs when the critical depth is equal to or greater than the mixed layer depth (MLD). However, less mixing also

prevents nutrients from being drawn to the surface, and the bloom collapses when all nutrients in the euphotic zone are exhausted. Therefore, changes in mixed layer depth are expected to affect the timing and spatial extent of the bloom.

While it is generally accepted that a period of mixing followed by a period of water column stability are necessary precursors to development of a spring bloom (Mann and Lazier 2006), the importance of a mixed layer for phytoplankton productivity varies between regions. For example, the influence of MLD on phytoplankton productivity may not be consistent across marine ecosystems because spring blooms were shown to occur in the absence of a mixed layer in Norwegian fjords (Eilersten 1993) and the Gulf of Maine (Townsend et al. 1992). In Auke Bay, Alaska, inter-annual differences in the timing of the spring bloom could not be explained by differences in MLD (Ziemann 1991). Evans and Parsons (1985) simulated a phytoplankton bloom even in the absence of shoaling of the MLD, and Huisman et al. (1999), using another model of phytoplankton production, inferred that phytoplankton blooms occur even in a very deep mixed layer if turbulence is low.

Recent studies have examined the effect of climate on interannual variability in primary productivity in the North Pacific. Decadal changes in primary productivity that follow climate cycles have been observed (Venrick 1987, Saitoh et al. 2002, Yatsu 2005). Aita et al. (2007), using the physical-biological coupled model 3D-NEMURO, were able to reconstruct phytoplankton and zooplankton biomass for the North Pacific from 1948 to 2000. They showed

how primary productivity experienced a shift synchronous to the climate regime shift of the late 1970's. The decrease in phytoplankton biomass in the eastern and sub-tropical northwestern Pacific Ocean, and the increase in phytoplankton biomass in the north central Pacific have been linked to variability in PDO. It was concluded that the change in PDO triggered a change in the MLD; regions with an increase in MLD showed an increase in phytoplankton biomass, while in regions where the MLD shoaled, a lower biomass was simulated.

In order to understand how fish production is affected by phytoplankton dynamics and climate cycles, it is appropriate to investigate what physical factors influence primary productivity at an appropriate geographic scale. Studies show that that the greatest impact on salmon survival rates occurs in their early ocean migratory stage (Peterman 1987, Francis and Hare 1994). Sockeye salmon (*Oncorhynchus nerka*) survival rates co-vary only within regions smaller than 500 km (Mueter et al. 2002, Peterman et al. 1998), implying that sockeye salmon survival is largely determined by regional factors.

Rivers Inlet is a fjord on the central coast of British Columbia, which until the mid-seventies was home to the third largest sockeye salmon fishery in Canada. The stock experienced a period of instability beginning in the late 1970's and it crashed in the early 1990's. Rivers Inlet sockeye has yet not recovered, even in the absence of fishing, and reasons for the decline remain unknown, but appear to be related to marine survival (McKinell et al. 2001).

The goal of this study was to learn how physical and chemical oceanographic characteristics in Rivers Inlet affect phytoplankton dynamics; the intent was to contribute to the ecosystem based management of this sockeye salmon stock. The ultimate goal is to stimulate the development of a mechanistic model explaining dynamics of phytoplankton, zooplankton, and sockeye salmon production. The physical driving variables of primary productivity in temperate coastal fjords are not well understood because most models of phytoplankton dynamics were developed and validated with observations for open ocean environments and shallow, nutrient rich estuaries. We compared differences in nutrients, wind events, critical depth, MLD, and temperature to try to discover the basis for the observed changes in the timing of the spring bloom in Rivers Inlet.

Methods

Survey Area

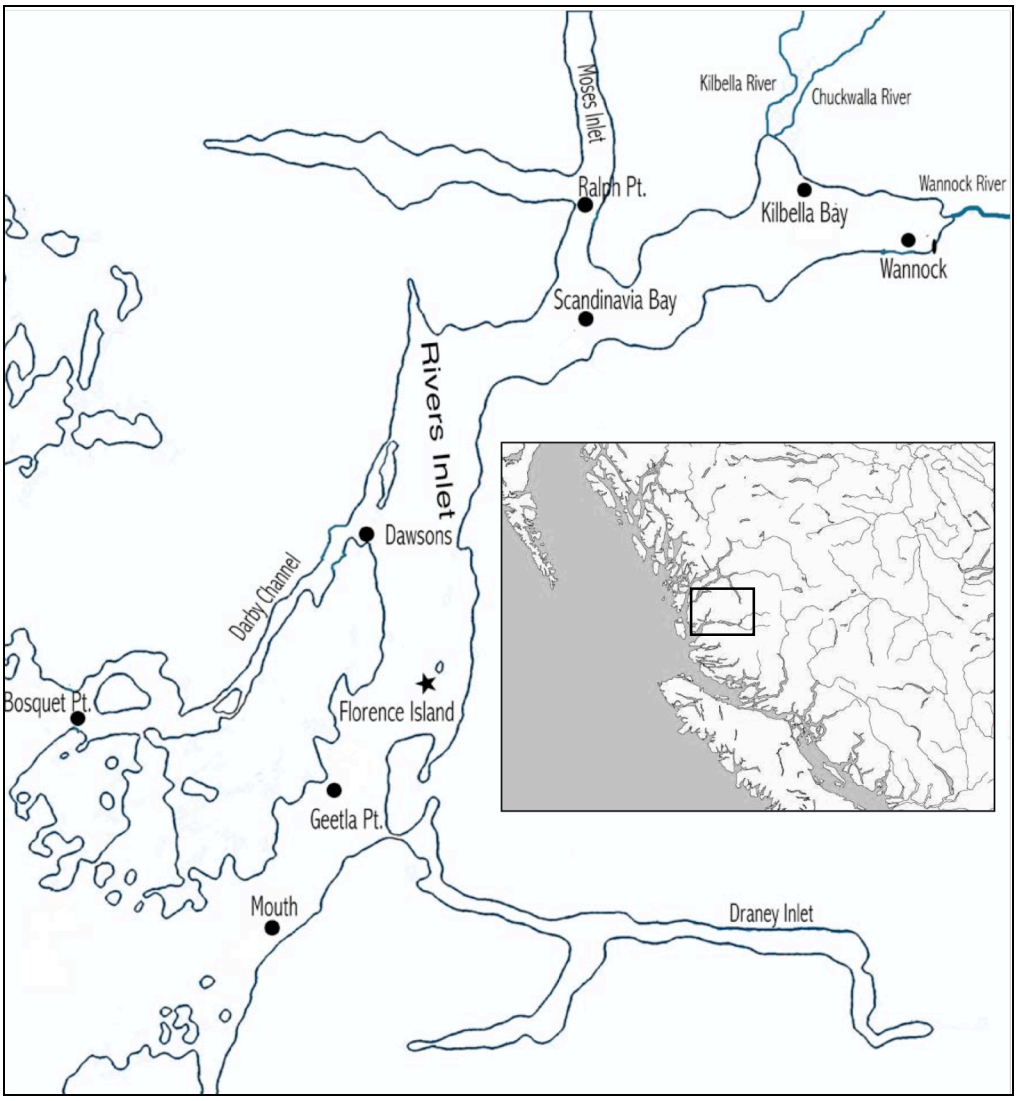
Rivers Inlet (51^{o} 26', 127^{o} 38') is deep (400 m maximum depth), 3 km wide and 40 km long fjord of glacial origin on the central coast of British Columbia, Canada. The inlet is 500 km northwest of Vancouver. It is characterized by an estuarine circulation whereby a shallow surface layer transports freshwater out to the inlet mouth into Queen Charlotte Strait and nutrient-rich waters enter the inlet at depth periodically over a shallow (110 m) sill at the mouth of the inlet. This process is enhanced in late spring and summer months as winter southeasterly winds ease and freshwater discharge increases (Whitney et al. 2005). Three side inlets, Moses Inlet, Darby Channel, and Draney Inlet, merge with the main arm at Scandinavia Bay, Bickle Passage, and Draney Narrows, respectively. The major

input of fresh water is from Oweekeno Lake via the Wannock River. The lake is large (78 km^2) and oligotrophic. It is fed by two glaciers and drains an area totaling 4100 km^2. Oweekeno Lake is the main sockeye salmon spawning area in the region. The Chuckwalla, Kilbella, and Clyak Rivers are the other significant sources of fresh water. The first two drain into Kilbella Bay, while the last flows into Moses Inlet (Fig. 1).

Field Sampling

The sampling locations were the same ones used by Buchanan (2007) to collect juvenile sockeye salmon and zooplankton in Rivers Inlet over 2002-2005 (Fig. 1). A list of these sites and their co-ordinates is available in Appendix 1. An additional site was added in 2007 to increase the sampling frequency for chlorophyll *a* to daily measurements to obtain a more detailed picture of phytoplankton dynamics. This new site was mid-inlet (Fig. 1), near Florence Island and easily accessible from our field station. The field seasons lasted approximately four months. They extended from March 11 until June 24 in 2006, and from March 10 to June 22 in 2007.

Figure 1 Map of Rivers Inlet showing sampling stations. The Florence Island station marked by a star was only sampled in 2007. The inset shows Rivers Inlet in the context of the entire British Columbia coast.



Chlorophyll a and Water Properties

Information on chlorophyll *a* concentration and water properties was collected during casts made with a Hydrolab® DS5X sonde equipped with a fluorometer. The sonde was deployed to a depth of 30 m at each site, and depth profiles of fluorescence, salinity, temperature, pH, TDS (total dissolved

solids), dissolved oxygen, and PAR (photosynthetically active radiation) were obtained. 30 m was a depth that was logistically feasible to sample frequently, and which included the entire depth of the euphotic zone, as from in situ underwater PAR measurements, and the halocline region. Sampling was conducted bi-weekly in 2006 and weekly in 2007 at each of the eight sites. Profiles were duplicated after the March 30, 2007 sampling event. Additional daily profiles of chlorophyll *a* were collected at the Florence site. No daily samples were collected on April 1, April 13, April 21, and May 29 2007 due to bad weather. On the third cruise in 2006, we were only able to obtain surface measurements at two of the eight sites, at Geetla and Scandinavia. Bi-weekly samples were always conducted in the afternoon in 2006 and at any time during the day in 2007. Daily sampling was conducted in the morning between 0800 and 1000 h if weather allowed.

Water samples were collected to calibrate the Hydrolab® optical fluorometer readings and convert voltages to μg L^{-1} cholorophyll *a*. They were collected bi-weekly at all sites at 0, 1, 3 and 5 m in 2006, and daily at Florence Island and bi-weekly at all sites at a depth of 5 m in 2007. Samples were collected at depth with a Van Dorn bottle, and a fraction of each water sample was filtered through a Whatmann GF/F filter. The sample water was filtered in 60 ml aliquots until the filter looked brown, at which point the volume filtered was recorded. Thus, the fraction filtered was dependent on the amount of chlorophyll in the water. The filter was folded, wrapped in aluminium foil, stored in a cooler and then frozen at the field station. Samples were sent subsequently to the

Canadian Department of Fisheries and Oceans' Institute of Ocean Sciences, Sidney, B. C., in 2006 and to the University of British Columbia in 2007 for chlorophyll *a* determination.

Calibration curves were developed by regressing log-transformed fluorometer readings on log-transformed chlorophyll *a* concentrations from the filtered samples. Least-squares regression fits, R^2 values, and parameter estimates are available in Appendix 2.

Nutrients

Nutrient samples were collected using the same Van Dorn bottle water samples as for chlorophyll. Therefore, samples were collected bi-weekly at depths of 0, 1, 3, and 5 m in 2006 and depths of at 0, 5, and 25 m in 2007 at each of the eight sites. Sampling was extended to 25 m in 2007 to measure nutrient concentrations below the halocline. Samples were also collected at Florence Island in 2007. They were collected weekly at depths of 0, 5, and 25 m and bi-weekly at 100 m. Nutrient samples were sent subsequently to the Canadian Department of Fisheries and Oceans' Institute of Ocean Sciences, Sidney, B. C., in 2006 and to the University of British Columbia in 2007 to determine nitrate, phosphate, and silicate concentrations.

Wind

Data on hourly average wind speed from Herbert Island (50.57^{o}, 127.38^{o}), 80 km southeast of Rivers Inlet, were downloaded from Environment Canada's Climate Data Online database

(http://www.climate.weatheroffice.ec.gc.ca/climateData/canada_e.html). A storm event was defined as daily averaged wind speeds higher than 11 m s^{-1} (20 knots) because wind speeds greater that this were observed to mix the water column in the inlet.

Visibility

PAR or sunlight data were not available from any Environment Canada weather station in the general proximity of the study system. Therefore, data on hourly average visibility in kilometers from the Port Hardy airport (50.40^{o}, 127.22^{o}), 100 km southeast of Rivers Inlet, were downloaded from Environment Canada's Climate Data Online database (http://www.climate.weatheroffice.ec.gc.ca/climateData/canada_e.html) and used as a surrogate measure of sunlight.

River Discharge

Mean daily discharge for the Wannock River was obtained from Environment Canada's hydrometric database (http://www.wsc.ec.gc.ca/hydat/H2O/index_e.cfm?cname=main_e.cfm).

Statistical Analysis

Analyses of variance (ANOVA) were used to test for significant effects of year, sampling cruise and location on nutrient concentration (for each nutrient at 0 and 5 m), surface salinity, surface temperature, MLD and critical depth. Nutrient concentrations, surface salinity, and MLD data were log transformed to normalize the residuals.

The MLD can be defined using the threshold method, as the depth where the density exceeded the surface density by 0.01 kg m^{-3} (Thomson and Fine 2003). This value corresponds to a change of 0.013 ppt in the salinity gradient for the temperatures and salinities observed in Rivers Inlet. To calculate the MLD we used a value of 0.04 ppt for the salinity difference instead of 0.013 ppt to account for the noise in the data and the resolution of our sonde (0.01 ppt).

Critical depth was defined as the depth where integrated phytoplankton production is the same as phytoplankton respiration (Mann and Lazier, 2006). It was calculated using the PAR profiles as the depth (*crit*) where

$$\int_{0}^{comp} (P - P_c)\delta z = \int_{comp}^{crit} (P_c - P)\delta z$$

where P is the measured PAR at depth, P_c is PAR at the compensation depth = 7 μE m^{-2} s^{-1} (Mann and Lazier, 2006), *comp* is the compensation depth where the rate of photosynthesis equals the rate of respiration and PAR = 7 μE m^{-2} s^{-1}.

ANOVA's were calculated using JMP®. Analysis was restricted to samples collected until the sampling cruise prior to the spring bloom in each year to try to identify the factors that trigger a spring bloom. Year, date, site and the year*site interaction were incorporated as effect terms. Other two-way interactions were not added to the generalized linear model because only one cruise was conducted before the 2006 spring bloom. The test for critical depth did not contain a year*site interaction because PAR was not measured at Ralph Point during the first 2006 cruise. An ANOVA of a second linear model with salinity as an extra exploratory variable was also performed on the nutrient concentration

data to tease out explanations for the observed variability between sites, date and year. The significance of differences in wind speed, visibility and river discharge were tested with day and year as main effects.

A model used to estimate the timing of peaks in chlorophyll a was developed using daily-integrated chlorophyll observations from the Florence site until the end of the spring bloom on May 15. The curve was constructed as a straight line plus an exponential curve followed by a decay curve (Fig. 15), as defined by the equation below.

If $t < c$ $C_t = a + ge^{d(t-b)}$

Else $C_t = a + ge^{d(c-b)}e^{f(t-c)}$

Where

t = sampling day (day 1 = March 10),

C_t = estimate of integrated chlorophyll biomass on day t,

and the five parameters are as follows:

a = background biomass,

b = date of growth initiation,

c = date of the peak,

d = growth rate,

f = decay rate,

g = 1 mg m^{-2}.

The five model parameters were estimated using maximum likelihood. We assumed that the data were normally distributed with uniform variance. Residual plots showed this to be a reasonable assumption. With the likelihood function based on the probability density function for a normal distribution, the likelihood function could then be minimized by ordinary least squares to obtain estimates of model parameters (Kapadia et al. 2005).

Furthermore, marginal likelihood profiles were computed to asymptotically determine marginal 95% confidence intervals for each of the parameter estimates. The marginal likelihood was constructed for each parameter separately. For example, to find the marginal likelihood for *a*, the other parameters were always optimized, while *a* was allowed to vary. The 95% confidence interval for each parameter estimate can be determined visually from the marginal likelihood plots, but it was computed in R using a root finding method. The critical level for the 95% confidence interval was determined as the maximal likelihood plus 1.921, corresponding to $\frac{1}{2}\chi^2_{0.05,1}$.

The same curve, as defined by the best parameter estimates for the daily data, was then fit to the weekly 2007 data. To obtain the fit, the original curve was allowed to shift vertically and horizontally, and two extra parameters defining the time shift and scale expansion were added to the model for each site. It was assumed that once the optimal growing conditions are reached, chlorophyll grows exponentially at the same constant rate at each site, and that the shape of the growth curve is maintained at each site and is comparable to the one at the Florence site. Phytoplankton has indeed been observed to grow exponentially

once the bloom is underway (Boney 1989). The following is an example of the modification of the phytoplankton growth model; the location is Bosquet:

$Bq_t = v\, C_{(t-s)}$

Where

t = sampling day (day 1 = March 10),

Bq_t = estimate of integrated chlorophyll biomass on day t at Bosquet,

C = model equation for daily data with best fit parameters,

and the two parameters are as follows:

v = scale expansion parameter,

s = time shift parameter.

To assess the spatial variability in bloom timing, the estimated time shift parameter was then added to the date of the peak obtained from the daily model fit to compute an estimate of the date of the peak for each site in 2007. Similarly, the daily peak biomass estimate was multiplied by the estimated scale expansion parameter to obtain an estimate of the peak biomass at every site in 2007. Again, confidence intervals for the parameters were found asymptotically.

The null hypothesis of no variation in maximum chlorophyll biomass or timing of the bloom between sites in 2007 was evaluated using a test that compared the difference in likelihood between a model with either the same time or vertical shifts for all the sites to that of one were both were optimized differently for each site. The test statistic corresponded to $½\ \chi^2_{0.05,7}$. Multiple

comparisons of time and biomass differences between sites were computed with tests of the difference between the likelihood of the model where the time and scale parameters were optimized differently for each site and that of a model with two sites having the same time or scale parameters. The critical value used was 4.77, ½ $\chi^2_{0.05,1}$ adjusted by a Bonferroni correction to an alpha level of 0.002.

A different model was applied to the 2006 data, because the one described, with scale expansion and time shift parameters, was found to overestimate the initial chlorophyll biomass at every site. Also, we felt that we needed to allow for more variability in the duration of the bloom, because environmental conditions differed substantially between years. We again used the same model as for the 2007 daily Florence site. The best estimates for rate of growth, decay, and initial biomass obtained from the daily fit (see Table 3) were inputted as constants, the two parameters determining the date of initiation and peak of the bloom were estimated using maximum likelihood, and confidence intervals were again determined asymptotically.

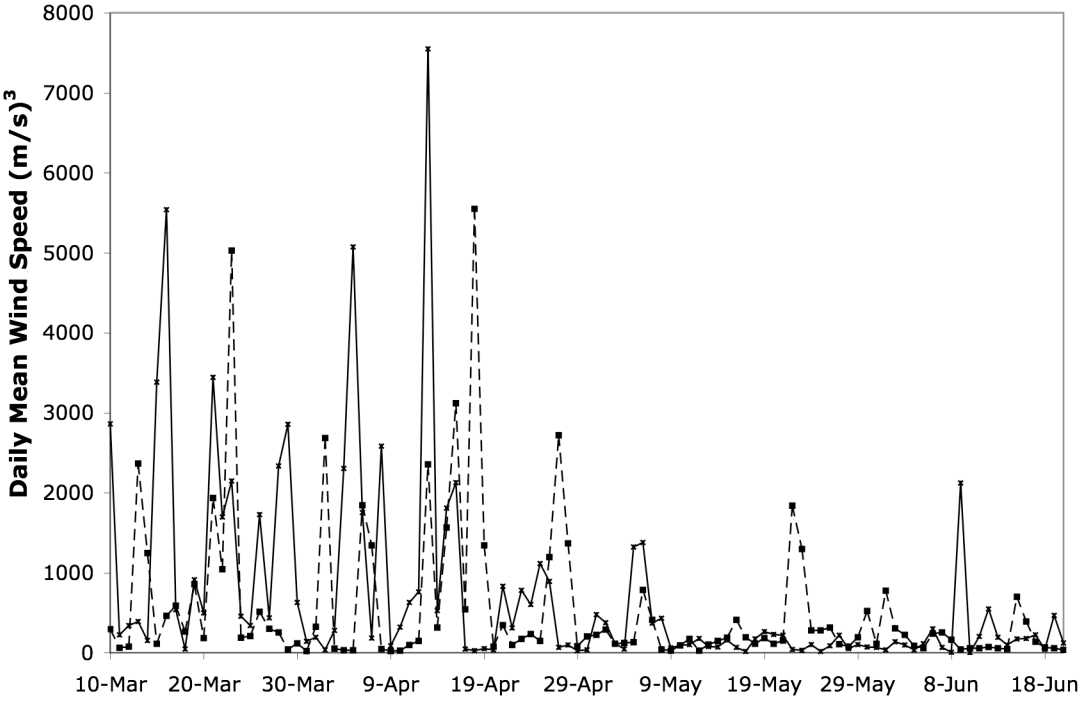
No attempt was made to perform multiple comparisons of timing among sites for the 2006 data because of the low (bi-weekly) sampling frequency. The likelihood analysis was performed in R.

Results

Physical Properties

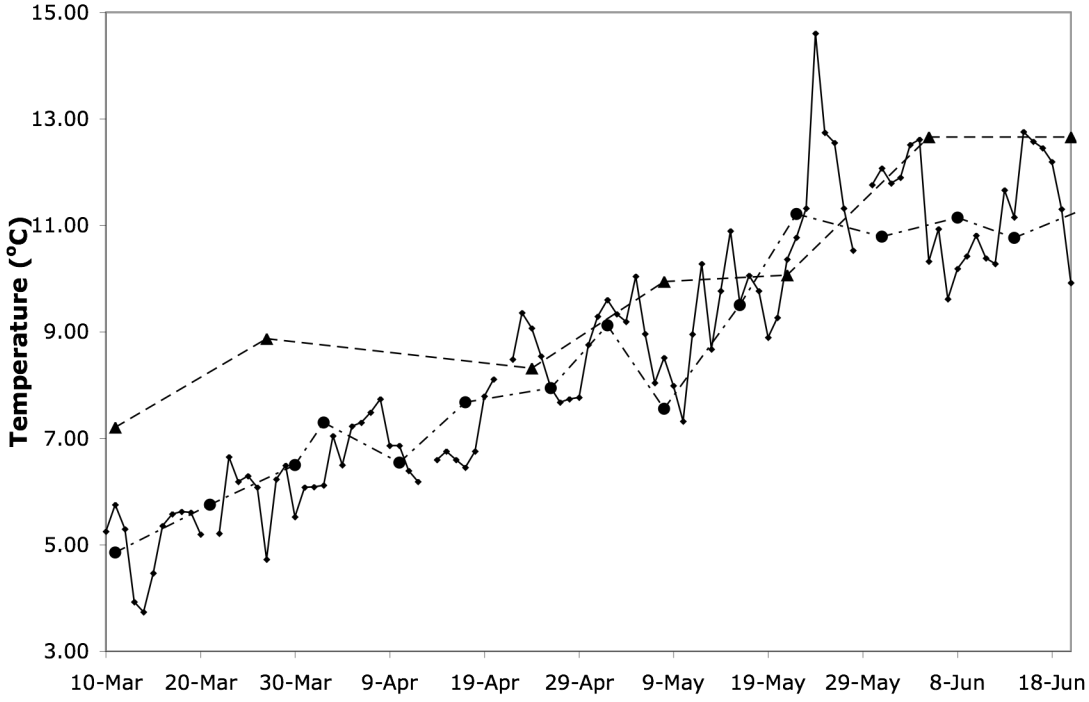
In general, we observed substantial interannual variations in meteorological conditions, river discharge, and water properties prior to the spring bloom in Rivers Inlet. The spring of 2007 had a higher frequency of storms. Wind data from Herbert Island shows that wind events in March and April 2007 were more frequent than in 2006, but not more severe (Fig. 2). The average time interval between storms was 6 ± 2 days (mean ± SD) in 2006 and 3.8 ± 1 day (mean ± SD) in 2007, with the longest break of 9 storm free days happening prior to the 2006 bloom from March 24 to April 1. Winds lessened in the latter half of April in both years (Fig. 2).

Figure 2 Mean cubed daily wind speed at Herbert Island from March 10 to June 20 2006 (dashed line) and 2007 (solid line).



Atmospheric visibility in March and April was significantly higher in 2006 than 2007 ($p = 0.013$), and the critical depth prior to the bloom, averaged over all the sites, was also significantly deeper in 2006 than in 2007 ($p = 0.0308$) by an estimated 6 m (SE = ± 3 m). No significant differences in critical depth were detected among sites in either year. 2006 surface water temperatures prior to the spring bloom were significantly higher than in 2007 ($p < 0.0001$), averaging 8.05 ± 0.35 °C across all sites. In 2007, surface temperatures prior to the spring bloom averaged 5.70 ± 0.16 °C (Fig. 3).

Figure 3 Surface water temperature averaged over all the sampling stations in 2006 (triangles) and in 2007 (circles), and at the 2007 daily the Florence site (solid line). Standard error is 0.4 ºC for both 2006 and 2007 weekly averages.



River discharge in March and April was substantially lower in 2006 than in 2007 (Fig. 4). As a consequence, the water column was less strongly stratified in 2006 with significantly higher surface salinities ($p < 0.0001$) than in 2007 (Fig. 5 and 6). In 2006, prior to the bloom, the mixed layer was present at every site, but at the upper sites (Wannock, Kilbella, Ralph, and Scandinavia) it was shallow (0.5 to 1 m) with fresher surface salinities, while the other sites had a deeper MLD (4 to 7 m), but were not as strongly stratified (Fig. 5). By contrast, in 2007, all sites were strongly stratified with a shallow MLD of 0.5 to 1 m (Fig. 6). However, in both years, the MLD prior to the bloom remained much shallower than the critical depth (Fig. 7).

Figure 4 Mean Wannock River daily discharge from March 10 to April 30 2006 (dashed line) and 2007 (solid line).

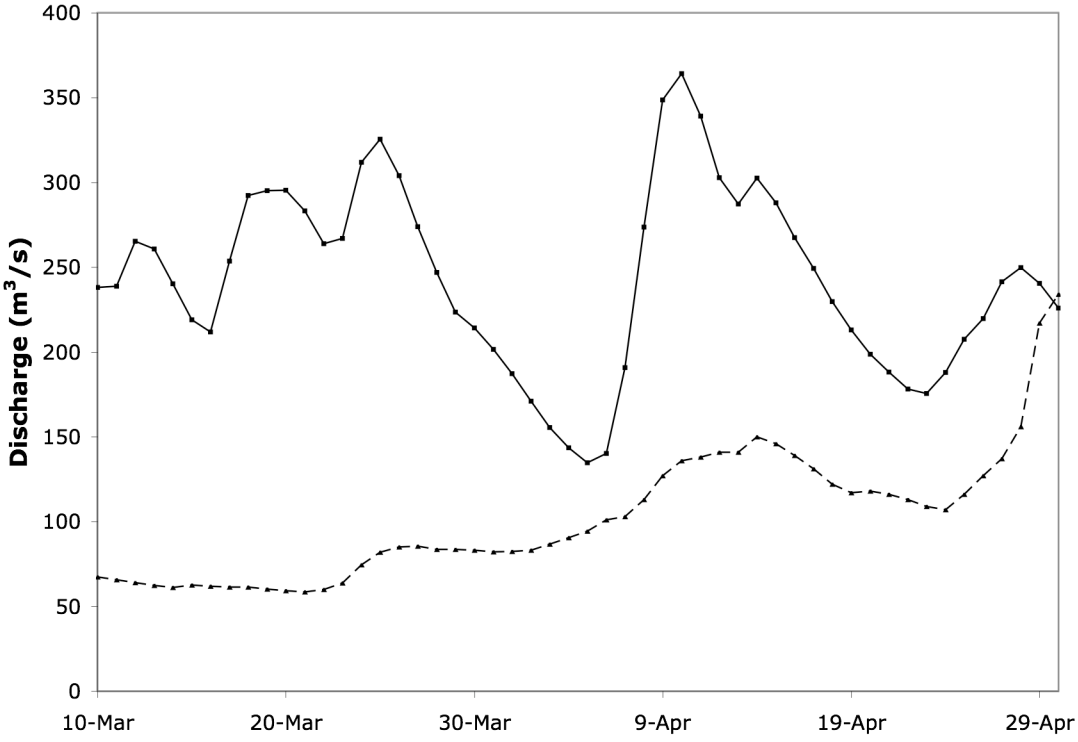


Figure 5 Salinity depth profile at Rivers Inlet weekly sampling stations on March 11 2006.

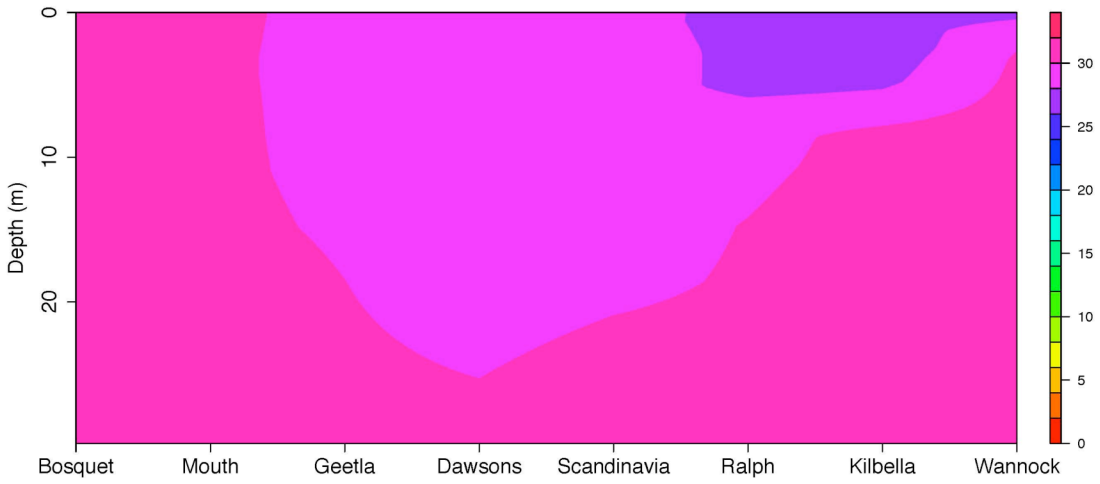


Figure 6 Salinity depth profile at Rivers Inlet weekly sampling stations on March 11 2007.

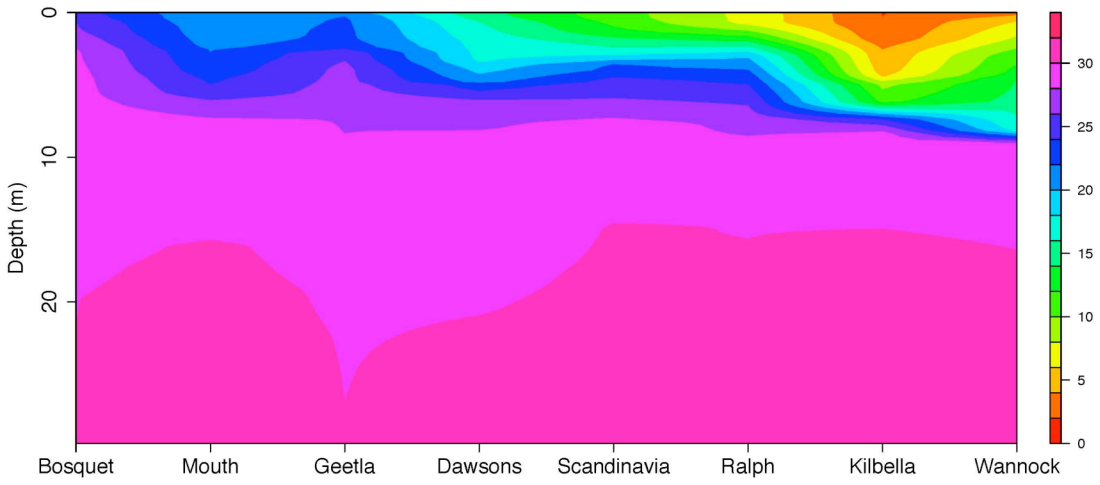
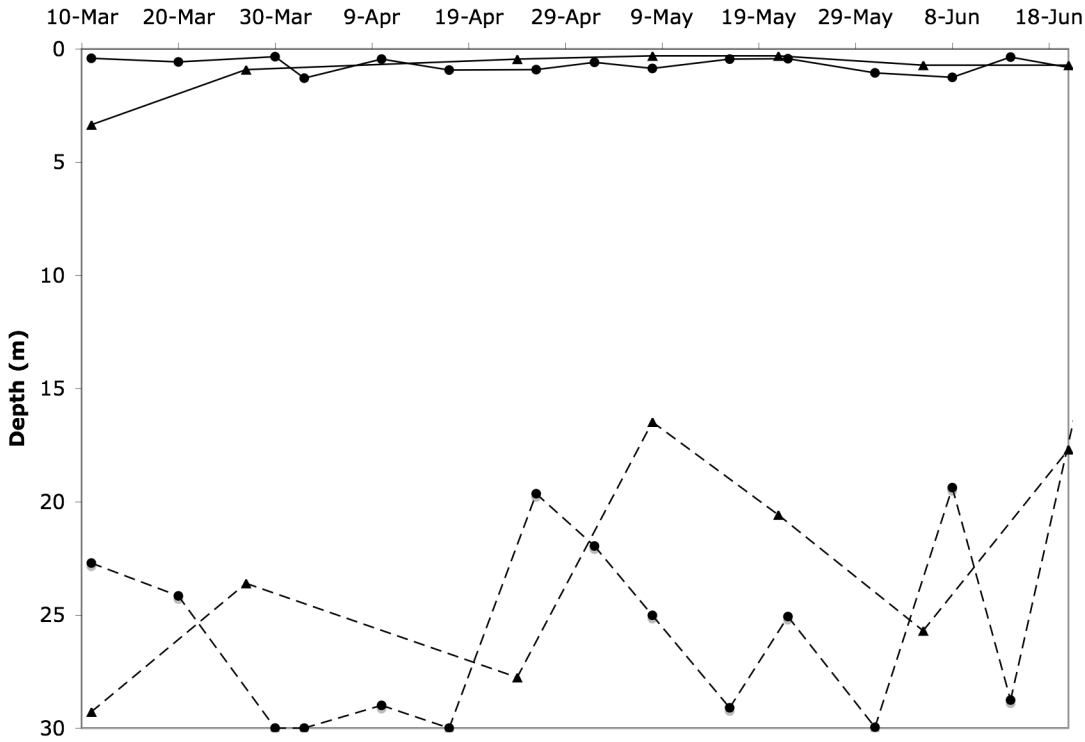


Figure 7 Critical depth (dashed line) and mixed layer depth (MLD) (solid line) for 2006 (triangles) and 2007 (circles) averaged over all the sampling stations. The standard error is 1.1 and 1.3 m for MLD in 2007 and 2006 respectively, and 2.3 m for the critical depth in both 2007 and 2006 except for the first cruise in 2006, where the SE for critical depth was 2.5 m. The phytoplankton bloom occurred in late March/early April in 2006 and on April 26 in 2007.



Spring to summer variations in MLD and the critical depth were monitored at the Florence Island station in 2007. The water was stratified to the surface since the beginning of the sampling season and the MLD remained relatively constant at 0.5-1 m (Fig. 8). The salinity profile shows a major wind-driven mixing event, which resulted in higher surface salinities, occurring on April 4, April 5, and April 7 (Fig. 9). Two minor wind mixing events were also observed on March 25 and March 29 (Fig. 9). The critical depth was always deeper than the MLD (Fig. 8).

Figure 8 Critical depth (dashed line) and mixed layer depth (solid line) at the Florence site in 2007.

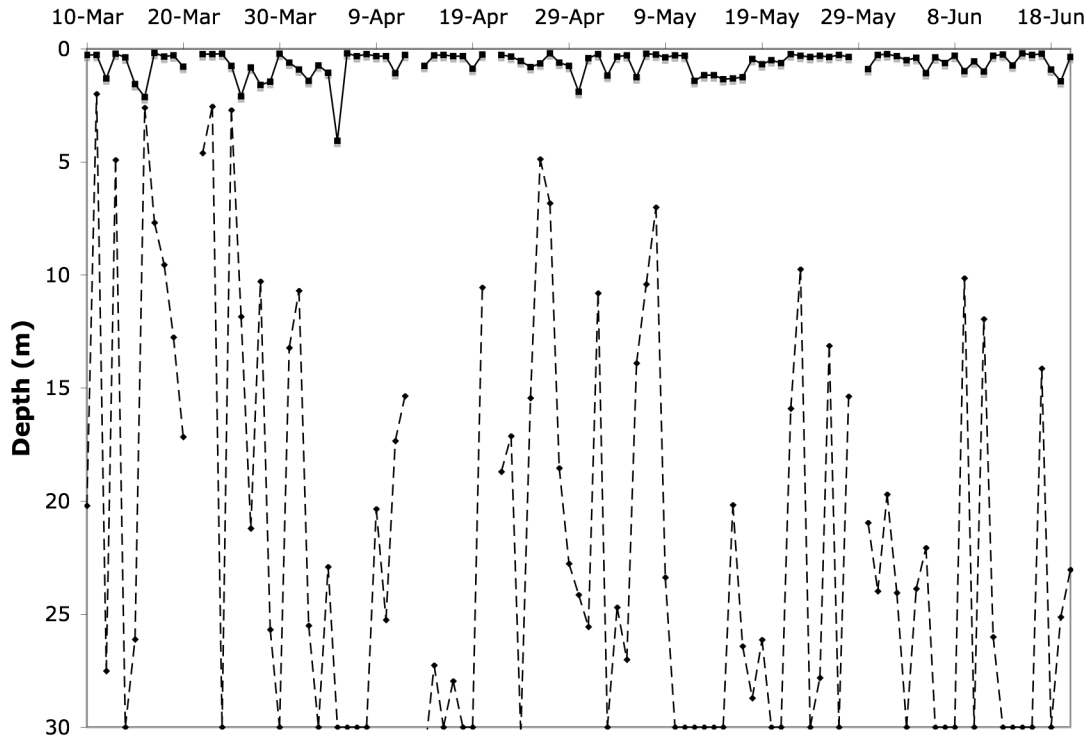
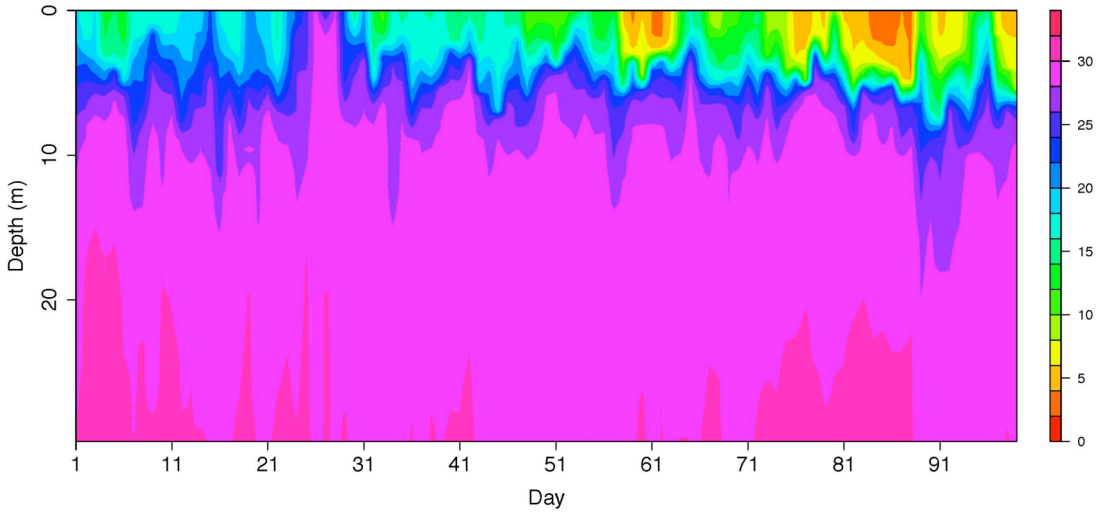


Figure 9 Daily salinity depth profile at the Florence site.



The ANOVA of surface nutrient concentrations showed a significant effect of year on the concentration of phosphates and nitrates at the surface, but not silicates (Table 1).

Table 1 ANOVA summary of the linear model: nutrient concentration at 0 m = Year + Date + Site + Year*Site. For each year, only data for the sampling cruises prior to the bloom was inputted in the linear model.

	Effect	F Ratio	p-value
P	Year	30.97	<0.0001
	Date	3.62	0.0539
	Site	2.17	0.1027
	Year*Site	1.18	0.3724
N	Year	11.35	0.0046
	Date	2.81	0.0944
	Site	1.99	0.1293
	Year*Site	1.59	0.2185
Si	Year	4.17	0.0604
	Date	3.57	0.0557
	Site	1.88	0.1484
	Year*Site	1.16	0.3819

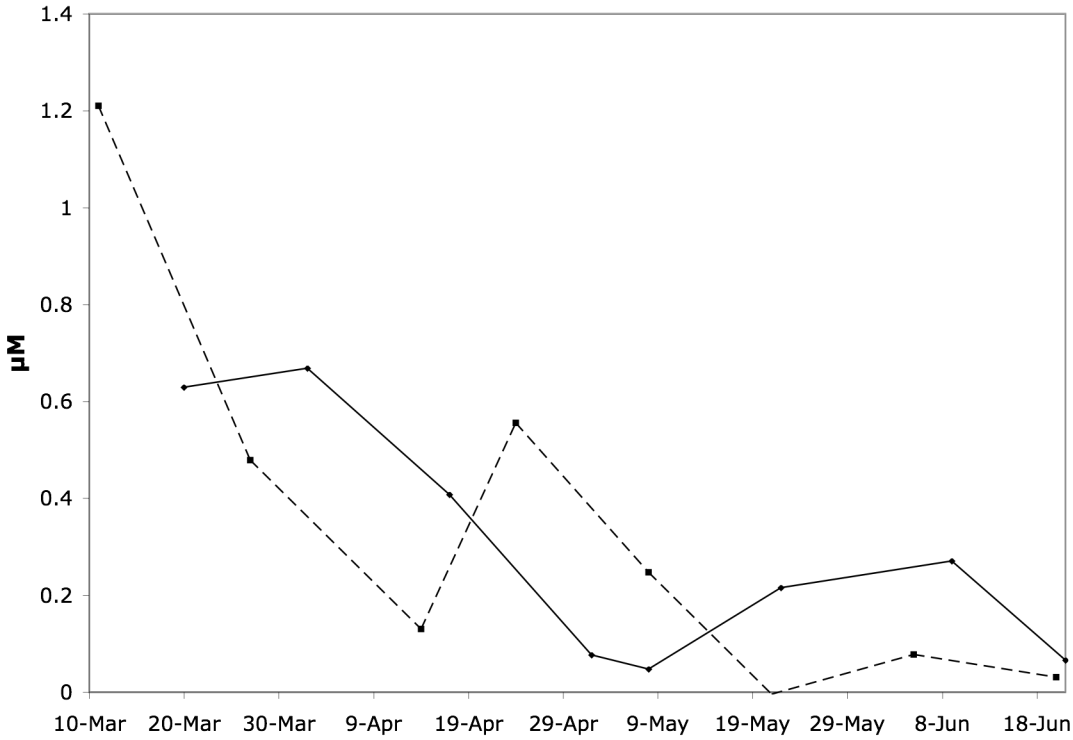
The subsequent analysis, which evaluated the additional effect of surface salinity, suggests that the differences in nitrate and phosphate concentrations were positively associated with differences in surface salinity (Table 2).

Table 2 ANOVA summary of the linear model: nutrient concentration at 0 m = Year + Date + Site + Salinity + Integrated Chlorophyll biomass. For each year, only data for the sampling cruises prior to the bloom was inputted in the linear model.

	Effect	F Ratio	p-value
P	Year	0.15	0.7002
	Date	1.71	0.2196
	Site	1.91	0.1494
	Salinity	12.84	0.0033
	Year*Site	1.33	0.3115
N	Year	0.51	0.4870
	Date	2.82	0.0964
	Site	2.11	0.1157
	Salinity	9.54	0.0086
	Year*Site	1.77	0.1768
Si	Year	0.18	0.6789
	Date	1.05	0.3770
	Site	1.83	0.1651
	Salinity	0.34	0.5700
	Year*Site	0.95	0.5042

There was no significant effect of year or station on silicate concentration at the surface or in any nutrient at 5 m. However, even at the surface, all nutrients were non-limiting before the spring bloom in both years (Fig. 10, 11 and 12).

Figure 10 Surface phosphate concentrations averaged over all the sampling stations in 2006 (dashed line) and in 2007 (solid line). Limiting phosphate concentrations are < 0.1 µM (Reynolds 2006). The standard error is 0.07 µM for 2006 and 0.09 µM for 2007.



In 2007 average N, and P concentrations over all the sites became limiting on May 2 after the bloom, while average Si concentrations were never limiting (Fig. 10, 11 and 12). Similarly, in 2006, average N, and P concentrations were depleted after the bloom on March 27, and Si was never limiting (Fig. 10, 11 and 12).

At 25 m nutrient concentrations were relatively constant and non-limiting (P=1.3, N=15.2 Si=25.6 µM), while they slightly increased over time at 100 m (P=0.9 to 2.0, N=8.1 to 26.1, Si=14.5 to 44.8 µM), possibly due to the increase in estuarine circulation as freshwater discharge increased over the sampling season.

Figure 11 Surface nitrate concentrations averaged over all the sampling stations in 2006 (dashed line) and in 2007 (solid line). Limiting nitrate concentrations are < 2 µM (Reynolds 2006). The standard error is 0.5 µM for 2006 and 1.03 µM for 2007.

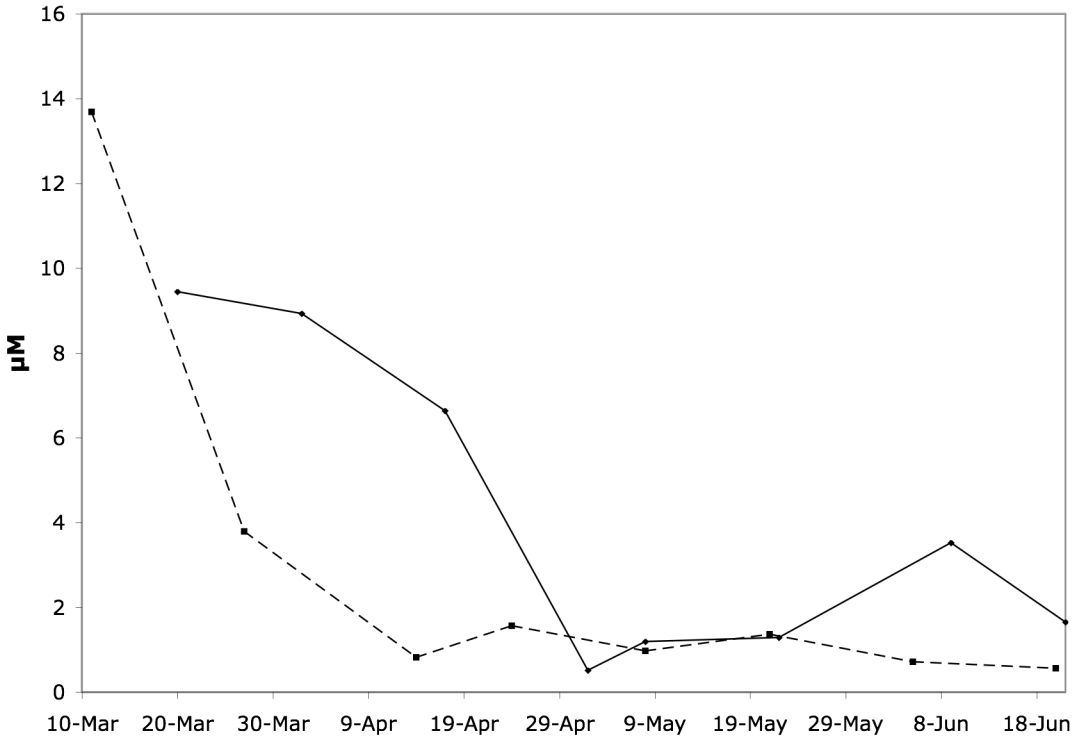
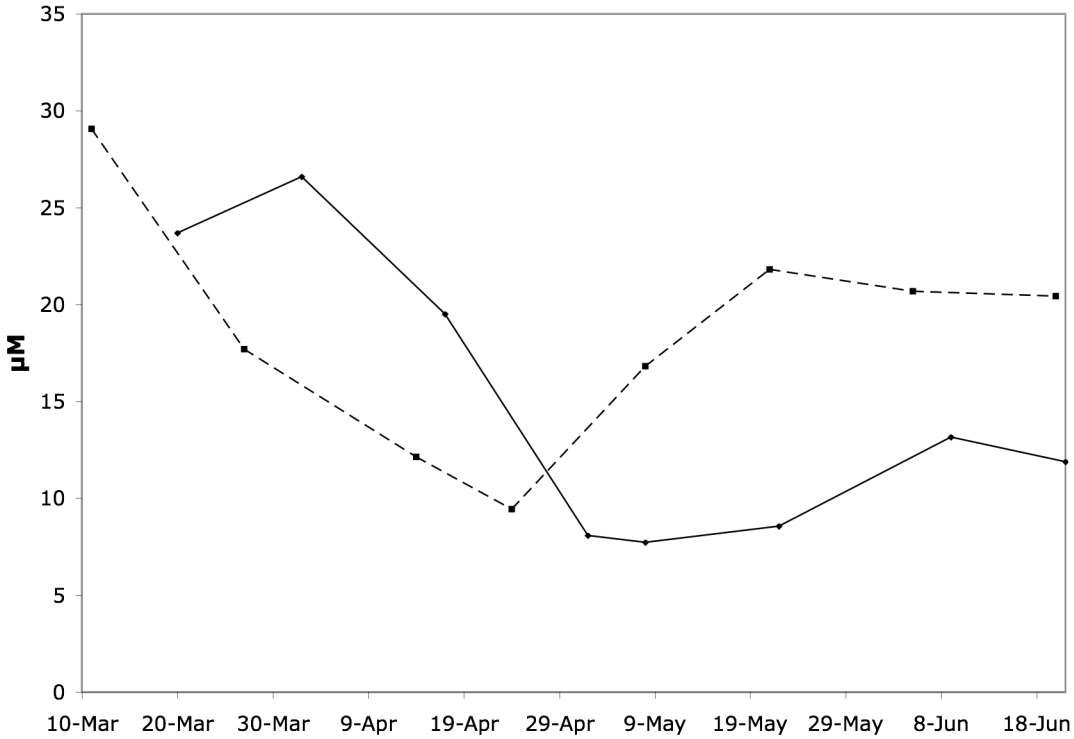


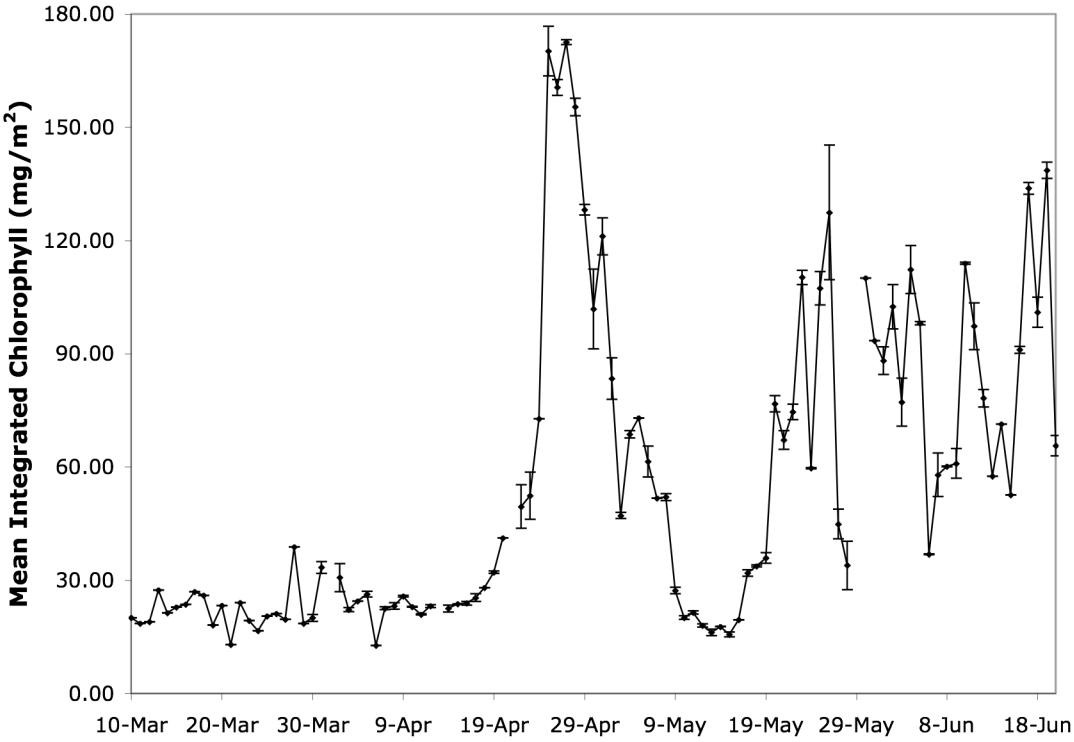
Figure 12 Surface silicate concentrations averaged over all the sampling stations in 2006 (dashed line) and in 2007 (solid line). Limiting silicate concentrations are < 2 µM (Reynolds 2006). The standard error is 3.4 µM for 2006 and 2.2 µM for 2007.



Chlorophyll *a* Dynamics

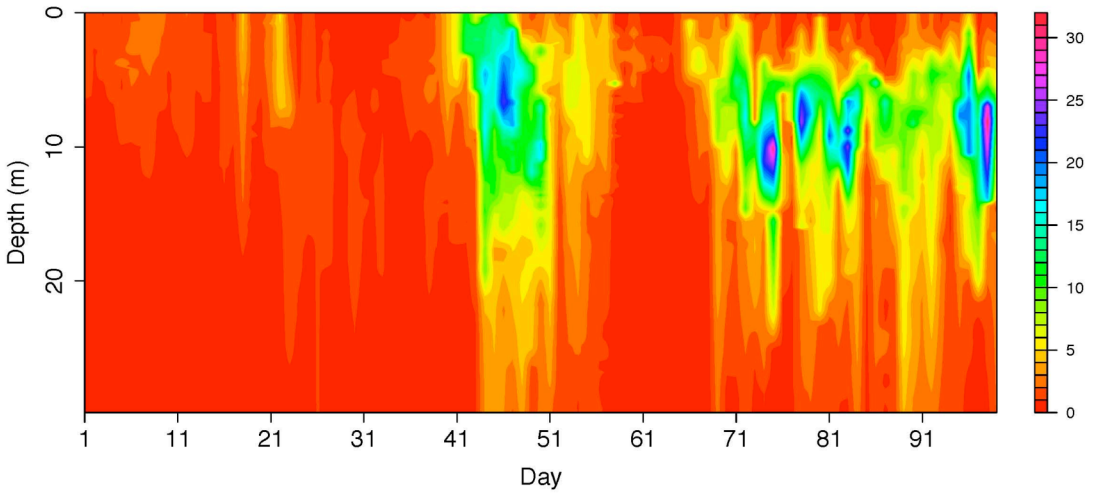
There was considerable seasonal variability in chlorophyll *a* concentrations at the Florence Island sampling location. Maximum chlorophyll biomass was observed on April 27 at 173 mg m^{-2}, after an initial period of low biomass averaged at 22 mg m^{-2} (Fig. 13).

Figure 13 Integrated chlorophyll *a* (to 20 m) as a mean of the two depth profiles taken daily at the Florence station from March 10 to June 20 2007. Error bars denote one standard error. No data was collected on April 1, April 13, April 21, and May 29.



Chlorophyll biomass declined and then increased in late May (Fig. 13). It then fluctuated frequently and widely, but averaged about 100 mg m^{-2} until the end of the sampling season. The highest chlorophyll a concentration (18 mg m^{-3}) on April 27th occurred at 4.5 m (Fig. 14). The blooms later in the season were about a meter deeper, and while not as extensive through water column, reached higher chlorophyll *a* concentrations (Fig. 14). The chlorophyll maximum was also at or below the MLD, with relatively high chlorophyll concentrations extending below to about 20 m at the time of the bloom (Fig. 14).

Figure 14 Daily depth profile of chlorophyll *a* at the Florence station. Legends unit is mg m^{-3}



The modeled chlorophyll curve fit the data quite well (Fig. 15, Appendix 3). However, major deviations occur on April 27, where the observed biomass was 21 mg m^{-2} lower than estimated, on May 1 when decay slowed down and where biomass was overestimated by 23 mg m^{-2}, and on May 3, where the observed biomass was 29 mg m^{-2} lower than estimated. The date of the spring bloom obtained from the model is April 26, with a chlorophyll biomass value of 199 mg m^{-2}. The optimized parameters are reported in Table 3.

Figure 15 Best fit of estimated integrated chlorophyll concentrations during the spring bloom over the daily samples collected at the Florence site in 2007. Dot represents daily observations.

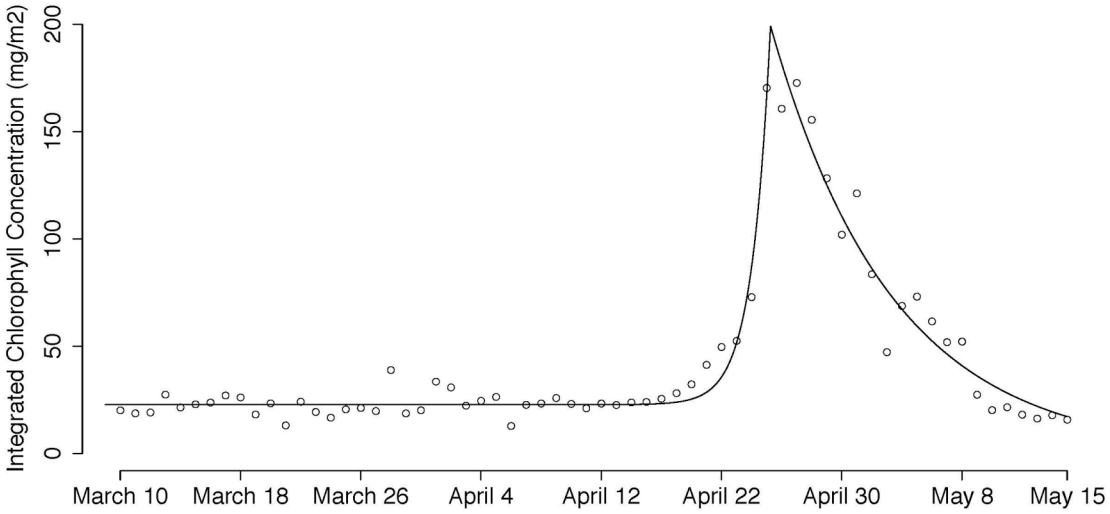


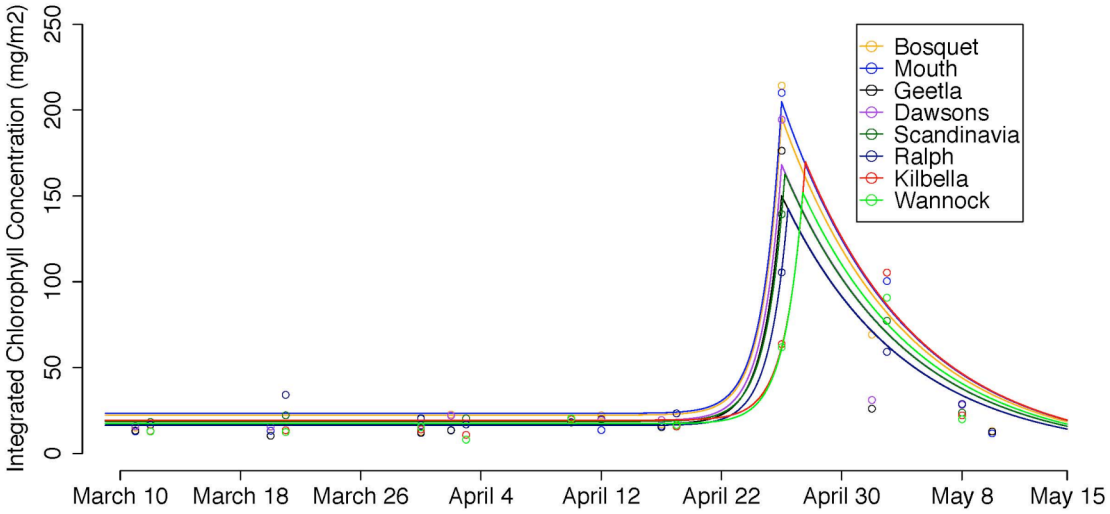
Table 3 Optimized parameters for the model fit to the daily 2007 data from the Florence station. Day 44 is April 26.

Parameter	Optimal Value	Confidence Interval
Background Biomass	23 mg m^{-2}	21 - 25 mg m^{-2}
Date of Growth Initiation	37.8	36.4 – 39.1
Date of the Peak	44.3	44.1 – 44.4
Growth Rate	0.80 d^{-1}	0.64 - 0.99 d^{-1}
Decay Rate	-0.12 d^{-1}	-0.11 - -0.13 d^{-1}

The model proved to be a reasonable good fit to the weekly data (Fig. 16, Appendix 3). However, a small increase in chlorophyll biomass on March 21 at the Ralph site was not captured by the model. Furthermore, data points after the peak were fit more poorly, especially at Dawsons and Geetla, where the spring bloom seems to have started declining earlier. These two sites have the widest

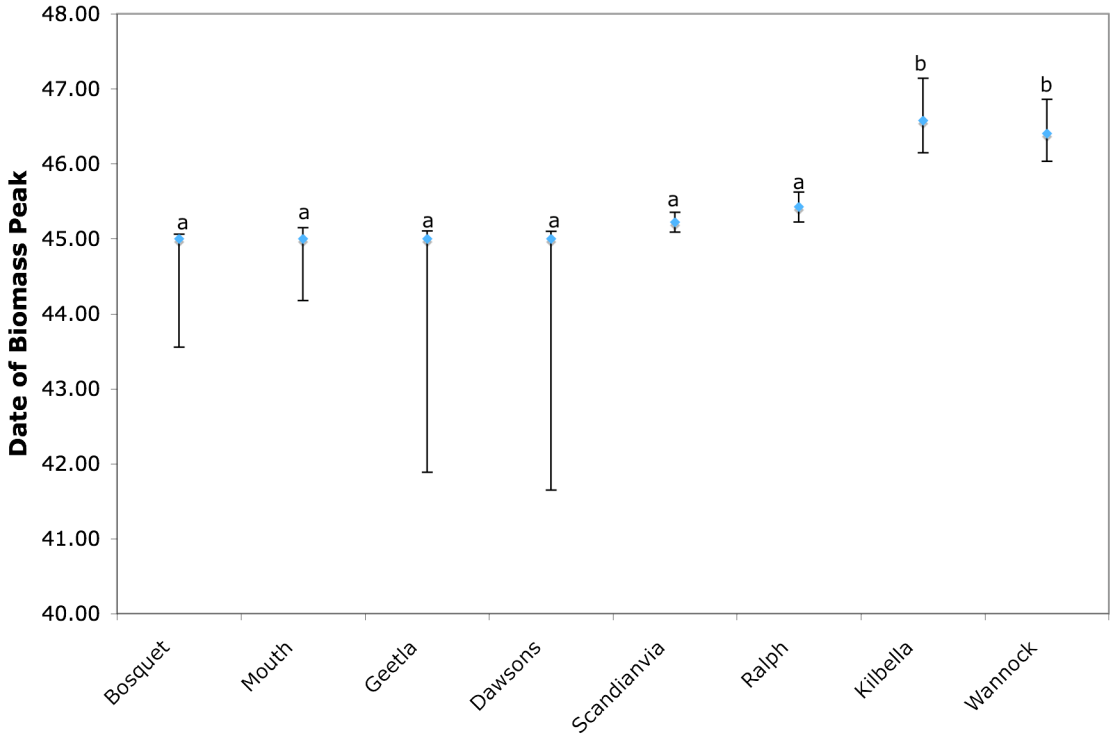
confidence intervals for both the estimate of date of the peak and peak biomass (Figs. 17 and 18).

Figure 16 Best fit of model estimates of integrated chlorophyll concentrations during the spring bloom at different sites in 2007. Dots represent weekly observations.



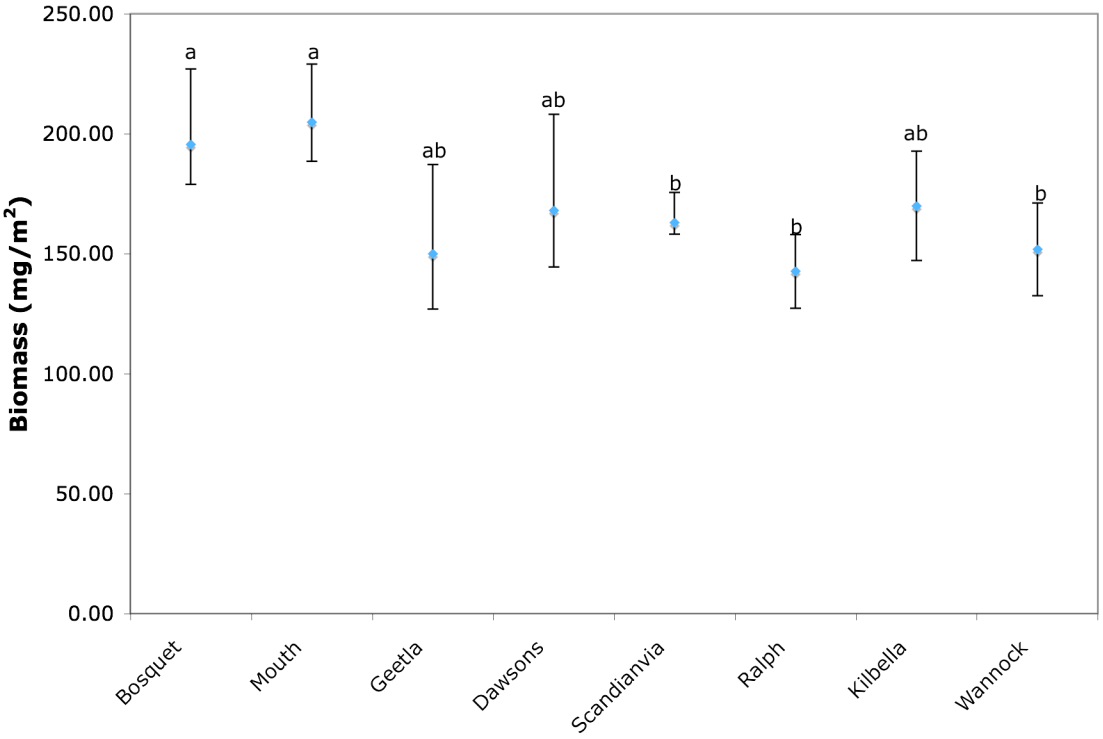
Generally, the timing of the spring bloom was spatially uniform throughout the inlet, with chlorophyll *a* concentrations peaking on April 27 at most of the inlet stations (Fig. 17).

Figure 17 Model estimates of the date of the spring bloom at different sites in 2007. Error bars denote upper and lower confidence intervals. Points marked by different letters are significantly different. Day 44 is April 26.



Model output suggested that the bloom peaked significantly later (1.5 days) at the Kilbella and Wannock stations but the biological significance of this is questionable. Estimated peak chlorophyll *a* concentrations were significantly greater at the two outer stations (Bosquet, Mouth), intermediate at the Geetla, Dawsons and Kilbella stations and lowest at the Scandinavia Bay, Ralph Point, and Wannock stations (Fig. 18). The intermediate stations were not consecutive geographically. These differences in peak chlorophyll *a* biomass among stations were greater than the within station variability observed between duplicate casts. On April 26, the standard deviation of duplicate casts was 12, 19, 5, 10, 9, 15, 3, and 6 mg m^{-2} for the Bosquet, Mouth, Geetla, Dawsons, Scandinavia, Ralph, Kilbella and Wannock sites respectively.

Figure 18 Model estimates of integrated peak biomass during the spring bloom at different sites in 2007. Error bars denote upper and lower confidence intervals. Points marked by different letters are significantly different.

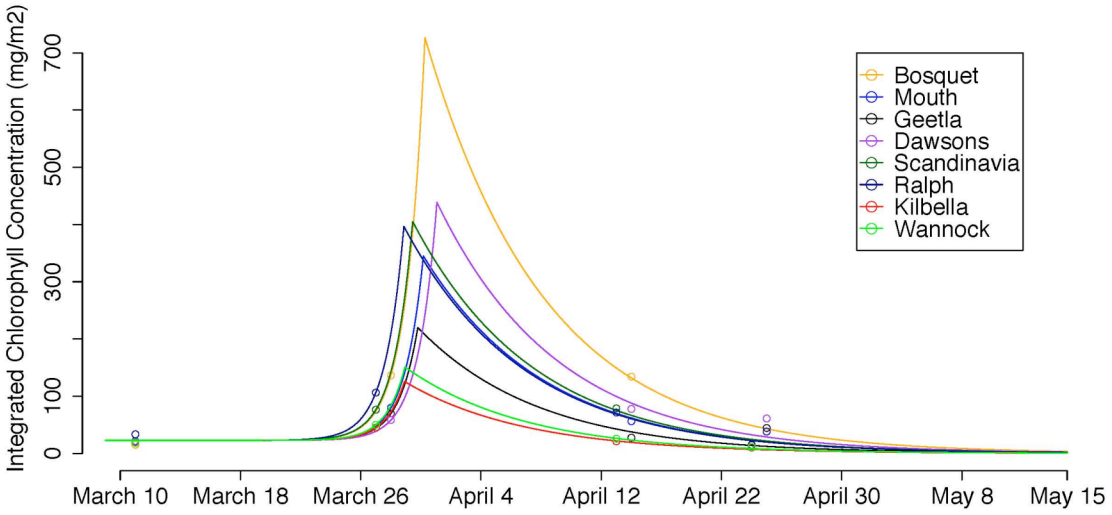


The bloom in 2006 was estimated to be earlier (March 29 – March 31) (Table 4). The model fit the 2006 data well (Appendix 3). The estimated peaks were higher than in 2007 (Fig. 19). It is difficult to define the temporal trend in chlorophyll *a* concentration in 2006 because of the low sampling frequency and classically rapid phytoplankton growth rates. For example, it is plausible that the data from the April 15th 2006 cruise could be part of second bloom, or that the bloom was shallower, but more prolonged.

Table 4 Estimated dates of spring bloom initiation and of the peak in integrated chlorophyll in 2006 at each of the 8 stations in Rivers Inlet. The dates were obtained by fitting the model of the daily spring bloom dynamics to the profiles collected biweekly at the 8 stations along the inlet. Day 20 is March 29.

Site	Estimated Date of the Peak	Confidence Interval		Estimated Date of Initiation	Confidence Interval	
Bosquet	21.3	21.2	21.4	13.1	13.0	13.2
Mouth	21.2	20.8	21.6	14.0	13.7	14.3
Geetla	20.8	19.3	21.9	14.2	13.7	15.2
Dawsons	22.1	21.4	23.6	14.6	13.9	16.3
Scandinavia	20.5	20.2	20.7	13.0	12.9	13.3
Ralph	19.9	19.7	20.1	12.5	12.3	12.7
Kilbella	19.9	19.6	20.2	14.1	13.9	14.4
Wannock	19.9	19.7	20.2	13.9	13.7	14.1

Figure 19 Best fit of model estimates of integrated chlorophyll concentrations during the spring bloom at different sites in 2006. Dots represent weekly observations.



Discussion and Conclusion

The phytoplankton bloom in Rivers Inlet occurred approximately 20 days later in 2007 than in 2006, apparently as a consequence of different environmental conditions experienced in the two years by phytoplankton in March and April. According to the Sverdrup (1953) mechanism of bloom development, the bloom should have occurred at the same time in both years, as the mixed layer depth (MLD) in late March and in April was shallower than the critical depth in both years. However, Ziemann et al. (1991) showed that bloom initiation was not dependent on the shoaling of the MLD as Auke Bay, Alaska, was already stratified in early spring. Thus, in Rivers Inlet, where freshwater discharge stratifies the water column by establishing a permanent shallow mixed layer in early spring, a shallow mixed layer is not indicative of optimal bloom conditions. This is in contrast with conditions observed in open ocean environments, where phytoplankton are thought to be mixed throughout a very deep mixed layer until spring warming allows a shoaling of the MLD (Sverdrup 1953). Lucas et al. (1998) modelled spring bloom dynamics in shallow estuaries and observed that that system was also not consistent with the classic Sverdrup model. They proposed that, unlike in pelagic systems where the mixed layer is often hundreds of meters deep, leakage of phytoplankton from the shallow surface layer of permanently stratified estuaries by sinking or turbulent diffusion is important and needs to be included in models of bloom dynamics (Lucas et al. 1998). Like in shallow estuaries, we observed permanent stratification and a very shallow MLD in Rivers Inlet. However, Rivers Inlet is deep, and turbulent

diffusion losses of phytoplankton may occur because of wind mixing rather than from the interaction of tidal currents with the bottom bathymetry.

The MLD measures the depth of the layer that has become mixed and this might not be the same as the mixing depth, the depth of active mixing (Noh and Lee 2008). Thus, under high wind stress, even in the presence of a surface stratified layer, phytoplankton can experience turbulent leakage. Wind events in 2007 were more frequent, but because of the high continuous input of freshwater the mixed layer appeared relatively constant. On the other hand, the mixing layer was likely deeper. Many studies have proposed that spring blooms may be delayed by wind stress (Kim et al. 2007, Saitho et al. 2002, Ware and McQueen 2006, Goebel 2005, and Ziemann et al. 1991). In 2007, the MLD was observed to be shallow in early March at all sites, but strong winds could have increased leakage of phytoplankton from the surface layer into the aphotic zone, leading to a net negative phytoplankton growth. Our data shows that there is a span of 6-8 days between bloom initiation and the peak in spring phytoplankton biomass (Fig. 13). In 2007, a window of calm weather optimal for phytoplankton growth was delayed until April 16. In 2006, the 9 days of calm winds after March 24 could have been enough to allow a bloom to develop.

The early spring in 2007 was also characterized by a higher freshwater discharge. Stronger horizontal advection, caused by the higher river discharge, would have also increased phytoplankton loss rates. In 2007, phytoplankton growth rates might have had to be higher or sustained for a longer period than in 2006 to achieve bloom concentrations, leading to a later bloom.

Higher freshwater discharge in 2007 not only influenced the timing of the spring bloom: it might also have reduced spring bloom biomass and overall production. The magnitude of the spring bloom is set by the initial amount of nutrients available (Cloern 1996), and results show that in Rivers Inlet nutrients are linked to salinity. The fresher mixed layer present prior to the spring bloom in 2007 was poorer in nutrients, and this might have contributed to the shorter bloom or lower estimated spring phytoplankton biomass than in 2006. However, the estimated integrated biomass for 2006 assumes that phytoplankton had the same growth rate as in 2007, and the poor sampling frequency in 2006 does not allow us to validate this assumption. Integrated peak biomass estimates for 2006 are comparable to those reported for Auke Bay, Alaska, (415 mg m^{-2}) (Ziemann et al.1991), but are substantially higher than those observed during monthly observations of a Norwegian fjord (200 mg m^{-2}) (Eilertsen and Frantzen 2007) or in the Strait of Georgia (101 mg m^{-2}) (Yin et al. 1997). Maximum chlorophyll concentrations at depth during both the 2007 and 2006 spring bloom were also higher than those measured in April 1992 in the Strait of Georgia (Yin et al. 1997), and chlorophyll concentrations at 3 m were higher than those observed in April 1980 in Hecate Straight or Queen Charlotte Sound (Ware and McQueen 2006). However, maximum chlorophyll concentrations were comparable to those observed on the Greenland shelf in 2002 (Waniek et al. 2005), in a New Zealand fjord in the late 1990's (Goebel et al. 2005), and in Chesapeake and Delaware Bay in the late 1980's (Fisher et al. 1988), and were 10 or more mg m^{-3} less than those detected in San Francisco Bay (Cloern 1996), a nutrient enriched, shallow

estuary. Substantial inter-annual differences in phytoplankton production will result in differences in the amount of organic matter available to upper trophic levels, and thus, in Rivers Inlet, inter-annual changes in phytoplankton biomass under different nutrient conditions warrant further investigation. Future studies should maintain a frequent chlorophyll *a* sampling strategy to better quantify these interannual differences in peak integrated chlorophyll biomass.

While temperature in coastal waters is not the main determinant of water column stability, it still affects growth rates of phytoplankton (Reynolds 2006), and might explain the spatial difference in bloom timing observed in the inlet. The blooms were modeled to occur two days later at Wannock and Kilbella, the only two sites with temperatures below 7 ^{o}C on April 26, the date of the bloom elsewhere in the inlet. Nevertheless, in Auke Bay, phytoplankton blooms occurred at temperatures lower than 7 ^{o}C, and phytoplankton productivity rates were not correlated with water temperature (Ziemann et al. 1991). Thus, temperature might not be a factor limiting phytoplankton biomass. The critical depth and MLD at these two sites were comparable to those in other locations in the Inlet. However, these two sites are the closest to the head of the inlet, where the input of freshwater is high. The freshwater would be free of saltwater phytoplankton, and this might be the cause of the delayed bloom at these sites.

Interannual variability in the timing of the spring bloom in Rivers Inlet is similar to that observed elsewhere (Henson and Thomas 2007, Kim et al. 2007, Ware and McQueen 2006), and the differences can have repercussions on upper trophic levels dynamics. For example, Cassin auklet's nestling growth rates are

influenced by the timing of the spring bloom (Bertram, 2001) and herring growth rates in Hecate Strait have been observed to be positively correlated to primary productivity (Ware and McQueen, 2006).

Variation in climate indices and fish catch have been shown to be correlated (e.g. Beamish et al. 1999), but predictions made by incorporating climate variability into fisheries forecasts have been disappointing because the mechanisms that link climate fluctuations to changes in biological variables are still not well understood (Lehodey et al., 2006). This analysis has started to elucidate such mechanisms in Rivers Inlet. High March and April discharge from the Wannock River during the sockeye juvenile out-migrating year has been shown to be negatively correlated to sockeye survival in the inlet (Routledge et al., in prep.), and this study has provided the first evidence of an interaction between high early spring discharge and phytoplankton processes. A higher freshwater discharge will lower nutrient concentrations in the euphotic zone, and will increase horizontal advection and phytoplankton loss rates. Furthermore, early springs with higher discharge are likely associated with higher wind speeds, a factor that also increases phytoplankton loss rates. Intense Aleutian Lows, a pressure system dominating the region in winter, are associated with higher wind speeds and precipitation (Mantua et al. 1997), and an analysis of historical climate records for this region should be undertaken to illustrate the likelihood of such climatic scenarios. Routledge et al. (in prep.), found survival rates in years of low discharge more variable. This variability could be explained by variation in those environmental factors, other than river discharge, that we have found to

influence phytoplankton dynamics. For example, a low discharge, but windy early spring could still delay a spring bloom if the increase in phytoplankton growth due to the reduced horizontal advection rates were to be offset by the higher vertical mixing rates, and if optimal growth conditions were not constant over a 6-8 days period.

In conclusion, this research has found evidence of a large interannual variation in the timing of the spring bloom and has highlighted the main physical drivers of phytoplankton dynamics in a coastal fjord; it appears that a windy early spring with high freshwater discharge will delay the spring phytoplankton bloom. More specifically, it is hypothesized that the frequency and duration of wind events and the amount of horizontal and vertical advection play a major role in determining the timing of the bloom by influencing phytoplankton loss rates. These findings present exciting possibilities for the development of a mechanistic model of phytoplankton dynamics for the inlet. Such a model could re construct spring blooms in the past and relate them to observed sockeye salmon survival, forecast future phytoplankton biomass in the inlet and assess changes in productivity following climate change. In coastal fjords, where inlet hydrodynamics determine water structure, nutrient availability in the euphotic zone, and horizontal advection rates, such models should not only include predictions of increased temperatures and irradiances, but also expected changes in turbulent diffusion and phytoplankton leakage from the mixed layer due to wind speed and river discharge.

CHAPTER 2: SEASONAL AND INTERANNUAL VARIABILTY IN ZOOPLANKTON BIOMASS AND SPECIES COMPOSITION

Introduction

It has now been well documented that the dynamics of many marine organisms parallel fluctuations in climate trends (Lehodey et al. 2006). For example, interannual variations in the abundance of many species of Pacific salmon (*Oncorhynchus* sp.) have been shown to correlate with changes in the Pacific Decadal Oscillation, the El Nino Southern Oscillation (ENSO), the Aleutian Low pressure system, sea surface temperature, and river flow (Mantua et al. 1997, McGowan et al. 1998, Beamish et al., 1999, Beamish et al. 2000). It is believed that these environmental fluctuations act via bottom-up effects through changes in primary and then secondary productivity (Iverson 1990, Ware and Thomson 2005). Indeed, the abundance of Atlantic cod has been shown to follow trends in the size, abundance, and timing of its zooplankton prey (Beaugrand et al. 2003), and some of the variability in Pacific herring (*Clupea pallasi*) and coho salmon (*Oncorhynchus kisutch*) recruitment can be predicted by changes in the timing and abundance of euphausiids (Tanasichuk 2002).

In the Northeast Pacific, zooplankton dynamics do vary at some of the same temporal scales as climate indexes, sea surface temperatures, and fish stocks. Zooplankton biomass in the California Current declined following the well-documented climate regime shift in 1977 (McGowan et al. 1998), and shifts in

zooplankton community composition have been observed during ENSO events (Mackas and Galbraith 2002, Keister and Peterson 2003, Zamon and Welch 2005). In addition, interannual changes in the timing of the winter to summer transition in copepod communities have been reported in the Northern California Current (Peterson and Keister 2003), and in the Northeast Pacific, decadal shifts in zooplankton assemblages and in the seasonality of the subarctic copepod *Neocalanus plumchrus* appear to parallel sea surface temperature changes (Mackas et al. 2007).

However, the biological mechanisms linking environmental parameters to salmon fisheries or zooplankton productivity are still not well understood (Gargett et al. 2001, Lehodey et al. 2006, Mackas et al. 2007), reducing our ability to conserve salmon stocks or predict future impacts of climate change on salmon productivity. Environmental forcing variables fluctuate at a variety of scales, and their relationship with salmon marine survival rates are complex because they may act via many trophic linkages, may change over time, and may operate over different temporal and spatial scales. For example, at northern latitudes, environmental conditions in late winter and early spring can set the stage for the annual seasonality in primary productivity, and thus the seasonality in secondary production. As a result, environmental conditions in winter and spring might impact food availability for salmon juveniles in early summer. Furthermore, unlike large-scale climate indices, such as the PDO, salmon survival rates from different stocks have been found to be correlated only at a regional scale (Mueter et al. 2002). Therefore, to understand the ecological processes driving fluctuations in

salmon marine survival, it is important to study changes in secondary productivity and environmental forcing variables at this same spatial scale.

The system under investigation is Rivers Inlet, a fjord on the central coast of British Columbia, which until the mid-seventies was home to the third largest sockeye salmon (*O. nerka*) fishery in Canada. The stock has experienced a period of instability since the late 1970's and crashed in the early 1990's. It has yet not recovered, even in the absence of fishing, and reasons for its decline remain unknown, but are most likely related to marine survival (McKinell 2001). The sockeye juveniles are some of the smallest in British Columbia (Foskett 1958), and the inlet is an important feeding ground for them; they have been observed to double in size during their 2-3 week migration though the fjord (Buchanan 2007). Furthermore, the sockeye juveniles' migration appears to consistently peak during the first new moon in late May or early June (Buchanan 2007), and this might make them particularly vulnerable to large changes in the timing of peak zooplankton biomass in the inlet.

However, although zooplankton may be important in controlling sockeye salmon juveniles' survival and growth in the inlet via bottom-up effects, data on zooplankton seasonality, species composition, and abundance is sparse or non-existent for the Central coast and Rivers Inlet in particular. The aim of this study is to present the first detailed data series on zooplankton dynamics in the fjord from early spring to early summer, and to tentatively link observed bi-weekly and interannual changes in zooplankton abundance and species composition to phytoplankton biomass and other environmental forcing variables. It is hoped that

these data will be the first step in the understanding of the biophysical links and ecological mechanisms impacting the early marine survival of this depleted sockeye salmon stock.

Methods

Study Area

Rivers Inlet (51^{o} 26', 127^{o} 38') is a deep (400 m maximum depth), 3 km wide and 40 km long fjord of glacial origin on the Central Coast of British Columbia, Canada. It is located 500 km north of Vancouver. The inlet is characterized by an estuarine circulation whereby a shallow surface layer transports fresh water out to the inlet mouth into Queen Charlotte Strait and nutrient-rich waters enter the inlet periodically over a shallow (110 m) sill at the mouth of the inlet. This process is enhanced in late spring and summer months as winter southeasterly winds ease and freshwater discharge increases (Whitney et al. 2005). Three side inlets, Moses Inlet, Darby Channel, and Draney Inlet, merge with the main arm at Scandinavia Bay, Bickle Passage, and Draney Narrows, respectively (Fig. 1). The major input of fresh water is from the Wannock River, flowing out from Oweekeno Lake, a large, oligotrophic lake fed by two glaciers and draining an area totaling 4100 km^2. Oweekeno Lake is the main sockeye salmon spawning area in the region. The Chuckwalla, Kilbella, and Clyak Rivers are the other significant sources of fresh water. The first two drain into Kilbella Bay, while the last flows into Moses Inlet (Fig. 1).

Field Sampling

Zooplankton vertical hauls were made every two weeks at eight sites along the length of Rivers Inlet from March 11 to June 22 in both 2006 and 2007, for a total of eight cruises each year. However, only one sample, at the Geetla site, was collected during the second cruise in 2007, and only two, at the Geetla and Dawsons sites, were collected during the fourth cruise in 2007. Zooplankton samples were also collected in Rivers Inlet during a study on juvenile sockeye salmon ecology from 2002-2005, albeit only from May to early July and every month (Buchanan 2007). To allow for a future comparison with the 2002-2005 results, the same eight sites selected by Buchanan (2007) were used in this study (Fig. 1). A list of these sites, their co-ordinates, and depths is available in Appendix 1.

Hauls were conducted at night using a 50 cm diameter, 250 cm length, 153 μm mesh bongo net with an attached TSK flowmeter. The net was lowered manually, and retrieved with a winch at approximately a speed of 2 m/s. Depth of haul was determined for each site by subtracting 30 m from the bottom depth as on the depth sounder. On deck, the net was rinsed and the sample from one cod end was kept and preserved in a 5 % formalin solution. The vertical towing distance was obtained from the number of revolutions recorded on the flowmeter after each net deployment. The volume of water filtered by the net was calculated by multiplying the towing distance by the net mouth area, and this value was used to express zooplankton abundance and biomass on a unit volume basis.

Al Hirst of Jensyd Biotech in Nanaimo, B.C., analyzed all the zooplankton samples as follows. Each sample was filtered over 1000 µm and 250 µm sieves and the wet weight of each size fraction was measured and then added together to obtain a total sample wet weight. Then plankton in each sample were counted and identified. If a large quantity of organisms was observed, the sample was split with a Folsom plankton splitter to generate subsamples with 80-100 individuals. When possible, copepods were identified to species and life-history stage as either juveniles or adults. Copepod nauplii were counted but not identified. Cladocerans were also identified to species, but all other organisms were grouped into larger taxonomic categories (e.g. euphausiids, decapods, amphipods, etc.).

A Hydrolab® sonde was deployed at each site as part of each zooplankton sampling cruise. It was lowered to a depth of 30 m and depth profiles of fluorescence, salinity, temperature, pH, TDS (total dissolved solids), dissolved oxygen, and PAR (photosynthetically active radiation) were obtained. On the third cruise in 2006, we were only able to obtain surface measurements at two of the eight sites, at Geetla and Scandinavia.

Water samples were collected to calibrate the Hydrolab® optical fluorometer readings and convert voltages to µg L^{-1} cholorophyll *a*. They were collected bi-weekly at all sites at 0, 1, 3 and 5 m in 2006, and daily at Florence Island and bi-weekly at all sites at a depth of 5 m in 2007. Samples were collected at depth with a Van Dorn bottle, and a fraction of each water sample was filtered through a Whatmann GF/F filter. The sample water was filtered in 60

ml aliquots until the filter looked brown, at which point the volume filtered was recorded. The filter was folded, wrapped in aluminum foil, stored in a cooler and then frozen at the field station. Samples were sent subsequently to the Canadian Department of Fisheries and Oceans' Institute of Ocean Sciences, Sidney, B. C., in 2006 and to the University of British Columbia in 2007 for chlorophyll *a* determination.

Calibration curves were developed for both 2006 and 2007 data by regressing log-transformed fluorometer readings on log-transformed chlorophyll *a* concentrations from the filtered samples. Least-squares regression fits, R^2 values, and parameter estimates are available in Appendix 2.

Chlorophyll concentrations were then integrated over the first 20 m to obtain chlorophyll biomass estimates for each site and cruise.

Statistical Analysis

We conducted an ANOVA to assess yearly, bi-weekly, and spatial changes in zooplankton abundance (total # of individuals per sample per m^3) and zooplankton biomass (total wet weight of sample per m^3). Abundance and biomass data were both log transformed to normalize the residuals. The regression models used is presented below:

Log (Density or Biomass) = Year + Cruise + Site + Year*Cruise + Cruise*Site + Year*Site + e

A second ANOVA that used data from only the May and June cruises was also calculated to highlight differences in zooplankton abundance and biomass

during the time of the juvenile sockeye salmon migration through the inlet. Chlorophyll and surface salinity were added as extra explanatory variables. Surface salinity and chlorophyll biomass were log transformed to normalize the residuals. Multiple comparisons of significant effects on the least square means were conducted using the Tukey HSD test with α = 0.05.

Multivariate analysis was performed to explore patterns in species composition between years, seasons, and sites. The abundance of each taxon in each sample was log(*x* + 1) transformed to reduce the influence of the more abundant species on the rest of the data (Field et al. 1982). Then, a samples-by-taxa matrix of the transformed abundances was used to generate a Bray-Curtis similarity matrix. This measure of similarity is particularly robust when many of the entries are zeroes, because it does not take into account joint absences when comparing samples (Field et al. 1982). It is defined as

$$S_{jk} = 1 - \frac{\sum_{i=1}^{p} |Y_{ij} - Y_{ik}|}{\sum_{i=1}^{p} (Y_{ij} + Y_{ik})}$$

where S_{jk} is the similarity between samples j and k, Y_{ij} is the abundance of species *i* in sample *j*, Y_{ik} is the abundance of species *i* in sample *k*, and *p* is the number of species. S_{jk} ranges from 0, indicating no species in common between the samples, to 1, indicating the samples have the same relative abundance and species composition.

In order to visualize which samples had similar species compositions a hierarchical sorting strategy, group-average sorting, was used to produce a dendrogram from the similarity matrix. Samples that shared more than 50% similarity were considered as belonging to the same cluster. To assess which species were characteristic of each cluster and contributed the most to difference between clusters we used similarity percentages analysis (Clarke 1993). The contribution of each species to the average dissimilarity between two clusters was computed and the species were ranked according to their contribution. The average dissimilarity between two clusters with *n* and *m* samples respectively was defined as

$$\overline{\delta} = \frac{\sum_{j=1}^{n}\sum_{k=1}^{m}\left(1 - S_{jk}\right)}{nm}$$

where S_{jk} is the similarity between the *j*th and *k*th sample.

The average contribution of species *i* to the average dissimilarity between two clusters with *n* and *m* samples respectively was computed as

$$\overline{\delta}_i = \frac{\sum_{j=1}^{n}\sum_{k=1}^{m}\left[\frac{\left|Y_{ij} - Y_{ik}\right|}{\sum_{i=1}^{p}\left(Y_{ij} + Y_{ik}\right)}\right]}{nm}$$

where Y_{ij} is the density of the *i*th species in sample *j*; Y_{ik} is the density of the *i*th species in sample *k*, and *p* is the number of species.

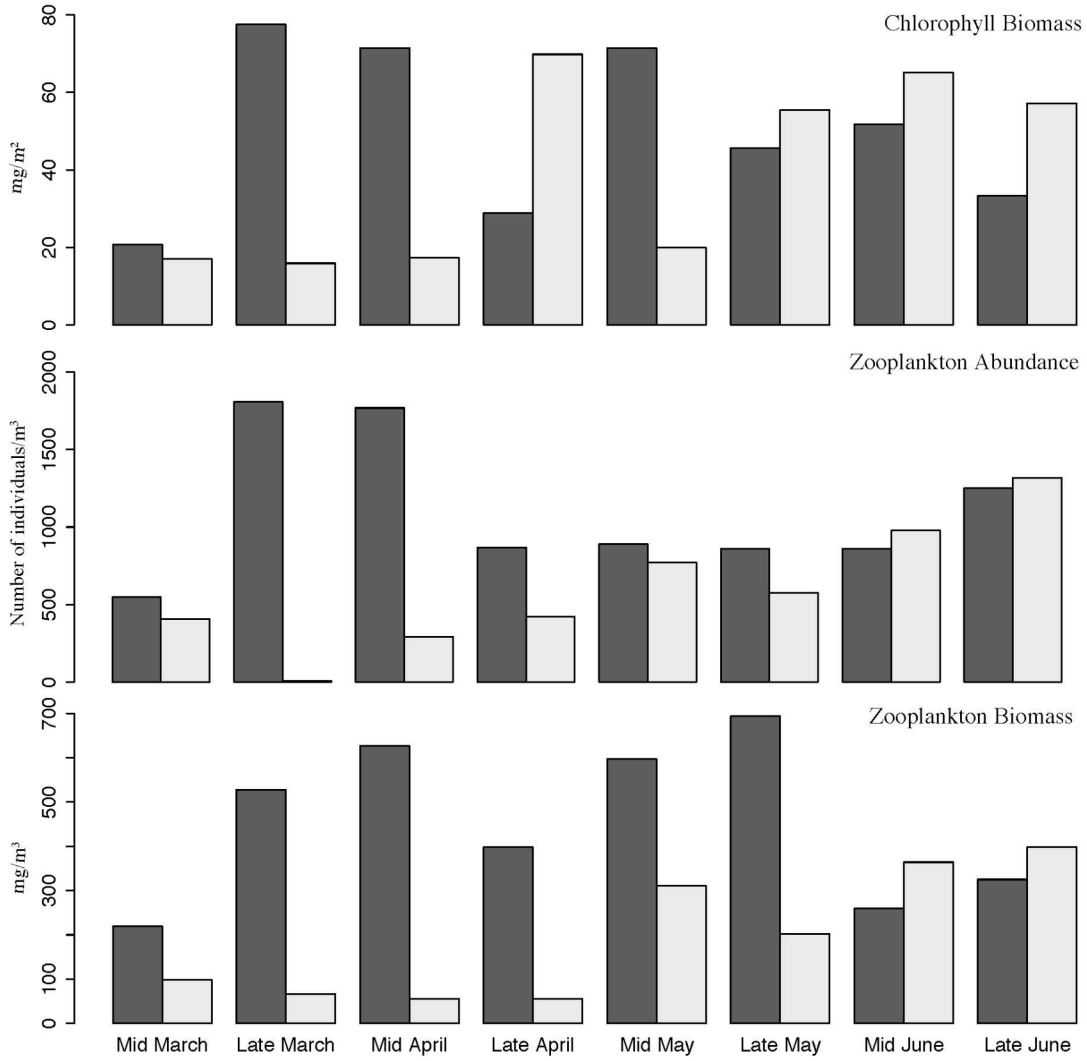
The similarity matrix was also summarized with a NMDS ordination. Samples were ordered in a multidimensional space so that the distance between samples was comparable to the ranks of the similarity matrix; points closer together have a more similar species composition. The goodness of fit of the MDS distance measure with the rank similarities is computed by a stress value, and it increases with each addition of an ordination axis. If the stress value is greater than about 0.2, the MDS is a poor representation of the sample similarities, and another axis is required to explain the remaining variability (Clarke 1993). All the multivariate computations were performed using the software PRIMER.

Results

There were interannual differences in the temporal trends of zooplankton biomass, and in the apparent relationship between chlorophyll a and zooplankton biomasses. In 2007, the seasonal increase in zooplankton biomass was delayed, happening in mid May, a month later than in 2006 (Fig 20). Indeed, the interaction effect of year*cruise was significant ($p < 0.0001$), implying that differences in biomass between the two years were not consistent over time. Both years were characterized by a two-month long period of high zooplankton biomass marked by a slight drop after the initial increase (Fig. 20). However, the duration of the 2007 zooplankton biomass peak cannot be well resolved, as biomass had not yet declined at the end of the sampling period. Not only was the seasonal cycle in biomass delayed in 2007; total zooplankton biomass was also

significantly lower (year effect $p = 0.0002$). However, in May and June, when juvenile sockeye salmon would have been present in the inlet, zooplankton biomass was higher in 2006 than in 2007 in May only ($p = 0.0030$). In 2006, zooplankton biomass seasonal dynamics appeared to closely match phytoplankton dynamics with a first increase timed with the spring phytoplankton bloom in mid March, a slight drop during phytoplankton depletion in late April, and a second increase in mid May corresponding to the second peak in chlorophyll biomass (Fig. 20). By contrast, in 2007, zooplankton biomass did not parallel fluctuations in chlorophyll as closely, and the increase in biomass occurred in mid May when chlorophyll was low following the chlorophyll peak in late April (Fig. 20). A slight drop in biomass was observed at a lag of two weeks instead of a month after the initial biomass increase, and, unlike in 2006, this did not correspond to low chlorophyll abundance (Fig. 20).

Figure 20 Mean chlorophyll biomass, zooplankton abundance, and zooplankton biomass and at the eight sampling cruises in Rivers Inlet in 2006 (dark grey bars) and in 2007 (light grey bars). In each year, each variable was an averaged over the eight sampling stations. The standard errors (SE) of the least square means for the year*cruise effects are 1.2 mg m^{-2}, 1.3 individuals m^{-3}, 1.3 mg m^{-3} for chlorophyll, zooplankton abundance, and zooplankton biomass respectively. In 2007 only one site (Geetla) was sampled for zooplankton in late March, and only two were sampled in late April (Geetla and Dawsons) and the SE for these cruises are 2.8 and 2.0 individuals m^{-3} for abundance and 2.7 and 2.0 mg m^{-3} for biomass.



Spatial differences in zooplankton biomass were observed between stations in May and June, and they reflected spatial variation in chlorophyll *a* and salinity. Zooplankton biomass was consistently higher at Bosquet than at Geetla, Kilbella, and Ralph (site effect $p = 0.0053$), with the other sites being

intermediate. This difference was consistent between cruises as there was no significant cruise*site interaction (*p = 0.6394*). The year*site interaction was also not statistically significant (*p = 0.0930*), with Bosquet being a productive site in both years. Thus, while differences between-years were substantial at some sites, they were not statistically significant. At Bosquet, zooplankton biomass decreased from 1247 mg m^{-3} in 2006 to 394 mg m^{-3} in 2007, at the Mouth it fell from 439 to 249 mg m^{-3} and at Ralph from 360 to 152 mg m^{-3}. Biomass at Wannock increased from 178 mg m^{-3} to 502 mg m^{-3}, and it remained comparable at the other sites (Fig. 21). Spatial differences in zooplankton biomass mirrored differences in chlorophyll biomass, with Bosquet showing significantly higher zooplankton and chlorophyll biomass than Geetla and Kilbella (Fig. 21). Additionally, the only sites that showed a decrease in zooplankton biomass from 2006 to 2007 were the same sites that showed a significant decrease in surface salinity between the two years (Fig. 21). Indeed, when chlorophyll and salinity are included as effects into the model describing zooplankton biomass variation, the site effect is no longer significant (*p = 0.1247*). However, salinity and chlorophyll effects explained only 21% of the total variance in zooplankton biomass (Table 5).

Figure 21 Mean surface salinity, chlorophyll biomass, zooplankton abundance, and zooplankton biomass at the eight sampling stations in Rivers Inlet in 2006 (dark grey bars) and in 2007 (light grey bars). In each year, each variable was averaged over the four sampling cruises in May and June. The standard errors (SE) of the least square means for the year*site effects are 1.2 ppt, 1.3 mg m^{-2}, 1.5 individuals m^{-3}, and 1.5 mg m^{-3} for salinity, chlorophyll, zooplankton abundance, and zooplankton biomass respectively.

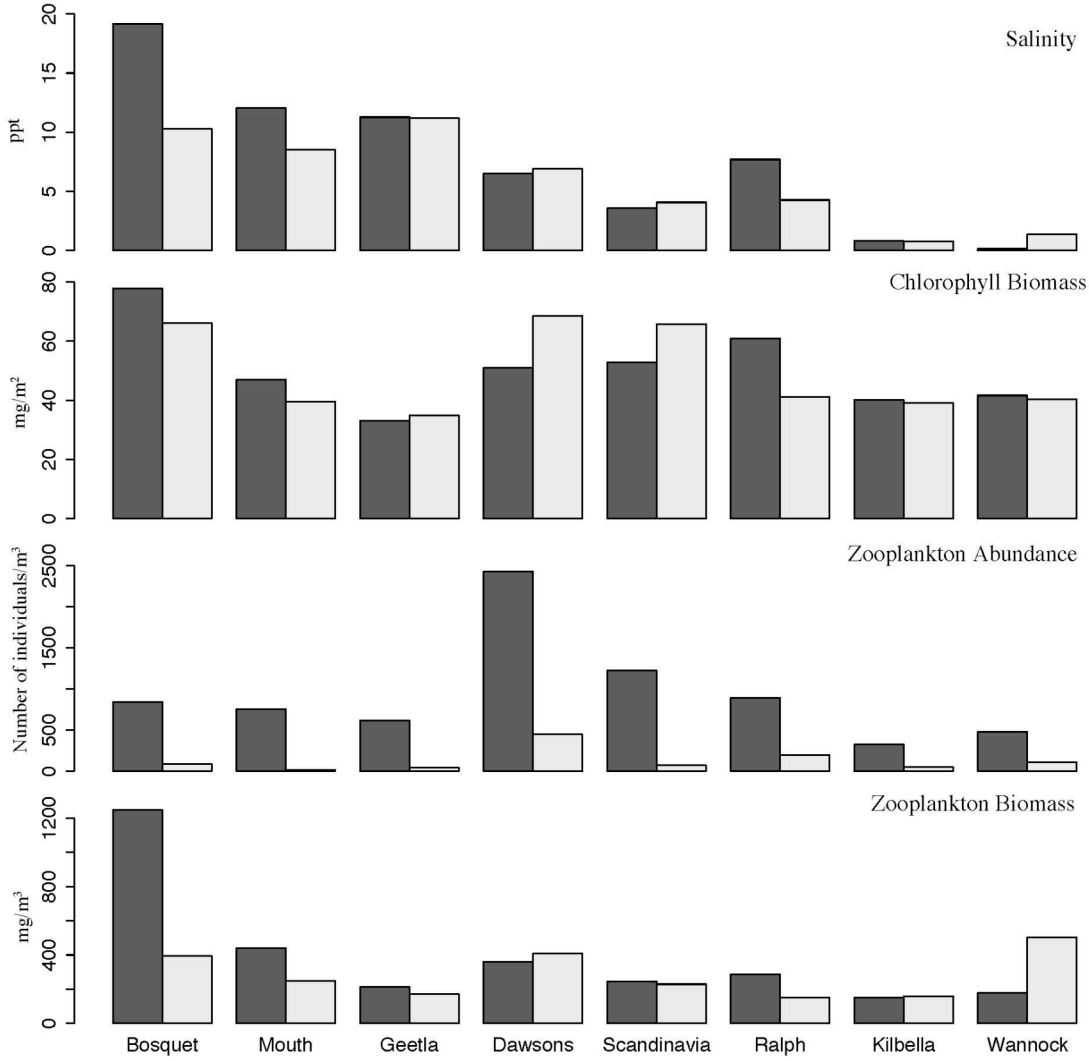


Table 5 Model summary of the ANOVA of zooplankton biomass sampled in May and June with salinity and chlorophyll as main effects.

	Salinity	Chlorophyll	Model
DF			62
F statistic			8.207
R^2			0.21
p-value	0.0108	0.0373	

The temporal trend in zooplankton abundance and its apparent association with chlorophyll *a* concentrations differed between years. As with zooplankton biomass, zooplankton abundance in 2006 peaked earlier in late March and mid April, during the spring phytoplankton bloom (Fig. 20). It then remained at intermediate levels until the end of the sampling season (Fig. 20). In 2007, abundance was low prior to the spring bloom, and increased in mid May. However, while in 2006 the peak in abundance lasted about two weeks and coincided with the spring bloom, in 2007 it was not well defined, did not coincide with the spring bloom in late April, and was comparable to abundances later in the season (Fig. 20). Thus, in 2007, zooplankton abundance was lower over the entire seasonal cycle as compared to 2006. Total zooplankton abundance was significantly higher in 2006 than in 2007 (year effect $p < 0.0001$). However, in May and June, zooplankton abundance showed no significant differences between years (year effect $p = 0.1730$, cruise*year effect $p = 0.5603$) (Fig. 20).

Spatial differences in zooplankton abundance were observed in the inlet in May and June, but unlike for zooplankton biomass, spatial differences in zooplankton abundance did not parallel spatial differences in chlorophyll or in

salinity. The Dawsons and Wannock sites showed higher abundances than the Mouth and Geetla sites ($p = 0.0006$) (Fig. 21). These differences were consistent between cruises ($p = 0.8678$) and years ($p = 0.5603$). Adding chlorophyll or salinity into the linear model of zooplankton abundance ($p = 0.0863$ and $p = 0.5564$, respectively) did not decrease the variance in abundance explained by the site effect, which remained significant ($p = 0.0125$).

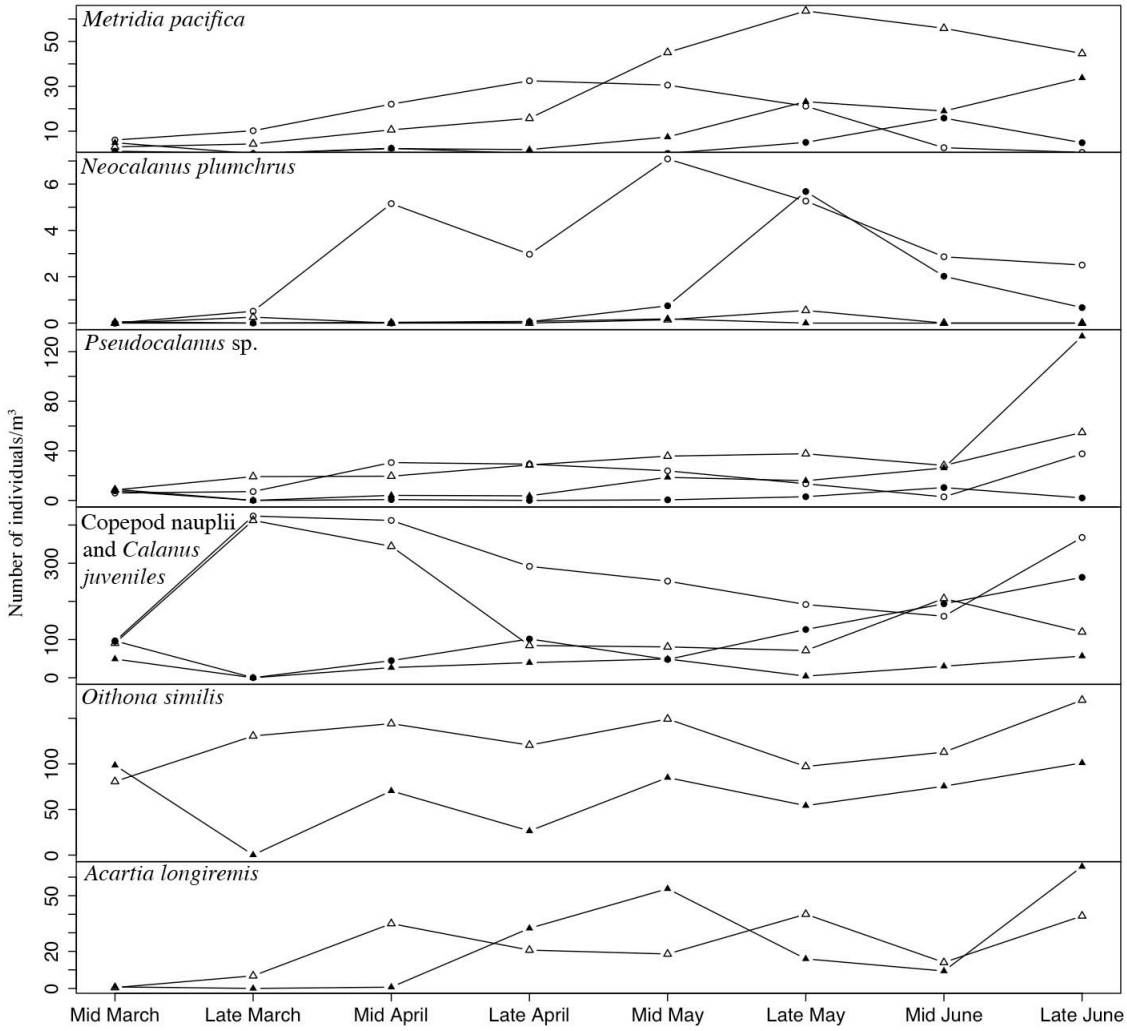
Interannual differences in the abundance and the temporal dynamics of copepods, the most abundant taxa in both years (Table 6), were detected. Cyclopoids were the most abundant order of copepod adults, with 14,277 individuals m^{-3} in 2006 and 8,719 individuals m^{-3} in 2007 (Table 6). *Oithona similis* was the most abundant cyclopoid; total adult abundance was 8,041 individuals m^{-3} in 2006 and 3,775 individuals m^{-3} in 2007. *O. similis* showed similar temporal dynamics during both years, albeit with lower abundances observed in 2007 (Fig. 22). Adult calanoid copepods were also very abundant with 9043 and 6213 individuals m^{-3} in 2006 and 2007 respectively (Table 6). *Metridia pacifica*, *Acartia longiremis*, and *Pseudocalanus* sp. were the most abundant adult calanoids. In 2006, *M. pacifica*, the most common calanoid copepod in the inlet, reached peak adult densities in late May. This occurred after the peak in *M. pacifica* juvenile abundance in late April, and two months after the peak in phytoplankton when abundance of copepod nauplii was highest (Fig. 22).

Table 6 Total abundance (individuals m^{-3}) over all the hauls collected in 2006 and in 2007. Taxa shown are those with a relative abundance > 2%. Species in bold had > 2% in 2007, but not in 2006, and species in bold were the opposite. Total abundance for each of the main copepod orders is also shown.

	2006	2007
Juvenile calanoida	12,853	4,983
Copepod nauplii	11,289	1,733
Oithona similis	8,041	3,775
Barnacle nauplii	4,668	2,629
Oithona sp.	3,258	2,839
Eggs	2,646	1,303
Oikopleura sp.	2,551	39
Unknown Cyclopoid sp.	2,348	1,911
Metridia pacifica	1,943	717
Pseudocalanus sp.	1,859	1,634
Ostracods	1,488	956
Acartia longiremis	1,397	1,181
Cladocera Evadne	883	2,540
***Microsetella* sp.**	627	734
***Acartia* sp.**	299	758
Barnacle cyprids	172	1,035
Calanoids	9,043	6,213
Cyclopoids	14,278	8,719
Harpacticoids	627	734

In 2007, the peak in juvenile *M. pacifica* densities was delayed, occurring in mid June, and adult abundances were still increasing during the last sampling cruise (Fig. 22). Furthermore, both juvenile and adult *M. pacifica* abundances were lower during the 2007 sampling season. Unlike *M. pacifica,* peak abundances of *A. longiremis* were higher in 2007, coinciding with the chlorophyll peak in late April and mid May (Fig. 22). In both years, abundances peaked again in late June (Fig. 22). By contrast, as *M. pacifica,* adults of *Pseudocalanus* sp. peaked in late May 2006, but also showed a higher later peak in late June (Fig. 22).

Figure 22 Mean abundance of selected copepod species in Rivers Inlet from March to June. Abundance of adults (triangles) and juveniles (circles) for each of the eight Rivers Inlet sampling cruises in 2006 (open symbols) and in 2007 (black symbols) was averaged over the eight sampling stations along the inlet. Copepod nauplii are represented by triangles. Note that in 2007 only one site (Geetla) was sampled during the second cruise (Late March).



These two peaks might be due to two different *Pseudocalanus* species increasing at different times. In 2007 the late May peak is absent, but June adult abundances were higher than in 2006 (Fig. 22). Abundances of *Pseudocalanus* sp. juveniles were lower throughout the season in 2007 and peaked later, in mid June 2007 instead of mid April as in 2006 (Fig. 22). Densities of juveniles of *Neocalanus plumchrus*, a species rich in lipids, were also lower and delayed in

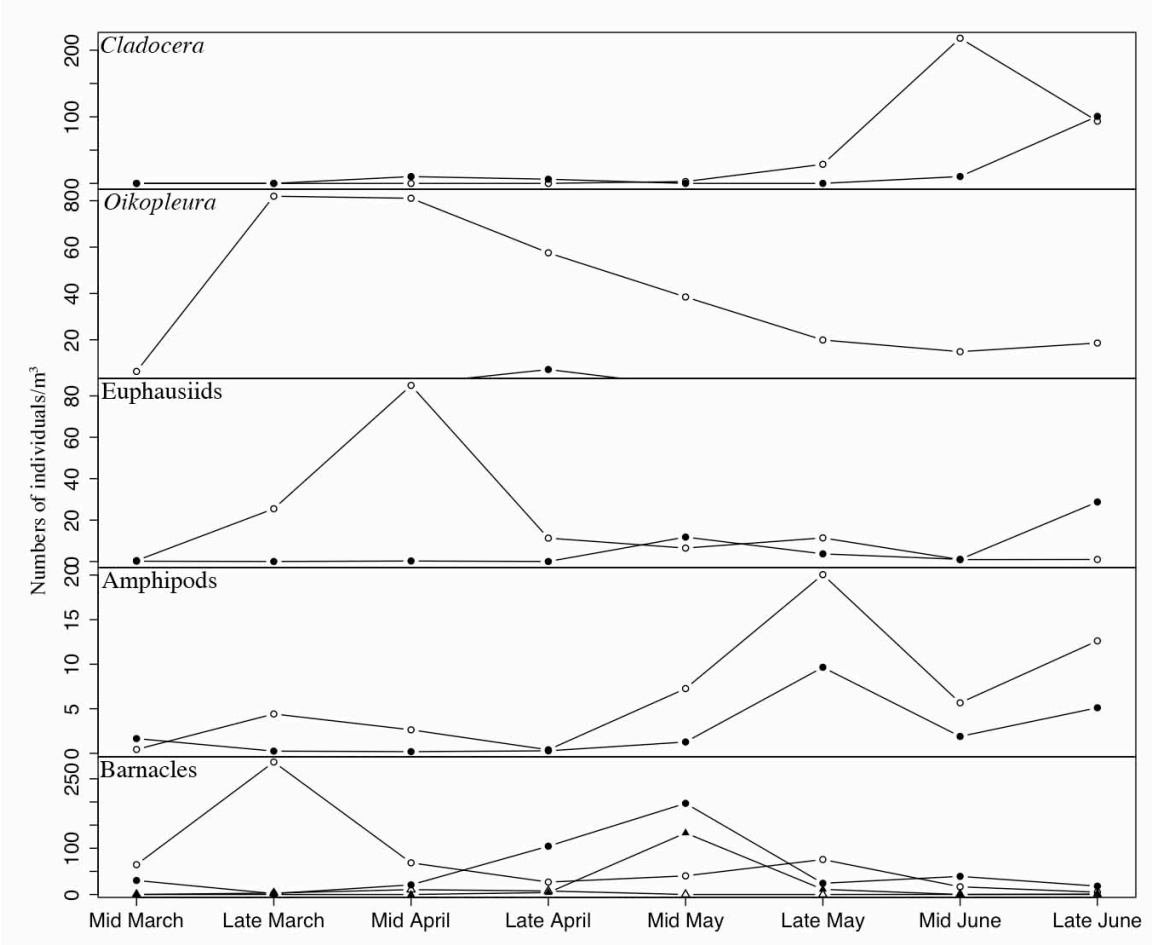
2007 (Fig.22). Adult specimens were not common in our samples (Fig. 22). *Calanus* juveniles were the most abundant group overall, showing total densities of 12,853 individuals m^{-3} in 2006 and of 4,982 individuals m^{-3} in 2007 (Table 6). In 2007, numbers of copepod nauplii and *Calanus* juveniles were lower and peaked later in late April during the phytoplankton bloom (Fig. 22). A second peak in *Calanus* juveniles and copepod nauplii was observed later in June in both years, possibly signifying a second reproductive event for some copepod species (Fig. 22). Harpacticoid copepods of the genus *Microsetella* showed moderate abundances in both years, but unlike most of the species mentioned above, did not show lower abundances in 2007 (Table 6).

Differences in the timing of peak abundance between adult copepods and the smaller, more numerous copepod nauplii and juveniles are reflected in the contrasting temporal patterns in zooplankton abundance and biomass. In 2006, zooplankton biomass increased with abundance, but remained high until late May, even if abundance was decreasing (Fig. 20). The May increase in biomass in the absence of an increase in abundance appears to be due to the seasonal development of the larger calanoid copepods species, such as *M. pacifica*, which developed from nauplii to heavier adults.

Abundances of non-copepod taxa varied between years. Barnacle nauplii were most abundant (Table 6) and their densities peaked during the phytoplankton spring bloom in both years (Fig. 23). By contrast, barnacle cyprids were more abundant in 2007 (Fig. 23). *Oikopleura* sp. was more abundant in 2006 (Table 6), and in both years abundances peaked during the spring

phytoplankton bloom (Fig. 23). The cladoceran *Evadne* was more abundant in 2007 (Table 6) and its temporal dynamics were similar in both years, peaking in late June (Fig. 23). Amphipods were more abundant in 2006 and their temporal dynamics were also quite comparable between years (Fig. 23).

Figure 23 Mean abundance of selected non-copepod zooplankton taxa in Rivers Inlet from March to June. Abundance for each of the eight Rivers Inlet sampling cruises in 2006 (open symbols) and in 2007 (black symbols) was averaged over the eight sampling stations along the inlet. Barnacle cyprids are represented by triangles, while abundances of barnacle nauplii are shown as circles. Note that in 2007 only one site (Geetla) was sampled during the second cruise (Late March).



On the other hand, abundances of euphausiid larvae were higher and peaked earlier in 2006 (Fig. 23). In 2007, a later increase in the abundance of larvae was observed in June (Fig. 23). A list of all the species collected and of their total abundances is available in Appendix 4.

Cluster analysis identified five outlier samples, which were excluded from the final analysis, with their own, distinct species composition. These were samples collected at Wannock and Kilbella during the 2006 second and fourth cruise, very poor in species diversity and abundance, with only some copepod and barnacle nauplii and cyclopoids, and sharing only 20% similarity with the other samples in the inlet. Two other outliers were samples from Geetla on the second cruise and from the Mouth on the third cruise in 2007, which showed extremely low abundances across all taxa, and shared less than 10% similarity with the remaining samples. Finally, the sample from Wannock for the fourth 2006 cruise formed a cluster on its own; its species composition was similar to that in cluster 4, but at lower abundances and with no gastropods. These samples were treated as outliers and not included in the final dendrogram.

Cluster analysis of the remaining samples identified 8 clusters with similar zooplankton species composition: Cluster 1, the early season group, Cluster 2, the 2007 bloom community, Cluster 3, the late season, inner 2006 community, Cluster 4, the 2006 Dawsons community, Cluster 5, the *Metridia* community, Cluster 5a, the 2007 Wannock community, Cluster 6, the late season, outer 2007 community, and Cluster 7, the low abundance community (Fig. 24).

The distribution of these clusters changed over time, space and between years. Clusters are described below in order of seasonal appearance. Cluster 7, a very poor community dominated by adult *Metridi*a sp. and barnacle nauplii, found in the 2007 pre spring phytoplankton bloom period, was quite distinct, sharing only 35% similarity with the other clusters (Table 7, Fig. 24). At the outer sites of Geetla, the Mouth and Bosquet, this cluster, with the lowest zooplankton density and abundance, persisted even after the phytoplankton bloom in late April (Table 7).