EXAMINING THE ENVIRONMENTAL FORCING OF ZOOPLANKTON POPULATION DYNAMICS: A LIFE HISTORY APPROACH USING DATA FROM A BRITISH COLUMBIA FJORD

by

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Abstract

Zooplankton play a pivotal role in marine ecosystem by cycling carbon and energy up the food chain. The species composition of a zooplankton community can influence such energy transfer pathways in a marine ecosystem. For example, when large calanoid copepods dominate a food web, more of the energy produced by phytoplankton is transferred up the food chain and high biomass of large, lipid-rich calanoid copepods or euphausiids has been associated with higher recruitment of upper trophic levels compared to a system dominated by smaller copepod species. Thus, understanding how environmental forcing drives fluctuations in zooplankton community composition is essential to assessing how the structure of marine ecosystems may vary in the future. However, knowledge of what zooplankton life history strategies or functional traits (e.g. feeding guild) make some species more successful under specific environmental conditions remains limited. Here, using three years of field data on zooplankton abundance, biomass, and species composition from a fjord in British Columbia, Canada, I identified the zooplankton seasonal succession cycle and the controlling effects of different environmental forcing factors on the recruitment success of various zooplankton functional traits. Zooplankton succession was delayed when the spring bloom was late. Furthermore, herbivorous, ontogenetically migrating copepods with a short reproductive season, such as *Calanus marshallae* and *Eucalanus bungii*, had reduced recruitment when the spring bloom was delayed or in years of high spring temperature, as compared to omnivorous copepods with a long reproductive season. A population dynamics model was employed to determine the environmental drivers of the observed temporal variability of *C. marshallae* and *E. bungii*. Interannual differences in mortality and advection
drove the observed change in the recruitment of the two copepod species. High mortality was associated with conditions of low chlorophyll biomass and high temperatures. I suggest that the success of these copepod species may depend on the presence of a low predation-high chlorophyll window in early spring.
Preface

All the research chapters in this thesis were prepared for publication in peer-reviewed scientific journals.


I participated in most of the sampling cruises and I am responsible for zooplankton taxonomic analysis, the majority of data analysis and writing of this manuscript. Dr. B. Hunt, Dr. E. Pakhomov, and Dr. D. Mackas provided extensive feedback on data analysis. Dr. B. Hunt and Dr. E. Pakhomov also helped with field data collection, and contributed editorial feedback and invaluable comments on all drafts prior to publication.

A version of Chapter 3 has been submitted for publication. The co-authors are D. Tommasi (first author), Dr. B. Hunt, Dr. S. Allen, and Dr. E. Pakhomov. Dr. S. Allen provided extensive feedback on the coupling of hydrodynamic model outputs to zooplankton data, as well as on sensitivity analysis. She also contributed editorial feedback. Dr. B. Hunt and Dr. E. Pakhomov provided feedback on the analysis of vertical zooplankton data, helped with field data collection, and contributed editorial feedback to numerous drafts prior to submission. I participated in most of the sampling cruises and I am responsible for most of the writing and data analysis and for the zooplankton taxonomic analysis.

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# Table of Contents

Abstract............................................................................................................................................. ii
Preface................................................................................................................................................ iv
Table of Contents ............................................................................................................................. vi
List of Tables ........................................................................................................................................ xii
List of Figures ..................................................................................................................................... xv
Acknowledgements ........................................................................................................................... xxv
Dedication ........................................................................................................................................... xxvii

Chapter 1: Introduction ...................................................................................................................... 1
  1.1 Motivation ................................................................................................................................... 1
  1.2 Background ............................................................................................................................... 3
  1.3 Thesis main objectives .............................................................................................................. 7
  1.4 Thesis structure ........................................................................................................................ 7

Chapter 2: Mesozooplankton community seasonal succession and its drivers: insights from a British Columbia, Canada, fjord ................................................................................................................................................. 11
  2.1 Introduction .............................................................................................................................. 12
  2.2 Methods .................................................................................................................................. 15
    2.2.1 Study area ......................................................................................................................... 15
    2.2.2 Field sampling ................................................................................................................ 17
    2.2.3 Zooplankton taxonomic analysis .................................................................................... 20
    2.2.4 Data analysis .................................................................................................................. 21
  2.3 Results ...................................................................................................................................... 27
2.3.1 Environmental parameters ................................................................. 27
2.3.2 Zooplankton abundance ................................................................. 30
2.3.3 Zooplankton biomass ........................................................................ 36
2.4 Discussion .............................................................................................. 42
2.4.1 Pattern of zooplankton succession ...................................................... 42
2.4.2 Environmental forcing of zooplankton succession .............................. 43
2.4.3 Spatial variation in zooplankton composition ...................................... 48
2.4.4 Implications for higher trophic levels ............................................... 53
2.5 Conclusions .......................................................................................... 53
2.6 Figures .................................................................................................. 55
2.7 Tables ................................................................................................... 72

Chapter 3: Variability in the vertical distribution and advective transport of eight mesozooplankton taxa in Rivers Inlet, British Columbia, Canada, in spring .................. 77

3.1 Introduction .......................................................................................... 78
3.2 Methods ................................................................................................ 82
3.2.1 Field sampling .................................................................................. 82
3.2.2 Zooplankton taxonomic analysis ...................................................... 83
3.2.3 Data analysis ..................................................................................... 83
3.2.3.1 Water velocities ........................................................................... 84
3.2.3.2 Zooplankton vertical distribution ............................................... 85
3.2.3.3 Zooplankton daily exchange rates .............................................. 86
3.2.3.4 Total advective transport ............................................................ 87
3.3 Results ................................................................................................ 89
3.3.1 Water velocities ........................................................................................................ 89
3.3.2 Zooplankton vertical distribution ............................................................................. 90
3.3.3 Daily exchange rates ................................................................................................ 95
  3.3.3.1 Sensitivity to bottom layer depth distribution .................................................. 102
3.3.4 Potential importance of advection to population size ......................................... 103
3.4 Discussion .................................................................................................................. 107
  3.4.1 Water velocities ..................................................................................................... 107
3.4.2 Zooplankton vertical distribution ........................................................................... 108
3.4.3 Daily exchange rates .............................................................................................. 112
  3.4.4 Importance of advection relative to local processes ........................................... 115
3.5 Conclusions ................................................................................................................ 119
3.6 Figures .......................................................................................................................... 121
3.7 Tables .......................................................................................................................... 133

Chapter 4: Differential response of distinct copepod life history types to spring environmental forcing ................................................................................................................................. 134

4.1 Introduction .................................................................................................................. 134
4.2 Methods ....................................................................................................................... 140
  4.2.1 Zooplankton taxonomic analysis ......................................................................... 140
  4.2.2 Determination of development times ................................................................. 141
  4.2.3 Determination of egg production rates .............................................................. 143
4.3 Results .......................................................................................................................... 145
  4.3.1 Hydrography ...................................................................................................... 145
  4.3.2 Modeled development times .............................................................................. 145

viii
4.3.3 Phenology and population structure................................................................. 147

4.3.3.1 Paraeuchaeta elongata ..................................................................................... 147

4.3.3.2 Metridia pacifica ............................................................................................. 147

4.3.3.3 Eucalanus bungii ............................................................................................. 149

4.3.3.4 Calanus marshallae .......................................................................................... 150

4.3.3.5 Acartia longiremis .......................................................................................... 151

4.3.4 Modeled egg production rates............................................................................. 152

4.4 Discussion................................................................................................................ 154

4.4.1 Life history strategies............................................................................................ 154

4.4.2 Relationship between phenology, overwintering strategy, and spring environmental forcing.................................................................................................................. 157

4.4.3 Relationship between recruitment success, overwintering strategy and spring environmental forcing.................................................................................................................. 162

4.4.4 Implications for upper trophic levels.................................................................... 164

4.5 Conclusions................................................................................................................. 166

4.6 Figures....................................................................................................................... 168

4.7 Tables......................................................................................................................... 183

Chapter  5: Investigating the environmental drivers of Calanus marshallae and Eucalanus bungii population dynamics: a modeling approach.................................................................185

5.1 Introduction.............................................................................................................. 185

5.2 Methods..................................................................................................................... 190

5.3 Results....................................................................................................................... 194

5.3.1 Eucalanus bungii ................................................................................................. 194
5.3.1.1 Refined parameterization of the fraction of mature, spawning females ........ 194
5.3.1.2 Comparison of simulated and observed abundances ............................ 197
5.3.1.3 Sensitivity analysis.................................................................................. 198
  5.3.1.3.1 Initial abundance.................................................................................. 198
  5.3.1.3.2 Temperature....................................................................................... 199
  5.3.1.3.3 Chlorophyll ...................................................................................... 199
  5.3.1.3.4 Mortality ......................................................................................... 200
  5.3.1.3.5 Advection .......................................................................................... 201
5.3.2 Calanus marshallae .................................................................................... 202
  5.3.2.1 Refined parameterization of the fraction of mature, spawning females .... 202
  5.3.2.2 Comparison of simulated and observed abundances ............................ 205
  5.3.2.3 Sensitivity analysis.................................................................................. 208
    5.3.2.3.1 Initial abundance.................................................................................. 209
    5.3.2.3.2 Temperature....................................................................................... 209
    5.3.2.3.3 Chlorophyll ...................................................................................... 209
    5.3.2.3.4 Mortality ......................................................................................... 210
    5.3.2.3.5 Advection .......................................................................................... 211
5.4 Discussion........................................................................................................ 212
  5.4.1 Model caveats ............................................................................................ 212
  5.4.2 Reproductive strategies of Eucalanus bungii and Calanus marshallae ........ 214
  5.4.3 Effect of differential survival on recruitment ............................................ 218
  5.4.4 Effect of advection on recruitment ............................................................ 220
  5.4.5 Effect of initial conditions on recruitment ................................................ 221
5.5 Conclusions .......................................................................................................................... 222
5.6 Figures ................................................................................................................................. 224
5.7 Tables .................................................................................................................................. 242

Chapter 6: Conclusion .............................................................................................................. 245

6.1 Summary ............................................................................................................................... 245
6.2 Implications and future work ............................................................................................... 250

Bibliography ............................................................................................................................. 259

Appendices ............................................................................................................................... 298

Appendix A .................................................................................................................................. 298

A.1 Rivers Inlet sockeye salmon returns .................................................................................. 298

A.2 Comparison of 2008 and 2009 sockeye salmon survival.................................................. 299

A.3 Generalized additive model of sockeye salmon survival................................................... 300

Appendix B .................................................................................................................................. 305

Appendix C .................................................................................................................................. 306

Appendix D .................................................................................................................................. 308

Appendix E .................................................................................................................................. 309

Appendix F .................................................................................................................................. 310

Appendix G .................................................................................................................................. 311

Appendix H .................................................................................................................................. 312
List of Tables

Table 2.1 Division of indicator species by feeding mode......................................................... 73
Table 2.2 List of environmental input variables used in the data analysis. ............................ 73
Table 2.3 Distribution of abundance-based clusters over space and time. Empty cells were outliers not included in cluster analysis and no samples were collected during the site/cruise combinations marked by NA. ........................................................................................................................................ 74
Table 2.4 Combination of the environmental variables yielding the best match of biotic and abiotic similarity matrices as measured by Spearman rank correlation, r. IWS is the inflow wind speed, S is daily 5 m salinity, TSB is the time since the spring bloom, and WRF is the Wannock River flow. ............................................................................................................................... 74
Table 2.5 Pearson correlation between each of the 3D MDS axis and each environmental variable selected by the abundance based-based BIO-ENV analysis. IWS is the inflow wind speed, S is daily 5 m salinity. TSB is the time since the spring bloom, and WRF is the Wannock River flow. Cluster means for the binned variables (e.g. S2) were divided by the length of the bin (days) and are presented as average daily values. Statistically significant correlations (p-value <0.05) are highlighted in bold............................................................... 75
Table 2.6 Abundance-based cluster means of each environmental variable selected by the abundance-based BIO-ENV analysis. IWS is the inflow wind speed, S is daily 5 m salinity, TSB is the time since the spring bloom, and WRF is the Wannock River flow. Cluster means for the binned variables (e.g. S2) were divided by the length of the bin (days) and are presented as average daily values. .................................................................................................................. 75
Table 2.7 Distribution of biomass-based clusters over space and time. Empty cells were outliers not included in cluster analysis and no samples were collected during the site/cruise combinations marked by NA. 76

Table 2.8 Biomass-based cluster means of each environmental variable selected by the biomass-based BIO-ENV analysis. IWS is the inflow wind speed, S is daily 5 m salinity, TSB is the time since the spring bloom, and WRF is the Wannock River flow. Cluster means for the binned variables (e.g. S5) were divided by the length of the bin (days) and are presented as average daily values. 76

Table 3.1 Ratio of abundance at DFO2 over the average inlet abundance for each cruise, taxa, and stage. A ratio of 4.0 implies that all the observed individuals were found at DFO2. 133

Table 4.1 Species and stage specific Belehrádek parameters used in the calculation of development times. Literature sources of the experimental data employed to derive the parameters are highlighted. 183

Table 4.2 Egg production rate equations derived from the literature. 184

Table 4.3 Species and stage specific development times and stage durations. Development times represent the days taken to develop to the specified stage and were computed from the species and stage-specific Belehrádek parameters listed in Table 4.1. Stage durations were computed from the difference of two consecutive development times. 184

Table 5.1 Timing and size of peak abundance of the C5 copepodite cohort as simulated by model runs for each species in each year. 242

Table 5.2 List of sensitivity test runs for Eucalanus bungii. The resulting timing and size of peak abundance of the C5 copepodite cohort was compared to that in the base run. 243
Table 5.3 List of sensitivity test runs for *Calanus marshallae*. The resulting timing and size of peak abundance of the C5 copepodite cohort was compared to that in the base run.
List of Figures

Figure 2.1 Map of Rivers Inlet showing sampling stations. The two insets show a regional map and a close up of the Florence Daily and Laska weather station locations........................................... 55

Figure 2.2 Along inlet temperature depth profiles collected on each fortnightly (2008 and 2009) and monthly (2010) cruise. .................................................................................................................................................. 56

Figure 2.3 Along inlet density depth profiles collected on each fortnightly (2008 and 2009) and monthly (2010) cruise. .................................................................................................................................................. 57

Figure 2.4 Along inlet salinity depth profiles collected on each fortnightly (2008 and 2009) and monthly (2010) cruise. .................................................................................................................................................. 58

Figure 2.5 Daily timeseries of Wannock River flow (daily average) from March 8 to June 18. . 59

Figure 2.6 Feather plots of the daily mean wind velocity vectors with components $u$ (x component) and $v$ (y component) as arrows emanating from equally spaced points along a horizontal axis. Data shown is from March 8 to June 18 in 2008, 2009, and 2010. Shaded boxes indicate periods of missing data.................................................................................................................................................. 60

Figure 2.7 Along inlet chlorophyll $a$ depth profiles collected on each fortnightly (2008 and 2009) and monthly (2010) cruise. .................................................................................................................................................. 61

Figure 2.8 Daily time series of integrated chlorophyll $a$ (0 to 20 m) at the Florence Daily station from March 8 to June 18.......................................................................................................................... 62

Figure 2.9 Dendrogram of group-averaged clustering from similarities of abundance.
Significantly different ($\alpha=0.05$) clusters are marked by a *.......................................................... 63

Figure 2.10 Average zooplankton abundance by cluster showing major taxonomic group composition (left panel), and for copepod species only (right panel)......................................................... 64
Figure 2.11 Representation of taxa with an IndVal of ≥ 25 for each of the sample groupings at each hierarchical level of the abundance-based dendrogram. If a cluster did not have a taxon with an IndVal ≥ 25, the taxon with the highest IndVal as compared to the other cluster at the same hierarchical level is presented. The highest IndVal across all clusters for each taxon is highlighted in bold. 

Figure 2.12 Two-dimensional MDS of Bray-Curtis similarities of abundance. Each sample is labeled with the cluster it belongs to.

Figure 2.13 Dendrogram of group-averaged clustering from similarities of biomass. Significantly different (α=0.05) clusters are marked by a *. 

Figure 2.14 Two-dimensional MDS of Bray-Curtis similarities of biomass. Each sample is labeled with the cluster it belongs to.

Figure 2.15 Representation of taxa with an IndVal of ≥ 25 for each of the sample groupings at each hierarchical level of the biomass-based dendrogram. If a cluster did not have a taxon with an IndVal ≥ 25, the taxon with the highest IndVal as compared to the other cluster at the same hierarchical level is presented. The highest IndVal across all clusters for each taxon is highlighted in bold.

Figure 2.16 Average zooplankton biomass by cluster showing major taxonomic group composition (left panel), and for copepod species only (right panel).

Figure 2.17 Conceptual model of zooplankton functional groups succession in Rivers Inlet.

Figure 3.1 Contours of daily profiles of water velocities at DFO2 from March 20 to June 28 2010 in the entire water column (a) and the top 30 m only (b). Red indicates an inflow, blue an outflow. The vertical resolution of the daily outputted model velocities is depicted by the column of *. (c) Average water daily exchange rates (flow at DFO2/inlet volume) for the top 10 m...
Figure 3.2 Grey bars represent the vertical distribution of cladocerans (a), larvaceans (b) and copepod eggs (c) by cruise and time of day. Weighted mean depth (WMD) ±SE is shown as a solid red line bounded by two dotted red lines.

Figure 3.3 Grey bars represent the vertical distribution of *Acartia longiremis* by cruise and time of day for different stages. Weighted mean depth (WMD) ±SE is shown as a solid red line bounded by two dotted red lines.

Figure 3.4 Grey bars represent the vertical distribution of *Calanus* spp. by cruise and time of day for different stages. Weighted mean depth (WMD) ±SE is shown as a solid red line bounded by two dotted red lines.

Figure 3.5 Grey bars represent the vertical distribution of *Eucalanus bungii* by cruise and time of day for different stages. Weighted mean depth (WMD) ±SE is shown as a solid red line bounded by two dotted red lines.

Figure 3.6 Grey bars represent the vertical distribution of *Metridia pacifica* by cruise and time of day for different stages. Weighted mean depth (WMD) ±SE is shown as a solid red line bounded by two dotted red lines.

Figure 3.7 Grey bars represent the vertical distribution of *Paraeuchaeta elongata* by cruise and time of day for different stages. Weighted mean depth (WMD) ±SE is shown as a solid red line bounded by two dotted red lines.

Figure 3.8 a) Mean daily exchange rate (DER) per taxa. Error bars represent standard errors. b) Boxplot of DER per taxa showing the median (horizontal line) and the 25th (upper hinge) and 75th (lower hinge) percentiles. The upper whisker extends from the hinge to the highest value that is within 1.5 * inter-quartile range (IQR) of the hinge. The lower whisker extends from the hinge to the lowest value within 1.5 * IQR of the hinge. AL= *Acartia longiremis*, MP= *Metridia*
pacific, CM=Calanus marshallae, EB=Eucalanus bungii, PE=Paraeuchaeta elongata,

CL=Cladocerans, EG=Copepod eggs, LR=Larvaceans. ................................................................. 128

Figure 3.9 Daily exchange rate (DER) per taxa and stage. Positive DERs (grey) are inflows,
negative (black) outflows. 0 DERs are also coloured in grey. Note that Calanus marshallae C1-
C3 are Calanidae C1-C3 individuals.................................................................................................. 129

Figure 3.10 Seasonal mean (March to June) daily exchange rate (DER) per taxa and stage. Error
bars represent standard errors. ........................................................................................................... 130

Figure 3.11 Percent change in the seasonal mean daily exchange rate (DER) per taxa relative to
the seasonal mean DER computed for each of the sensitivity analysis model runs. Top refers to a
distribution in the bottom layer from 100-120 m, mid to a distribution from 200 to 220 and
bottom to a distribution between 300-320 m. .................................................................................. 131

Figure 3.12 Inlet population size over time for those taxa most affected by advection. Grey dots
represent estimates of total inlet population size obtained from an average of field data among
sites on each cruise multiplied by the inlet volume. Black dots represent the population size after
advection (size of population on the previous day + size of population on the previous day*daily
exchange rate). Note that Calanus marshallae C2-C3 are Calanidae C2-C3 individuals........ 132

Figure 4.1 Seasonal depth profiles of chlorophyll (mg m$^{-3}$) and temperature ($^\circ$C) averaged across
inlet stations for the three years of observations. Note that in 2010 depth profiles were taken
monthly rather than fortnightly.......................................................................................................... 168

Figure 4.2 Average upper 30 m chlorophyll (panel A) and temperature (panel B) from March to
June at the Florence Daily station for the three years of observations. ........................................ 169

Figure 4.3 February depth profiles of chlorophyll (mg m$^{-3}$) and temperature ($^\circ$C) at DFO2 for
2008 and 2009................................................................................................................................. 170
Figure 4.4 Species and stage-specific estimates of development times averaged across inlet stations computed for each sampling cruise and sampling year. Error bars represents standard errors. ................................................................. 171

Figure 4.5 Left panel: stage-specific variation in abundance of Paraeuchaeta elongata averaged across inlet stations over the spring period (March to June). Right panel: stage-specific relative abundance at DFO2 over the winter, summer, and fall. ......................................................... 172

Figure 4.6 Left panel: stage-specific variation in abundance of Metridia pacifica averaged across inlet stations over the spring period (March to June). Right panel: stage-specific relative abundance at DFO2 over the winter, summer, and fall. ............................................................................. 173

Figure 4.7 Late December (LD) to late June (LJ) cohort development of Metridia pacifica. Solid boxes represent actual observations. Dotted boxes are back-calculated estimates using development times. In each box, the central black line represents the actual timing of sampling. Boxes were extended two weeks (2008 and 2009) or a month (2010) from this date to represent the uncertainty in the cohort appearance resulting from our fortnightly (2008 and 2009) or monthly (2010) sampling resolution. The C1 cohort has two potential timings because of the almost two-week duration of the C1 stage. See text for more details. The rectangle on the time axis represents the timing and duration of the spring bloom. Note that the C1 G1 cohort was not sampled within the sampling season timeframe in 2008 and 2010 and hence no observed C1 G1 cohort is shown. ........................................................................................................ 174

Figure 4.8 Left panel: stage-specific variation in abundance of Eucalanus bungii averaged across inlet stations over the spring period (March to June). Right panel: stage-specific relative abundance at DFO2 over the winter, summer, and fall. ............................................................................. 175
Figure 4.9 Late December (LD) to late June (LJ) cohort development of *Eucalanus bungii*. Solid boxes represent actual observations. Dotted boxes are back-calculated estimates using development times. In each box, the central black line represents the actual timing of sampling. Boxes were extended two weeks (2008 and 2009) or a month (2010) from this date to represent the uncertainty in the cohort appearance resulting from our fortnightly (2008 and 2009) or monthly (2010) sampling resolution. The rectangle on the time axis represents the timing and duration of the spring bloom.

176

Figure 4.10 Left panel: stage-specific variation in abundance of *Calanus marshallae* averaged across inlet stations over the spring period (March to June). Right panel: stage-specific relative abundance at DFO2 over the winter, summer, and fall.

177

Figure 4.11 Late December (LD) to late June (LJ) cohort development of *Calanus marshallae*. Solid boxes represent actual observations. Dotted boxes are back-calculated estimates using development times. In each box, the central black line represents the actual timing of sampling. Boxes were extended two weeks (2008 and 2009) or a month (2010) from this date to represent the uncertainty in the cohort appearance resulting from our fortnightly (2008 and 2009) or monthly (2010) sampling resolution. The rectangle on the time axis represents the timing and duration of the spring bloom.

178

Figure 4.12 Left panel: stage-specific variation in abundance of *Acartia longiremis* averaged across inlet stations over the spring period (March to June). Right panel: stage-specific relative abundance at DFO2 over the winter, summer, and fall.

179

Figure 4.13 Late December (LD) to late June (LJ) cohort development of *Acartia longiremis*. Solid boxes represent actual observations. Dotted boxes are back-calculated estimates using development times. In each box, the central black line represents the actual timing of sampling.
Boxes were extended two weeks (2008 and 2009) or a month (2010) from this date to represent the uncertainty in the cohort appearance resulting from our fortnightly (2008 and 2009) or monthly (2010) sampling resolution. The rectangle on the time axis represents the timing and duration of the spring bloom.

Figure 4.14 Seasonal variation in species-specific egg production rate estimates (egg female$^{-1}$ day$^{-1}$) at the Florence daily station (top panel).

Figure 4.15 Average of egg abundance estimates (# m$^{-2}$ day$^{-1}$) across inlet stations ± standard error.

Figure 5.1 Conceptual diagram of the 0 dimension, stage structured, mean age population model.

Figure 5.2 Simulated (blue line) abundances of Eucalanus bungii with parameterization of the fraction of mature females equal to the fraction of females observed in the upper 30 m during the 2010 stratified vertical hauls. Actual observed abundances averaged across inlet stations are displayed as black dots ± SE.

Figure 5.3 Functional relationship between egg production rate (epr) and temperature and epr and chlorophyll concentration for each species. Temperature was constant at 5 °C for the chlorophyll-epr relationship displayed, while chlorophyll concentration was maintained at 5 mg m$^{-3}$ for the temperature-epr relationship.

Figure 5.4 Simulated (blue line) abundances of Eucalanus bungii in 2009 with parameterization of the fraction of mature females equal to 0.45 if mean chlorophyll concentration in the upper 30 m > 2.1 mg m$^{-3}$ and equal to 0 when < 2.1 mg m$^{-3}$. Actual observed abundances averaged across inlet stations are displayed as black dots ± SE.
Figure 5.5 Daily variation in mean temperature and chlorophyll concentrations for the upper 30 m at the Daily Florence Station from March 8 to June 19. Optimal spawning conditions for *Eucalanus bungii* since the start of model simulation (March 20), when 0.45 of the females were mature, are highlighted as dotted boxes in the middle panel (blue border = 2008, red border = 2009, black border = 2010). The horizontal dotted line in the same panel represents chlorophyll concentrations of 2.1 mg m\(^{-3}\). The period of optimal spawning conditions for *Calanus marshallae*, when the fraction of mature females equals 0.2, is highlighted in the bottom panel. The green rectangle represents the first spawning period in 2009 supported by lipid stores, when 0.8 of females were mature. The vertical dotted line represents the start of the simulation. The horizontal dotted line represents chlorophyll concentrations of 1.7 mg m\(^{-3}\).

Figure 5.6 Simulated (blue line) abundances of *Eucalanus bungii* with final parameterization of the fraction of mature females. 0.45 of total females where mature for 15 consecutive days starting when mean chlorophyll concentration in the upper 30 m were first > 2.1 mg m\(^{-3}\) for at least 8 consecutive days and equal to 0 otherwise. Actual observed abundances averaged across inlet stations are displayed as black dots ± SE.

Figure 5.7 Relationships between the change in the size or timing of the C5 diapausing cohort and selected variables used in the sensitivity analysis.

Figure 5.8 Stage-specific advection rates of *Eucalanus bungii* and *Calanus marshallae* for the model run period in 2008, 2009, and 2010.

Figure 5.9 Stage-specific mortality rates ± SE of *Eucalanus bungii* and *Calanus marshallae* averaged over years and for the entirety of the model run period.

Figure 5.10 Stage-specific mortality rates of *Eucalanus bungii* and *Calanus marshallae* for the model run period in 2008, 2009, and 2010. The green rectangles represent the period of high
chlorophyll concentration from when chlorophyll concentrations were first > 4 mg m\(^{-3}\) to when they dropped below 4 mg m\(^{-3}\) for more than 10 consecutive 10 days. ........................................234

Figure 5.11 Simulated (blue line) abundances of *Calanus marshallae* with parameterization of the fraction of mature females equal to the fraction of females observed in the upper 30 m during the 2010 stratified vertical hauls. Actual observed abundances averaged across inlet stations are displayed as black dots ± SE.................................................................236

Figure 5.12 Simulated (blue line) abundances of *Calanus marshallae* with a *Calanus glacialis*-like parameterization of the fraction of mature females. Actual observed abundances averaged across inlet stations are displayed as black dots ± SE. ................................................................................................238

Figure 5.13 Simulated (blue line) abundances of *Calanus marshallae* with a *Calanus finmarchicus*-like parameterization of the fraction of mature females. This was the final parameterization in 2008 and 2010. Actual observed abundances averaged across inlet stations are displayed as black dots ± SE.................................................................................................................240

Figure 5.14 Simulated (blue line) 2009 abundances of *Calanus marshallae* with both a *Calanus glacialis*-like and a *Calanus finmarchicus*-like parameterization of the fraction of mature females. Actual observed abundances averaged across inlet stations are displayed as black dots ± SE.................................................................................................................240

Figure 5.15 Simulated (blue line) 2009 abundances of *Calanus marshallae* with both a *Calanus glacialis*-like and a *Calanus finmarchicus*-like parameterization of the fraction of mature females and adjusted advection rates for C4 copepodites during the high river discharge event on April 22. This was the final parameterization in 2009. Actual observed abundances averaged across inlet stations are displayed as black dots ± SE. .................................................................................................................241
Figure 6.1 Temporal variation of total mesozooplankton biomass, Type I copepods (*Calanus marshallae*, *Eucalanus bungii*, and *Neocalanus plumchrus*), and fish larvae. Superimposed in blue is an artificial juvenile salmon seasonal cycle. Their abundance peaks in late May and early June and their timing is comparable between years (Ajmani 2012). I maintained this seasonality but numbers were scaled down to the biomass of the zooplankton for ease of comparison. ..... 257

Figure 6.2 Historical (1961-2008) time series of Rivers Inlet sockeye salmon survival (Return/Spawner) and anomalies in mean April alongshore wind speed, sea surface temperature, and Wannock River flow. Winds from the south have a positive sign. 258
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Chapter 1: Introduction

1.1 Motivation

Zooplankton provide a variety of ecosystem services, such as fishery production and nutrient cycling (Morales, 1999, Beaugrand et al., 2003; Ware and Thomson, 2005, Steinberg et al., 2012). Long-term changes in zooplankton biomass and species composition have been linked to large shifts in the biomass and recruitment success of upper trophic levels in a variety of marine regions (McGowan et al., 1998, Beaugrand et al., 2003, Alheit and Niquen, 2004, Beaugrand and Reid, 2003, Mackas et al., 2007, Hipfner, 2008, Bi et al., 2011, Hunt et al., 2011, Tansichuk and Routledge, 2011). Therefore, the capability to predict changes in zooplankton dynamics is an essential contributor to our ability to assess the effects of environmental variability on marine systems.

There is ample evidence that zooplankton biomass and community structure respond to shifts in the climate system. Increases in sea surface temperature (SST) have been associated with reduction in zooplankton biomass or with a decrease in the range of cold-water assemblages in the California Current (Mackas et al., 2001, Peterson and Keister, 2003, Hooff and Peterson, 2006, Lavaniegos and Ohman, 2007, Mackas et al., 2007), the Humboldt current (Alheit and Niquen, 2004), the North Atlantic (Beaugrand et al., 2002, Pershing et al., 2010), the Bering Sea (Baier and Napp, 2003), and the Western North Pacific (Chiba et al., 2008). Such changes in zooplankton dynamics are often not a direct response to changes in temperature, which have been too small to produce substantial variability in development rates, but rather to shifts in alongshore transport (Keister et al., 2011), or in phytoplankton biomass following changes in
upwelling strength (Alheit and Niquen, 2004) or density stratification (Lavaniegos and Ohman, 2007, Chiba et al., 2008).

Zooplankton population dynamics are dependent on changes in its vital rates, such as egg production and mortality (Twombly, 2007). Therefore, in the same water mass, changes in zooplankton biomass are a response of zooplankton vital rates to environmental forcing, either through bottom-up processes or following changes in predation rates (e.g. Ji et al., 2013). Since knowledge of both the environmental factors that regulate zooplankton vital rates, particularly mortality (Ohman, 2012), and of how vital rates translate environmental forcing into changes in zooplankton population size is limited, mechanistic explanations of the linkages between environmental forcing and zooplankton are still poorly quantified (Gargett et al., 2001, Lehodey et al., 2006, Mackas et al., 2007), reducing our ability to predict future marine ecosystem responses to environmental change.

There is clearly a need to develop an understanding of how climate forcing is translated into fluctuations in zooplankton biomass and community structure via changes in zooplankton demographic processes. It is the overall aim of this thesis to identify commonalities between zooplankton life history strategies and response to environmental variability, and to test how the vital rates of the species most drastically influenced by environmental variation respond to shifts in environmental forcing. It is hoped that this study will improve our mechanistic understanding of how atmospheric variability affects zooplankton population dynamics as well as our ability to predict future changes in zooplankton species composition and abundance.
1.2 Background

This study forms a major component of the Rivers Inlet Ecosystems Project (RIES), which was started in 2008 and aimed to develop an understanding of the Rivers Inlet ecosystem, with special focus on how spring plankton productivity influences the early life history of Rivers Inlet sockeye salmon (*Oncorhynchus nerka*). RIES is led by Dr. S. Allen, Dr. B. Hunt, Dr. M. Maldonado, Dr. E. Pakhomov, and Dr. R. Pawlowicz, at the University of British Columbia (UBC), and Dr. R. Routledge at Simon Fraser University (SFU). RIES builds on the preliminary research conducted in Rivers Inlet by Prof. R. Routledge and his students (Buchanan, 2007, Tommasi, 2008).

Rivers Inlet, a deep (365 m maximum depth) fjord of glacial origin on the Central Coast of British Columbia, Canada, is part of a continuous deep fjord region that extends for 1500 km along the northwestern coastline of North America from southern British Columbia to Alaska (Pickard and Stanton, 1980). Similar coastal systems also exist in the Artic, Scandinavia, New Zealand and Chile (Pickard and Stanton, 1980). All deep fjord regions are found in relatively young mountainous areas where the fjords were created by glacial erosion in the Pleistocene (Pickard and Stanton, 1980). They all share a specific topography characterized by a length much greater than their width, and the presence of a deep basin followed by a shallower sill (generally one half to one tenth of the deep basin depth), which provides the only connection to adjacent marine waters (Matthews and Heimdal, 1980). All fjords also share similar hydrodynamics described by an estuarine circulation and density or wind-driven currents that either bring water into the fjord over the sill or take it out at the surface (Matthews and Heimdal, 1980). When the water coming over the sill is dense enough, it sinks into the deep basin, renewing it (Matthews and Heimdal, 1980).
Fjords are found in some of the most productive fisheries regions in the world oceans and their importance as nursery areas for many fish species, such as herring and cod, has long been recognized (Farmer and Hubbert, 1979, Matthews and Heimdal, 1980, Salvanes et al., 1992, Lucas et al., 2007). Fjords have also been referred to as “juvenile salmon highways”, as they provide food for millions of salmon juveniles during their seaward migration journey (Farmer and Hubbert, 1979). Despite the importance of fjord ecosystems to fish production, the effects of future climate change on their “nursery function” for upper trophic levels remain largely unknown.

Fjords are also perfect “laboratories” for oceanographic research as they are relatively contained systems, where advective inputs can be easily identified and quantified (Syvitski et al., 1987), but maintain a similar zooplankton composition to both shelf and open ocean regions given their large depth range. Therefore, knowledge on the effect of environmental variability on zooplankton dynamics in the Rivers Inlet “model system” may inform the understanding of zooplankton populations throughout the North Pacific Fijordland, similar fjord systems around the world, and more open ocean water masses.

Notwithstanding the more global applications of the oceanographic research carried out in Rivers Inlet, the original driving force for the establishment of the RIES research program was concern over the state of the local sockeye salmon fishery. Pacific salmon (Oncorhynchus spp.) hold a special ecological, economic and cultural significance to people living on the North Pacific coast. For centuries, salmon have provided sustenance for First Nations in the Pacific Northwest, and they remain an important source of income for commercial fishermen. In British Columbia alone the total commercial landed value of sockeye salmon in 2011 was $97 million (British Columbia Ministry of Agriculture, 2012). Rivers Inlet used to be a major contributor to
the total British Columbia sockeye salmon landings, being home to one of the largest sockeye salmon fisheries in the province until the late 1970s (McKinnell et al., 2001). However, returns showed a declining trend since then and crashed in the late 1990s (Appendix A.1). Commercial fishing of this stock has been closed since 1996. Even in the absence of fishing, the stock has yet to recover to historical levels. Reasons for its decline and lack of recovery remain unclear, although the relatively constant freshwater survival as compared to a declining returns to spawner ratio, points to reduced marine survival, possibly in response to climatically driven changes in bottom-up forcing (McKinnell et al., 2001).

The decline in Rivers Inlet sockeye salmon was symptomatic of declines in productivity of many Central and Southern British Columbia sockeye stocks (Riddell, 2004, McKinnell et al., 2011). A coherent change in salmon production and a variety of large-scale climate indices such as the Pacific Decadal Oscillation (PDO) and the Aleutian Low Pressure Index (ALPI) suggests that a bottom-up mechanism is driving the observed change in salmon dynamics (Hare et al., 1999, Peterson and Schwing, 2003). However, while the PDO provides a measure of high or low salmon productivity states (Hare et al., 1999, Peterson and Schwing, 2003), it is itself unable to forecast changes in salmon productivity within those climate regimes. For example, over the 1952-2006 time period, the PDO was not significantly correlated with the Oregon Production Index of coho marine survival or with the marine survival of Carnation Creek coho (Mackas et al., 2007). Moreover, forecast models of Fraser River sockeye salmon returns that included sea surface temperature (SST) or PDO data did not improve forecast performance (Cass et al., 2006). Conversely, Mueter et al. (2002) found that local variation in SST explained more of the variability in survival of different sockeye stocks than the PDO. Clearly, to be able to assess how climate variability influences salmon production through bottom-up forcing we first have to
understand what atmospheric forcing drives primary and secondary productivity at a local scale to allow for the selection of appropriate environmental variables to be inputted in models of salmon dynamics.

The greatest impact on salmon survival rates occurs in their early ocean migratory stage (Peterman, 1987, Pearcy, 1992). It appears that salmon juveniles need to reach a critical size by the end of their first summer at sea to survive their first winter (Beamish and Mahnken, 2001). Thus, bottom-up regulation of prey availability in their first spring and summer at sea may determine variation in year class strength (Beamish and Mahnken, 2001). Indeed, salmon survival rates co-vary only within regions smaller than 500-1000 km (Mueter et al., 2002), implying that regional processes largely determine sockeye salmon survival. Seaward migrating sockeye salmon juveniles spend three to six weeks in Rivers Inlet (Stocks, 2012), feeding on a variety of zooplankton prey (Ajmani, 2012, Buchanan, 2007). Sockeye juvenile growth rates, gut fullness, and stomach prey composition vary interannually and it has been hypothesized that a match between the timing of sockeye juvenile migration and the peak in spring zooplankton biomass may affect their survival (Ajmani, 2012). Indeed, higher spring zooplankton abundance appears to be associated with higher juvenile robustness (Buchanan, 2007). Zooplankton abundance, biomass, and species composition has been observed to vary interannually in Rivers Inlet (Tommasi et al., 2013a). However, an understanding of what drives zooplankton fluctuations in the region has yet to be achieved. Determining what drives variability in the zooplankton biomass and species composition available to the migrating sockeye juveniles will be of utmost importance to assess how climate forcing may have driven changes in the productivity of this sockeye salmon stock in the past and to assess the carrying capacity of this system for sockeye salmon in the future.
1.3 Thesis main objectives

The main objectives of this thesis are to:

1. Identify the zooplankton seasonal succession cycle in Rivers Inlet (Chapter 2);
2. Identify those functional traits and life history strategies that characterize a shared response of different zooplankton taxa to environmental change (Chapter 2 and 4);
3. Identify the main environmental drivers of *Calanus marshallae* and *Eucalanus bungii* temporal dynamics (Chapter 3 and 4);
4. Develop a model of zooplankton population dynamics of *C. marshallae* and *E. bungii* to test our conceptual understanding of their response to environmental forcing (Chapter 5).

Specific objectives for each aim are presented in the section that follows.

1.4 Thesis structure

Large interannual variations in the hydrography, primary productivity, and phytoplankton temporal dynamics have been reported for Rivers Inlet over the spring to summer season (Wolfe, 2010, Hodal, 2011, Shiller, 2013). The timing of the spring bloom can vary by almost a month (Wolfe, 2010, Shiller, 2013), but phytoplankton species composition remains relatively stable between years (Shiller, 2013). In Chapter 2, I determine if such changes in environmental forcing are associated with fluctuations in zooplankton community composition through an analysis of extensive zooplankton field data collected in Rivers Inlet over the spring to summer period in 2008, 2009, and 2010. Furthermore, I determine the zooplankton succession cycle and assess how different feeding guilds change in dominance interannually and seasonally. The specific objectives of Chapter 2 are to 1) detect patterns of spring to summer zooplankton seasonal
succession, 2) identify indicator species of zooplankton community succession, 3) determine the environmental variables associated with the observed changes in community structure.

Once it is established that zooplankton phenology, biomass, and species composition does vary in response to atmospheric forcing, one can explore mechanistic explanations for the observed changes. However, changes in zooplankton population size are impacted both by local changes in their vital rates and emigration/immigration via advection. Thus, to assess how environmental forcing drives variability in zooplankton vital rates, advection driven changes in zooplankton population dynamics have to be separated from fluctuations in population size driven by local processes. In Chapter 3, I couple a hydrodynamic model of the inlet with zooplankton vertical distribution data to determine zooplankton exchange rates between the fjord and outer waters for a variety of indicator zooplankton taxa in the system. Specific objectives of Chapter 3 are to 1) determine the seasonal vertical distribution of the zooplankton taxa, 2) assess if the different vertical distribution of zooplankton taxa interacts with horizontal flows to produce taxon-specific advection rates, 3) evaluate if advection rates differ between various developmental stages, and ultimately 4) assess if advection is an important term in determining changes in zooplankton population size as compared to local biological processes.

As different species have developed different life history strategies and trade-offs, the relative importance of each vital rate in determining successful recruitment differs among zooplankton species. It is these life history characteristics that will lead to their higher or lower success under different environmental regimes. Therefore, a detailed knowledge of zooplankton life history is required to develop an adequate explanation of zooplankton responses to varying environmental variables. In Chapter 4 I use a life history approach to assess what makes certain species assemblages dominant in some years and not in others. The life history characteristics of
five key copepod species, associated with the different feeding guilds and seasonal succession groups established in Chapter 2, are identified to gain a conceptual understanding of what drives changes in the recruitment of key zooplankton species in the system. Two species, *Eucalanus bungii* and *Calanus marshallae* are spring dominant, winter dormant, herbivorous copepods; *Paraeuchaeta elongata* is a carnivorous species, and *Metridia pacifica* and *Acartia longiremis* are omnivorous copepods dominant in the late spring/summer. Interannual differences in recruitment success are assessed by following seasonal changes in the copepods’ stage composition and the size of the G₁ adult cohort (*P. elongata, M. pacifica, A. longiremis*) or the G₁ C5 diapausing cohort (*E. bungii* and *C. marshallae*). Interannual variability in development and egg production rates, estimated using literature-derived empirical relationships of these rates to their environmental drivers, is also established. The objectives of Chapter 4 are to 1) present the seasonal cycle of these species in the region, 2) assess if the phenology of these copepods varied following interannual differences in spring bloom timing and spring temperature, 3) determine the interaction between overwintering strategy and spring bloom timing in recruitment success.

Evaluation of the factors driving changes in zooplankton recruitment has been hampered by the paucity of comprehensive zooplankton data and inadequate temporal or taxonomic resolution to resolve the demographic processes involved and test model performance (Fennel and Neumann, 2001, Richardson, 2008). These data provide one of the first comprehensive zooplankton datasets in British Columbia, Canada, collected at an adequate spatial, temporal, and taxonomic resolution to resolve zooplankton recruitment processes and test the mechanistic understanding of its drivers. It also offers a unique opportunity to integrate field observations and dynamical models to investigate competing hypotheses on the drivers of zooplankton variability.
In Chapter 5, I construct a model of zooplankton population dynamics for *C. marshallae* and *E. bungii* to test the conceptual framework of zooplankton recruitment processes developed in previous chapters. The objectives of Chapter 5 are to 1) build a population model that could successfully simulate the observed seasonal and interannual variability in the abundance of *E. bungii* and *C. marshallae* over the spring period, 2) test the hypothesis that *C. marshallae* recruitment is reduced when the spring bloom is delayed because of lower copepodite survival, 3) test the hypothesis that *E. bungii* recruitment is reduced when the spring bloom is delayed because of higher adult and/or copepodite mortality, 4) use the model to identify the environmental factors driving the observed interannual variability in both the phenology and size of the main spring cohort, 5) assess what knowledge gaps in our understanding of the life history of these two copepod species may need to be addressed in future studies.
Chapter 2: Mesozooplankton community seasonal succession and its drivers: insights from a British Columbia, Canada, fjord

The mesozooplankton dynamics in Rivers Inlet, a fjord in Central British Columbia, Canada, were studied from March to June of 2008, 2009 and 2010 to assess the interannual, seasonal, and spatial variability in zooplankton abundance and community structure under different physical environments and spring bloom scenarios. Samples were collected fortnightly during 2008-2009 and monthly in 2010 and provide one of the few multi-year zooplankton time series in the region. Two distinct zooplankton communities characterized the observed succession pattern. The winter-spring group was characterized by the presence of small, year-round omnivorous zooplankton: bryozoan cyphonautes, Microcalanus spp., Microsetella spp., Oithona spp., and Oncaea spp., as well as by large, diapausing copepods such as Eucalanus bungii, Neocalanus plumchrus, and Calanus marshallae, and by the euphausiid Thysanoessa spinifera. By contrast, the spring-summer community showed an increased abundance of Acartia longiremis, cladocerans, Limacina helicina, Metridia pacifica, Euphausia pacifica, appendicularians, Clione limacina, chaetognaths, polychaetes, Pseudocalanus spp., ostracods, and amphipods. The timing of zooplankton succession was consistently associated with the timing of the spring bloom, and was delayed in 2009 when the spring bloom occurred in May rather than April. The zooplankton succession dynamics are discussed in terms of dominant feeding guild structure to highlight the potential mechanisms of succession. Spatial variability in zooplankton distribution was mainly influenced by river flow and exchanges with adjacent coastal waters.
2.1 Introduction

Zooplankton perform a critical ecosystem function by transferring energy from phytoplankton to upper trophic levels. As such, changes in zooplankton community structure can have significant repercussions for higher trophic levels (Cooney et al., 2001, Tanasichuk, 2002, Beaugrand et al., 2003, Mackas et al., 2007, Hipfner, 2008, Bi et al., 2011, Tanasichuk and Routledge, 2011). These studies show that not only variation in bulk zooplankton biomass, but also changes in the composition of zooplankton communities are correlated with changes in the growth and survival of upper trophic levels. Therefore, monitoring and understanding changes in zooplankton community composition are essential if we are to assess and predict changes in ecosystem structure following variations in environmental forcing.

Substantial interannual fluctuations in zooplankton composition have been documented in many marine systems. A common pattern among them is a temporal switch, often in association with increases in sea surface temperature, from communities dominated by large zooplankton species to communities dominated by smaller-sized taxa (Coyle et al., 1990, Beaugrand et al., 2002, Mackas and Galbraith, 2002, Beaugrand et al., 2003, Chiba and Saino, 2003, Keister and Peterson, 2003, Zamon and Welch, 2005, Mackas et al., 2007, Chiba et al., 2008, Coyle et al., 2008, Richardson, 2008, Sastri and Dower, 2009, Keister et al., 2011). Although temperature changes are often correlated with the observed variability in zooplankton composition, they may not be the ultimate mechanism driving the change (Mackas et al., 2007). For example, alterations of current directions are understood to be driving interannual to decadal variability in zooplankton species composition in the Northern California Current (NCC) and on the continental shelf north and west of Vancouver Island, BC (Mackas et al., 2001, Keister and
However, switches in the timing of ontogenetic migration (Mackas et al., 1998, Chiba and Saino, 2003), or mismatches of key life history events (e.g. initiation of egg production, recruitment of early copepodite stages) with enhanced food supply (Chiba and Saino, 2003, Chiba et al., 2008, Eslinger et al., 2001) have all been put forward as possible mechanisms for decadal and interannual variations in zooplankton composition.

Seasonal variability in zooplankton composition is superimposed on such decadal and interannual changes in zooplankton dynamics. However, it remains to be assessed how the effect of interannual level variation in physical forcing (e.g. surface temperature or circulation pattern) on zooplankton composition scales down to affect seasonal level changes in zooplankton composition. For example, seasonally, there is a general trend for smaller zooplankton species (particularly within the Copepoda Subclass) to become more abundant both in summer, when waters are warmer (Gaard, 1999, Cooney et al., 2001, Plourde et al., 2002, Chiba and Saino, 2003, Debes and Eliasen, 2006, Madsen et al., 2008), and in winter (Madsen et al., 2008). It needs to be evaluated if the observed increased dominance of small copepods in warmer years is a result of a lengthening in the duration of summer-like conditions or of a direct increase in their overall biomass because of changes in, for example, circulation patterns, or of a combination of the two. A seasonal scale knowledge is particularly relevant to the understanding of the influence of physical forcing, through zooplankton community structure, onto upper trophic levels whose recruitment may depend on a match of their seasonal cycles with the seasonal biomass peak of preferred prey species (Hjort, 1914, Cushing, 1990a).
In temperate systems, zooplankton species recruitment is linked to a successful timing of important life history events such as ontogenetic migration and reproduction with favourable environmental conditions (Mackas et al., 2007). It is understood that climate change will alter the seasonality of physical forcing events, such as the arrival of upwelling winds (IPCC, 2007), and the phenology of organisms is expected to be sensitive to such shifts (Ji et al., 2010, Sydeman and Bogart, 2009). Recently, variation in the seasonal timing of the biomass peak in some copepods has been associated with increases in spring water temperature (Mackas et al., 2012).

Knowledge of the seasonal succession of zooplankton composition is fundamental to understand the interplay between species-level phenological responses and the observed interannual variability in community structure. In particular, species groups regularly occurring at the same time of year and responding to the same environmental forcing may be identified and assigned to specific functional groups based on their common feeding strategies. We would expect such functional groups to respond similarly to a varying seasonal forcing. However, while the concept of ecological succession has been applied to marine phytoplankton studies (e.g. Margalef, 1978) and in limnology (e.g. Sommer et al., 1986), the general temperate zooplankton community succession and the mechanistic underpinnings of the seasonal changes in zooplankton composition have yet to be proposed.

The lack of information on zooplankton community seasonality and its drivers is particularly evident for British Columbia’s coastal areas. Except for a year-long study of copepod seasonality in Knight Inlet (Stone, 1977), data on zooplankton community structure are scarce for fjords and bays on the North and Central coast, even though they are defining features of the region’s coastline, vital larval rearing areas for many fish species, and important feeding
grounds for marine birds and whales (Lucas et al., 2007). Results from a preliminary study of zooplankton community structure in Rivers Inlet, a typical fjord of the mainland coast of British Columbia, conducted in the spring and summer of 2006 and 2007 were the first to show substantial interannual variation in zooplankton community composition in the region (Tommasi et al., 2013a). *Metridia pacifica*, copepods, and larvaceans declined in abundance from 2006 to 2007, while *Acartia* sp., *Microsetella* sp., and cladocerans increased (Tommasi et al., 2013a). However, coarse taxonomic analysis used in the study precluded division of zooplankton into different life history strategies and an assessment of zooplankton succession pattern.

Here, we build on the preliminary study of Tommasi et al. (2013a) through an analysis of spring to summer zooplankton community succession in Rivers Inlet using three years of data (2008-2010). Specifically, we seek to detect patterns of spring to summer zooplankton seasonal succession based on analysis of the spatial and temporal patterns in zooplankton community composition. Furthermore, we aim to identify indicator species of zooplankton community seasonal succession and determine the environmental drivers of observed changes in community structure. Finally, in order to develop an understanding of the mechanisms driving zooplankton succession, and its relation to physical forcing, indicator species are described in terms of feeding modes and grouped into specific functional groups.

### 2.2 Methods

#### 2.2.1 Study area

Rivers Inlet (51° 26’, 127° 38’) is a deep (365 m maximum depth), 3 km wide and 46 km long fjord of glacial origin on the Central Coast of British Columbia, Canada (Pickard, 1961). It is located 500 km north of Vancouver. The inlet is characterized by a positive estuarine
circulation whereby a shallow surface layer transports fresh water out of the inlet into Queen Charlotte Sound (QCS) and nutrient-rich deep waters periodically enter the inlet over a shallow (137 m) sill at its mouth. As is typical of many fjords, most of the seasonal variation in salinity is therefore within the top 10-5 m of the water column (Freeland et al., 1980, Stanton and Pickard, 1981, Hodal, 2011). The estuarine circulation is enhanced in late spring and summer months as winter southeasterly winds ease and freshwater discharge increases (Whitney et al., 2005, Hodal, 2011). The switch from winter southerly to summer northerly winds creates offshore Ekman transport along the British Columbia coast, leading to coastal upwelling (Whitney et al., 2005), but also affects surface currents within the fjords. The presence of denser water on the shelf can trigger deep water renewal in the fjord at this time (Freeland et al., 1980, Hodal, 2011).

The major input of fresh water is from the Wannock River, flowing out from Owikeno Lake, a large, oligotrophic lake fed by two glaciers and draining an area totaling 3970 km² (Hodal, 2011). River runoff is at its minimum from January to March and maximum from May to July, during the freshet (Hodal, 2011, Pickard, 1961). The freshet is the sudden increase in river flow following the spring melting of the snowpack. The timing of the freshet was determined as the date of the highest river flow observed over the sampling season. The average daily Wannock River discharge, calculated for the period of 1962 to 2010, is 343 m³ s⁻¹, with a maximum of 2500 m³ s⁻¹ and a minimum of 43 m³ s⁻¹. The mean annual total discharge is 9.9 km³ per year.
2.2.2 Field sampling

Zooplankton vertical hauls with a bongo net equipped with a 150 μm mesh net were conducted in Rivers Inlet from March to the end of June, on a fortnightly basis in 2008 and 2009 and monthly in 2010 using the MV Western Bounty, a 10 m seine boat. A 150 μm was chosen to obtain a representative sample of the entire mesozooplankton community including small copepods, such as *Oithona similis*, as well as barnacle nauplii and cladocerans. All hauls were conducted during the day to a maximum depth of 300 m or to 10 m above the bottom across five sampling stations equally spaced along the length of the inlet (Fig. 2.1). Nets were retrieved at a speed of 1 m s$^{-1}$. A General Oceanics mechanical flowmeter was used to estimate volume filtered by each haul. After each haul the net was rinsed and the samples from one cod end were preserved in a 5 % formalin-seawater solution. The sample from the other cod end was used for other purposes. Wire angles were generally 0 degrees, but ranged up to a maximum of 30 degrees when surface currents were fast. No zooplankton samples were collected at DFO2 in the first 2008 cruise and at DFO5 in the late April 2008 cruise. During the early June 2009 cruise only a sample at DFO2 was collected. Samples from the remaining stations were collected from the *MV CCGS J. P. Tully* using a 236 μm bongo net during a routine biannual cruise of the Department of Fisheries and Oceans Canada. Initial cluster analysis of both abundance and biomass data identified these samples as belonging to a separate cluster and thus they were not included in the analysis. CTD profiles from the surface to the bottom depth were taken with a SBE 25 CTD following each bongo net deployment. No profiles were collected during the late May 2009 cruise at DFO5. Profiles were only to a maximum depth of 40 m in the early June 2009 cruise, and to 180 m in late March 2008.
Daily 30 m profiles of temperature (T°C), salinity (S), and fluorescence were conducted every morning from the Florence Daily site (Fig. 2.1). In 2008, data were sampled with a Hydrolab DS5X sonde. The Hydrolab sonde broke down on April 1st-9th, April 30th-May 15th, May 25th and 26th, June 8th, and June 14th-22nd and on these occasions profiles were taken with a SBE 25 CTD. In 2009 and 2010 daily 30 m profiles were measured with a RBR XR-620 CTD. Sampling to a depth of 30 m allowed the measurement of the bulk of the total water column chlorophyll a biomass, and definition of the halocline (Hodal, 2011). All sondes were calibrated in-factory prior to each yearly field season. Conductivity sensor accuracy was 0.001 mS cm\(^{-1}\) for the Hydrolab DS5X sonde, and 0.003 mS cm\(^{-1}\) for both the RBR XR-620 CTD and SBE 25 CTD.

Water samples for chlorophyll a biomass estimation were collected using a Van Dorn bottle at 5 m depth immediately following the daily 30 m casts and fortnightly or monthly CTD profiles. A known volume of seawater, between 60 and 300 ml, was filtered through a Whatmann GF/F filter. Pigments were extracted in 90% acetone for 24 hours at -20°C and measured with a fluorometer (Strickland and Parsons, 1972). The measured chlorophyll a biomass (mg m\(^{-3}\)) was used to calibrate the Hydrolab DS5X sonde fluorescence (volts), RBR XR-620 CTD and SBE 25 CTD fluorescence (mg m\(^{-3}\)) readings as described in Appendix B. Profiles of chlorophyll a biomass estimated from fluorometer profiles were then integrated to a 20 m depth to obtain values of daily integrated phytoplankton biomass (Chl a). A depth of 20 m was chosen as it was found to always contain the bulk of phytoplankton biomass in the water column (Hodal, 2011). The timing of the spring bloom was defined as the date when daily integrated chlorophyll a biomass was greater than 1.5 times the sampling season average.
Wind data (magnitude and direction) from 2008 were obtained from the Ethel weather station, maintained by Simon Fraser University. The Ethel weather station was replaced by the Laska weather station, maintained by the University of British Columbia, in March 2009. Wind data from 2009 and 2010 were obtained from the Laska weather station. The stations were located less than 15 m apart on Ethel Island, located close to the daily sampling site (Fig. 2.1). Both stations were left logging simultaneously from March 1 2009 to March 18 2009 to allow for intercalibration. It was determined that the Ethel wind data were calibrated to the Laska wind data using a root mean square error analysis. A correction of 69° was applied to the Ethel wind direction to calibrate it to that of the Laska weather station. The wind magnitude of the Laska weather station was determined to be 1.187 times larger than the wind magnitude at Ethel’s.

The direction of along channel wind speed is an important determinant of Rivers Inlet spring bloom timing and surface layer flow speeds (Wolfe, 2010). Thus, for our data analysis, in addition to overall wind magnitude (WS), we inputted measures of outflowing (OWS) and inflowing wind speed (IWS). Any wind magnitude with a direction between 10 and 80° was selected as an outflowing wind speed. Wind events with a direction between 180 and 260° were considered inflowing. Wind direction defines the direction the wind is blowing from.

Due to equipment malfunction, wind data were missing from April 24 to May 9 in 2008, and from April 10 to June 1 in 2009. To extrapolate missing wind data, wind speed (magnitude) and direction from the three closest Environment Canada weather stations to Rivers Inlet were downloaded from Environment Canada’s National Climate Data and Information Archive (http://climate.weatheroffice.gc.ca/climateData/canada_e.html) from March to June of each year sampled. Specifically, the weather stations used were: Herbert Island (50° 56’ 24”, 127° 38’
situated 72 km to the southwest, Cathedral Point (52° 11’ 14”, 127° 28’ 11”), 68 km to the northeast, and Bella Bella airport (52° 11’ 06”, 128° 09’ 24”), 84 km to the northwest. Next, a multivariate regression of Laska daily averaged wind speed against daily averaged wind speeds at the Environment Canada weather stations was run for each month in the sampling period. The wind speed data were log transformed to normalize the residuals. The same analysis was performed for the wind direction data. The correlation between estimated and actual Laska wind speed was poor (< 0.3) for May and June, when wind speeds were lowest. Therefore, to extrapolate missing wind speeds, we only used the April regression relationship, which gave an r of 0.59 and of 0.64 for wind speed and direction respectively.

Daily Wannock River flow (WRF) estimates were computed using Owikeno Lake water levels obtained from Environment Canada’s station 08FA007 (50° 41’ 26”, 127° 09’ 43”) and an empirical relationship between Owikeno Lake water levels and WRF. This empirical relationship was derived by M. Hodal from a table of both WRF and water levels obtained from Environment Canada (refer to Hodal, 2011 for details).

**2.2.3 Zooplankton taxonomic analysis**

Each sample was first examined for the presence of rare, large organisms such as hydromedusae, fish larvae, and euphausiids, which were counted and then removed from the full sample. The remaining sample was then split with a box plankton splitter to generate subsamples with approximately 100 individuals for the > 2 mm size fraction and 400 for the < 2 mm size fraction. Copepod adults and copepodites from stages 4 and 5 were identified to species. Copepodites 1 to 3 were identified to genus and to species for *Metridia pacifica, Eucalanus*
bungii, *Paraeuchaeta elongata*, and *Acartia longiremis*. Copepod nauplii were counted but not identified to species. Cladocerans, euphausiids, amphipods, chaetognaths, appendicularians, hydromedusae, siphonophores, pteropods and ostracods were also identified to species when possible. All other organisms, such as decapod zoea, eggs or polychaete larvae, were identified to genus or larger taxonomic categories. Total dry weights estimates for each taxa were calculated from a table of taxa-specific dry weight coefficients (Appendix C) obtained from the Institute of Ocean Sciences, Sidney, British Columbia, Canada (Moira Galbraith, personal communication). Zooplankton abundance and biomass were expressed on a unit volume basis (mg m\(^{-3}\)). Biomass estimates of larger taxa such as euphausiids, which are likely to avoid or be missed by small nets (Sameoto et al., 2000), are not quantitative. However, all samples have the same sampling bias and hence comparison of euphausiids variability between years was deemed appropriate.

### 2.2.4 Data analysis

To assess patterns in zooplankton composition across years, stations, and cruises a multivariate analysis of Bray Curtis similarities between samples was undertaken. Only taxa contributing more than 5% to the total abundance (or biomass) in any one survey were included in the analysis. Individual species of cladocerans, amphipods, chaetognaths, appendicularians, hydromedusae, siphonophores, and ostracods were grouped into these larger taxonomic categories before data analysis. For copepods, only adult female abundances were used in the analysis, as we were interested in the seasonal cycle and recruitment to the adult stage. Life history strategies and cohort development of key species will be discussed in a separate paper.
Prior to the computation of Bray Curtis similarities, the data were log-transformed to reduce the influence of the more abundant taxa on analysis outputs (Field et al., 1982). As the lowest non zero value of both abundance and biomass data was less than one, the $\log_{10}(x+1)$ transformation would distort the relationship between zeros and other small values in the dataset (McCune and Grace, 2002). Therefore, following the procedure outlined by McCune and Grace (2002) a $\log_{10}(x+0.1) +1$ was used for abundance (individuals m$^{-3}$) and a $\log_{10}(x+0.01) +2$ for biomass (mg m$^{-3}$). Similarity levels can range from 0, indicating no taxa in common between the cruises, to 1, indicating the cruises have the same relative abundance and taxonomic composition (Clarke, 1993). The similarities were then classified using non-metric multi-dimensional (MDS) scaling and group-average clustering using the PRIMER software version 6.1.12 (Clarke, 1993). Samples were not relativized prior to ordination. Group-average describes the linkage option of the clustering method. In group-average clustering the single-link dissimilarity between two different groups is computed by averaging the distance between all between-group pairs (Clarke and Warwick, 2001). Significant differences among clusters were computed with the SIMPROF permutation test available in PRIMER software version 6.1.12 (Clarke and Gorley, 2006). A two-dimensional MDS showed stress values greater than 0.2 and thus the three-dimensional MDS (stress = 0.17 for abundance and 0.18 for biomass) was deemed as the best representation of similarities between samples (Clarke and Warwick, 2001), and was used in further data analysis. However, we present the 2D MDS plot as they provide a more easily interpretable visualization of the sample ordination. The MDS ordination based on Bray Curtis similarities will be referred to as the biotic MDS.

Preliminary cluster analysis of abundance data identified three single-sample outliers, one in the early April 2008 cruise at DFO4, one in the late April 2008 cruise at DFO1, and the last in
the 2010 cruise at DFO1. The first was characterized by generally very low densities across all taxa, the second presented extremely high numbers of Cirripedia cyprids, and the last displayed high numbers of A. longiremis and Oithona spp.. The first two samples were also identified as outliers by the biomass cluster analysis. As for the abundance data, the first showed generally a very low biomass across all taxa, and the second displayed extremely high numbers of Cirripedia cyprids and of hydromedusae. Samples at DFO4 and DFO5 on the first 2008 cruise and at DFO5 on the early May 2008 cruise were also classified as outliers. The first two showed high biomass of Cirripedia cyprids, Cirripedia nauplii, polychaetes, Pseudocalanus spp. and siphonophores, and of Cirripedia cyprids, hydromedusae, and siphonophores respectively. The last was characterized by extremely high biomass of E. bungii and Limacina helicina. These samples were excluded from further analysis.

Following clusters analysis, IndVal indices (Dufrene and Legendre, 1997) were computed at each hierarchical level to identify indicator species of each cluster. Information on a species (i) relative abundance and its relative frequency of occurrence in the various samples belonging to the same cluster (j) are employed to obtain an IndVal value for each species in each cluster according to the following formulas:

Specificity of species i to cluster j = A_{ij} = \frac{N_{individuals_{ij}}}{N_{individuals_i}}

Fidelity of species i to cluster j = B_{ij} = \frac{N_{samples_{ij}}}{N_{samples_j}}

IndVal_{ij} = A_{ij} \times B_{ij} \times 100

Where \(N_{individuals_{ij}}\) is the mean number of individuals of species \(i\) across samples of cluster \(j\), while \(N_{individuals_i}\) is the sum of the mean numbers of individuals of species \(i\) over all
clusters at the hierarchical level of cluster $j$. $N_{samples_{ij}}$ is the number of samples in cluster $j$ where species $i$ is present. $N_{samples_j}$ is the total number of samples in the cluster.

Specificity is highest when species $i$ is only present in cluster $j$, whereas fidelity is maximum when species $i$ is present in all sites of cluster $j$. Therefore, $IndVal_{ij}$ is maximum (100%) when all the individuals of species $i$ are observed in all samples of only cluster $j$. Dufrene and Legendre (1997) proposed that only species with $IndVal$ values $\geq 25\%$ for a specific cluster should be considered as indicator species for that cluster. This would for example occur if an indicator species is present in at least 50% of the samples in a cluster, and if its relative abundance in that cluster reaches at least 50%. It also implies that if either fidelity or specificity are 100%, the other will never be less than 25% for an indicator species. Here an indicator species for a specific cluster is defined as that taxa which shows its highest $\geq 25\%$ $IndVal$ in that cluster.

In order to develop an understanding of the mechanisms driving zooplankton succession, indicator species were assigned to specific feeding modes and grouped into functional groups using data from the literature (Table 2.1). These groups are introduced in the results, but are assessed more exhaustively in the discussion section. Four taxa, *Metridia okhotensis*, Aetididae copepods, bivalve veligers and Cirripedia larvae, were not placed in functional groups either because lack of data on their life history made their association with one particular functional group difficult, or because, in the case of Cirripedia and bivalves, their dynamics may be more dependent on physical factors associated with the intertidal area and the feeding and spawning strategies of their sessile parents.
BIO-ENV (performed in PRIMER) was used to determine the set of environmental variables that best explained the observed ordination pattern of the biotic MDS. The BIO-ENV technique aims at selecting the environmental variables or subsets of variables that maximize the rank correlation between the biotic and environmental similarity matrices (Clarke and Ainsworth, 1993). The environmental similarity matrix was computed using Euclidean distance as a measure of dissimilarity between each pair of samples (1 - similarity) using different subsets of environmental variables (Clarke and Ainsworth, 1993). The best matching environmental similarity matrix selected by the BIO-ENV procedure for abundance and biomass data was used to create an environmental MDS ordination (based on Euclidean distances). Since they have different ranges and units, the environmental variables were normalized prior to analysis.

The environmental variables used in the BIO-ENV analysis are listed in Table 2.2. Spring bloom timing in Rivers Inlet has been observed to be spatially uniform throughout the inlet, with peak Chl a values occurring a maximum of three days apart across the different inlet stations (Tommasi, 2008). Furthermore, 5 m S and T from the Florence Daily site were well correlated with average 5 m conditions across all fortnightly and monthly stations (Appendix D). Therefore, environmental variables from the Florence Daily station were determined to be representative of average inlet conditions and tested as potential drivers of inlet zooplankton dynamics. One can expect zooplankton abundance and biomass to be affected by environmental conditions on the day of as well as some days leading up to the sampling cruise. Therefore, 5 m Chl a, T, and S from the Florence Daily station and WS, IWS, OWS, and WRF, were averaged into temporal bins of varying duration prior to comparison with the zooplankton data. In each year, daily sampling started only 11 days before the 1st zooplankton sampling cruise, and thus the maximum bin duration had to be set at 11 days. Each possible binning interval (1-11 days) for each
environmental variable was correlated with the first three MDS scores of the biotic matrix ordination. For each environmental variable, only the binning intervals with the highest correlation to one of the MDS scores were retained for input into the BIO-ENV analysis.

In addition to the selected binned variables described above we employed chlorophyll, salinity, density, and temperature station-specific data obtained during each fortnightly (2008 and 2009) or monthly (2010) cruise (Table 2.2). Chlorophyll data were vertically integrated over the first 20 m before input into the analysis. After inspection of temperature, salinity, and density profile plots (Fig. 2-4) only those specific depths that showed the highest variation in time and space were selected for the BIO-ENV analysis (Table 2.2). Three other environmental variables were used in the BIO-ENV analysis: intensity of incoming solar radiation or insolation (SR), a measure of the time since the spring bloom (TSB), and a measure of the distance from the beginning of deep water renewal (DWR). The intensity of insolation varies with the annual change of the earth’s axis relative to the sun, and is responsible for the seasonal temperature change observed over the planet. In the northern hemisphere, it is highest during the summer solstice and lowest during the winter solstice. We simulated the yearly insolation cycle using a sine curve with a maximum of 1 on June 21 and a minimum of -1 on Dec. 21. The values of this solar radiation (SR) sine curve for each cruise date were input as an environmental variable. The date of the spring bloom in each year was determined as the first peak in Chl a at the Florence Daily station 1.5 times higher than the sampling season average. For every year, the difference between this date and every cruise date was defined as the time since the bloom (TSB). Similarly, we defined DWR as the difference between the beginning of deep water renewal and each of the cruise dates. The date of the onset of deep water renewal was obtained from an
analysis of seasonal variation of density and oxygen concentration in deep water (270 m depth) conducted by M. Hodal (see Hodal, 2011 for details).

2.3 Results

2.3.1 Environmental parameters

Year 2010, an El Niño year, was the warmest year sampled, reaching temperatures of 8.5 °C at 100 m already in late March (Fig. 2.2). It also showed the lowest spatial temperature variability across stations, with a seaward gradient of warm to colder water being evident only in late March at 100-150 m (Fig. 2.2). By contrast, in 2008 and 2009, a warm to cold seaward temperature gradient was present for most of the season (Fig. 2.2). The gradient was strongest in March 2008, when a pool of warm water was concentrated at DFO4 and DFO5 m at 50 m, and a cooler water mass was present at DFO1 (Fig. 2.2). In the following cruise the cold water mass extended to DFO3, an indication of further inflow of water from the shelf into the inlet at 25-50 m (Fig. 2.2). By late April 2008, the 50 m cold water inflow had disappeared, but waters below 100 m became cooler across the length of the inlet following the start of deep water renewal (Fig. 2.2). The 50 m shelf water intrusion was again apparent from late May to June 2008 and extended to DFO3 (Fig. 2.2). A cold water mass was also observed at the outer stations in March 2009, the coldest year sampled, but it was deeper in the water column, centered at about 100 m, than in March 2008 (Fig. 2.2). In early April 2009 the cold water intrusion extended to 50 m, by late April it was concentrated at 50 m and by early May it shoaled to 30 m (Fig. 2.2). In early May 2009 a cold water mass was also present at DFO1 at depths > 100 m, which was a sign of deep water renewal (Fig. 2.2). No indication of deep water renewal was evident from the 2010 temperature profiles (Fig. 2.2). However, waters between 100 and 150 m became colder from
April to May 2010, suggesting a mid-water renewal may have occurred (Fig. 2.2). In April 2010 evidence of an inflow was apparent at the outer sites (Fig. 2.2). Unlike in 2008 or 2009, this was a warm water intrusion (Fig. 2.2), indicating that hydrographic conditions on the shelf were different during this El Niño year.

An increase in the amount of densest waters at DFO1 in late April 2008 and May 2009 (Fig. 2.3) confirmed the earlier start of deep water renewal in 2008. There was no evidence of deep water renewal in 2010 (Fig. 2.3). However, as the temperature data, density profiles showed an indication of a mid-water renewal at 100-150 m from April to May, with density increasing from 1025.5 kg m$^{-3}$ to 1026.5 kg m$^{-3}$ (Fig. 2.3). Waters in the upper 200 m were fresher and less dense at the beginning of the sampling season in 2010, the El Niño year, as compared to 2008 and 2009 (Fig. 2.3, Fig. 2.4). In 2008, the outflowing, fresher surface layer was deepest in early June (Fig. 2.4), after the Wannock River freshet on May 19 (Fig. 2.5). By contrast, in both 2009 and 2010 the outflowing surface layer was deepest in late June following the freshet on June 7 and June 3 respectively (Fig. 2.4, Fig. 2.5). Upper 30 m daily temperature and salinity profiles at the Florence Daily station reflected a similar seasonal and interannual pattern as fortnightly and monthly full depth profiles and will not be presented here.

Strong seasonality was observed in wind speed and direction. Winds were strongest in March and switched to northeasterly in May and June (Fig. 2.6). Summer winds off the coast of British Columbia are typically from the north (Whitney et al., 2005). A local orographic effect likely shifts the wind direction to northeasterly in Rivers Inlet. Early spring wind direction differed between years. In 2010 most winds were from the northwest, whereas in 2009 and 2008 strong wind events were from the south (Fig. 2.6). The seasonal switch to northerly winds in summer triggers offshore Ekman transport and coastal upwelling along the eastern North Pacific.
coast (Wilson and Overland, 1986). In Rivers Inlet, this dense water flowing onto the shelf leads to deep water renewal in spring and summer (Hodal, 2011). Deep water renewal (DWR) was strongest and earliest (April 24-July 20) in 2008, from May 4 to July 20 in 2009 (Hodal, 2011), and latest in 2010 (June 20) (M. Hodal, personal communication).

Chlorophyll concentration in late March was the lowest over the sampling season in all years (Fig. 2.7). The warm, stratified 2010 showed the highest late March chlorophyll values, while late March 2009 the lowest (Fig. 2.7). A chlorophyll bloom extending across all the inlet stations was apparent in late April 2008 and 2010, but only in early May in 2009 (Fig. 2.7). The timing of the chlorophyll bloom corresponded to the cruise when surface waters across all the inlet stations where greater than 7.5°C (Fig.2.4 and Fig. 2.7). In 2008, at DFO4 and DFO5, the bloom was already underway in early April (Fig. 2.7). A similar pattern was observed in 2009, with chlorophyll concentrations increasing earlier at the inner sites as compared to the rest of the inlet (Fig. 2.7). The 2010 sampling frequency was too low to discern if this pattern was maintained in 2010. The daily chlorophyll data also confirmed the timing of the spring bloom was latest in 2009, in early May (May 6) (Fig. 2.8). Furthermore, as illustrated by the monthly chlorophyll data, it demonstrated the 2010 bloom occurred in late April (April 22) (Fig. 2.8). However, it was evident that the fortnightly sampling frequency missed the start of the bloom in 2008, with the bloom at the Florence Daily station appearing on April 10, in between the sampling surveys of April 1 and April 24 2008 (Fig. 2.7 and Fig. 2.8). The magnitude of the bloom was highest in 2008 (Fig. 2.7 and Fig. 2.8).
2.3.2 Zooplankton abundance

Cluster analysis of abundance data revealed the presence of eight clusters of differing species composition (Fig. 2.9). The majority of the samples belonged to clusters f and g, two clusters sharing the highest similarity level (80%), but remaining nevertheless quite distinct even in the 2D ordination (Fig. 2.9 and 2.12). These clusters identified a seasonal cycle in zooplankton composition common to all the years sampled. Cluster f was present at the start of the sampling season in all years (Table 2.3), and will be referred to as the winter-spring zooplankton community. In 2010 and 2008 this cluster was only encountered in March or April, but in 2009 it dominated the inlet zooplankton abundance composition until early May (Table 2.3). In the mid to late sampling season, most stations switched to cluster g, the spring-summer zooplankton community (Table 2.3). Cluster g characterized most of the inlet sites in early May 2008, late May 2009, and April and May 2010 (Table 2.3).

Cluster g had a higher overall abundance than cluster f (Fig. 2.10), and was characterized by a higher abundance of appendicularians, cladocerans, and ostracods, the only three taxa showing a significant IndVal in this cluster (Fig. 2.11). They belonged to the winter omnivore-summer herbivore, winter non-feeding-summer omnivores, and carnivores functional groups respectively (Table 2.1). *A. longiremis*, amphipods, bivalves, Cirripedia cyprids, *L. helicina*, *M. pacifica*, and *Pseudocalanus* spp. also increased in abundance in this cluster as compared to cluster f (Fig. 2.10). These taxa, with the exception of Cirripedia cyprids, a non-feeding stage, and bivalves, also belonged to the winter omnivores-summer herbivores, winter non-feeding-summer omnivores, or carnivores functional groups (Table 2.1). By contrast, bryozoans, *Microsetella* spp., and *Microcalanus* spp., all belonging to the year-round omnivores functional group (Table 2.1), displayed a higher abundance in cluster f than cluster g (Fig. 2.10).
Furthermore, they were the only taxa showing a higher IndVal in cluster f than cluster g, albeit no IndVal was larger than 25.

Apart from clusters f and g, cluster h was the only cluster common to all years. It characterized the June zooplankton community at DFO4 in all years (Table 2.3). In June 2008 and 2010 this cluster was present also at DFO5, and in June 2009 and 2010 it extended to DFO3 (Table 2.3). Cluster h had a lower overall zooplankton abundance than cluster g, the spring-summer zooplankton cluster, but higher copepod numbers, due to high densities of Oithona spp. (Fig. 2.10). The abundance of two other year-round omnivorous copepod taxa, Microsetella spp. and Microcalanus spp., were also high in cluster h, while numbers of winter non-feeding-summer omnivores, and winter omnivores-summer herbivores were relatively low (Fig. 2.10). In particular, appendicularians, A. longiremis, Cirripedia nauplii, cladocerans, L. helicina, M. pacifica, and Pseudocalanus spp. decreased in cluster h as compared to cluster g (Fig. 2.10). Cluster h was always observed at the time of the freshet, in early June 2008, and late June 2009 and 2010 (Fig. 2.5), at a time when surface salinities were lowest and estuarine circulation strongest (Fig. 2.4).

In 2008 cluster h was also observed at DFO1 in March and early April, and at DFO2 in late April (Table 2.3). As compared to the winter-spring cluster, f, cluster h displayed a higher overall zooplankton abundance because of higher numbers of A. longiremis, bivalves, cladocerans, L. helicina, M. pacifica, Microcalanus spp., ostracods, and Oithona spp. (Fig.2.10). On the other hand, the abundance of Cirripedia nauplii, Oncaea borealis, and Pseudocalanus spp. was reduced as compared to cluster f (Fig. 2.10). Like cluster f, cluster h displayed a higher concentration of year-round omnivores than cluster g (Fig. 2.10). Temperature data showed that a colder water mass was present at 50 m at DFO1 in late March 2008 (Fig. 2.2). In late March of
2009 and 2010 the inflow was deeper than 50 m (Fig. 2.2) and a different community at DFO1 was not observed (Table 2.3).

The seasonal succession pattern described by the transition from cluster f to g, was not spatially uniform. The zooplankton community at the innermost site, DFO5, in late March 2008 and in 2009 differed from the general succession pattern and was characterized by clusters b and d respectively instead of cluster f (Table 2.3). Both clusters displayed higher abundances of year-round omnivorous copepods, Cirripedia nauplii, and *L. helicina* than the winter-spring cluster (Fig. 2.10). In both years temperature in the upper 100 m at DFO5 was warmer than the rest of the inlet. By contrast, both zooplankton composition and upper 100 m water temperature was quite uniform across the inlet length in early 2010 (Fig. 2.2). Cluster b differed from cluster d because of higher numbers of *A. longiremis*, *C. marshallae*, *M. pacifica*, *O. borealis*, *Pseudocalanus* spp., ostracods, and of *Microcalanus* spp. and Cirripedia cyprids, the two taxa showing their highest IndVal in this cluster, and lower abundance of bryozoans, and *Microsetella* spp., indicator taxa for cluster d, as well as bivalves, Cirripedia nauplii, *L. helicina*, and *Oithona* spp. (Fig. 2.10). The two different zooplankton associations occurred under two distinctive circulation patterns. Temperature profiles demonstrate that late March 2008 was characterized by an outflow between 25-50 m and by an inflow between 50-125 m (Fig. 2.2). On the other hand, in late March 2009 inlet waters were outflowing between 50-100 m and inflowing at 100-150 m (Fig. 2.2). As with the winter-spring cluster, f, both b and d clusters showed a lower abundance of winter omnivores-summer herbivores, winter non-feeding-summer omnivores, and carnivores than the spring-summer zooplankton community, cluster g (Fig. 2.10). More specifically, appendicularians, *A. longiremis*, cladocerans, *L. helicina*, *M. pacifica*, and ostracods were less numerous in cluster b and d than in cluster g (Fig. 2.10).
Zooplankton community composition at DFO3 transitioned from cluster f, the winter-spring cluster, to cluster e in April 2008 before switching to cluster g, the spring-summer cluster, in early May (Table 2.3). Cluster e shared a high similarity with cluster f and g (Fig. 2.9), and appeared to form an intermediate gradient in community composition between the two succession clusters. Like cluster f, cluster e had a higher abundance of bryozoans, and a lower abundance of bivalves, *M. pacifica*, *A. longiremis*, and *Pseudocalanus* spp. than cluster g (Fig. 2.10). However, as with cluster g, it showed a lower abundance of *Microsetella* spp., and higher abundance of *L. helicina* and cladocerans than cluster f. The relative abundance of Cirripedia cyprids, *Microcalanus* spp. and *O. borealis* was higher in cluster e than either cluster f or g (Fig. 2.10). This may indicate some mixing with a water mass characterized by a b cluster zooplankton community, as the b cluster showed a higher abundance of Cirripedia cyprids, *Microcalanus* spp. and *O. borealis* than either cluster f or g (Fig. 2.10). Indeed, the temperature profile shows that an outflowing layer was present at DFO3 in early April above 50 m and below 100 m (Fig. 2.2). This outflow would have carried the late March inner site community, cluster b (Table 2.3), to DFO3, mixing it with cluster f. In early May 2008, when water at 50 m was outflowing (Fig. 2.2), the cluster e zooplankton community would have been transported to DFO2 and transitioned to cluster h (Table 2.3). Cluster e and h show a relatively similar zooplankton composition (Fig. 2.10). However, cluster e, displayed a lower overall zooplankton abundance than cluster h because of the lower abundance of bivalves, *L. helicina* and *Oithona* spp. (Fig. 2.10). In late May 2008, water at 25-75 m was again inflowing (Fig. 2.2) and cluster h transitioned to a cluster b community extending to DFO3 (Table 2.3).

The late May 2008 zooplankton composition also differed from the spring-summer cluster, g, at DFO1, and was characterized by cluster c (Table 2.3). Cluster c displayed a higher
overall abundance than cluster g because of increased numbers of *L. helicina* and copepods (Fig. 2.10). All copepods except *Microsetella* spp. increased in abundance and *Calanus marshallae*, its indicator species (Fig. 2.11), displayed its highest abundance in cluster c (Fig. 2.10). Temperature data demonstrated that in late May, water was inflowing at DFO1 from 25 m downward (Fig. 2.2). This water mass may have carried into the inlet the cluster c community, which persisted until early June (Table 2.3). Cluster c also appeared at DFO5 in early May 2008 (Table 2.3). At this time, deep water renewal that started in late April 2008 had pushed waters below 100 m landwards (Fig. 2.2), possibly concentrating deeper dwelling copepods from mid-inlet stations up to DFO5, and resulting in the appearance of cluster c in early May. The same cluster was also observed at DFO5 in late June 2009 (Table 2.3).

Zooplankton composition in early June at DFO2 developed from cluster b into cluster a, while DFO1 remained characterized by cluster c (Table 2.3). Cluster a differed from cluster b by having a lower overall zooplankton abundance (Fig. 2.10). The only taxa showing a higher abundance in cluster a as compared to cluster b were *A. longiremis*, one of its indicator species (Fig. 2.11), appendicularians, and amphipods. All three taxa were also more abundant in cluster c than b (Fig. 2.10). The only taxon that showed a higher abundance in cluster a as compared to c was Cirripedia nauplii, its other indicator species (Fig. 2.10 and Fig. 2.11). Cirripedia nauplii were more numerous in cluster b than c (Fig. 2.10). Thus, cluster a may have resulted from a mix of cluster b and c taxa. The 50-75 m inflow at DFO1 and DFO2 in early June 2008 (Fig. 2.2) possibly carried *A. longiremis*, appendicularians, and amphipods landward, giving rise to cluster a. The inflow only persisted until DFO2 (Fig. 2.2). At DFO3, the b cluster transitioned back to a cluster c community (Table 2.3, Fig. 2.10).
Among all the input variables (Table 2.2), inflow wind speed, IWS (7 day bin), time since the bloom, TSB, 5 m salinity, S (2 day bin), and Wannock River Flow, WRF (9 day bin), were chosen by BIO-ENV as the best descriptors of the abundance data ordination (Table 2.4). These environmental factors explained 42% of the variation in community structure (Table 2.4). Correlations between each of the above variables and each MDS ordination axis scores revealed that most of the variance explained by the environmental variables was associated with changes in community composition along MDS axis 1, with TSB and WRF9 being both strongly positively correlated to MDS1 and S2 negatively correlated to MDS1 (Table 2.5). The TSB and WRF9 variables were also significantly correlated to MDS2, albeit less so than for MDS1 (Table 2.5). IWS7 was the only variable showing a significantly positive correlation with the MDS3 axis scores (Table 2.5). None of the environmental variables selected by the BIO-ENV analysis were station specific. Thus, the spatial variability in community composition could not be explained by any of the variables inputted in the analysis. Nevertheless, we can assess how clusters that appeared in different cruises are discriminated by the above variables.

Clusters f and d were both early season clusters and, except for two samples overlapping with cluster g in late April 2008 and in late May 2009, always occurred earlier than clusters g, c, and a (Table 2.3). They were associated with low MDS1 scores and displayed earlier TSB, lower WRF9, and higher S2 than clusters g, c, and a (Table 2.6). Cluster g, the late spring-early summer cluster, was associated with higher MDS1 and MDS2 and lower MDS3 than the winter-spring cluster, f. It showed lower IWS7 than cluster f and lower S2, later TSB, and higher WRF9 than cluster f and d (Table 2.6). Cluster c was also a late season cluster and was associated with high MDS1 and MDS2 values and low MDS3. It displayed the highest WRF9, and the second latest TSB of any cluster (Table 2.6). Another late season cluster, a, displayed the lowest MDS2
scores, even if it possessed the latest TSB, and one of the highest WRF9 (Table 2.6). Clusters h, b, and e overlapped with both early and late clusters (Table 2.3) and thus no environmental variable could clearly be associated with them.

2.3.3 Zooplankton biomass

Cluster analysis of the biomass data revealed the presence of ten clusters (Fig. 2.13). Most of the samples belonged to clusters g or h (Table 2.7). As with the abundance-based clusters f and g, biomass-based clusters g and h represented a common succession pattern across all years, with cluster g appearing prior to cluster h (Table 2.7). Similarly to the seasonal succession of abundance-based zooplankton composition, the transition to the spring-summer biomass cluster, h, occurred later in 2009 as compared to 2008 and 2010 (Table 2.7). Cluster h appeared in early May 2009, but was already present in late April in 2008 and 2010 (Table 2.7). The transition from the biomass-based winter spring cluster g, to the spring-summer cluster h occurred two weeks earlier than for the abundant-based clusters (Table 2.3, Table 2.7).

Clusters g and h shared 76% similarity and did not show a significant difference in species composition (Fig. 2.13). Nevertheless, the 3D biomass MDS demonstrated a clear distinction between them, and the remained quite distinct also in the 2D MDS (Fig. 2.14). Furthermore, major differences in species composition were highlighted by the IndVal analysis (Fig. 2.15). Thus, they were considered as separate clusters. Cluster g, the winter-spring cluster, displayed a lower overall biomass than cluster h, the spring-summer cluster, but a higher copepod biomass resulting from increased dominance of winter non-feeding-summer herbivores, as well as *M. okhotensis* (Fig. 2.16). *Neocalanus plumchrus* and *Thysanoessa spinifera* had their highest biomass in cluster g and were indicator species for this cluster (Fig. 2.15). By contrast,
biomass of *A. longiremis*, Aetididae spp., amphipods, appendicularians, Cirripedia cyprids, *Clione limacina*, *Candacia* spp., *Euphausia pacifica*, hydromedusae, *L. helicina*, *M. pacifica*, polychaetes, *Pseudocalanus* spp., and siphonophores was highest in cluster h (Fig. 2.16). With the exception of Cirripedia cyprids, all these taxa are winter-omnivores-summer herbivores, winter non-feeding-summer herbivores or carnivores (Table 2.1).

Cluster b was the only other cluster common to all years (Table 2.7). Like the abundance-based cluster h, it always occurred in June at DFO4 (Table 2.3 and Table 2.7). It also described the zooplankton communities in late June 2009 and early April 2008 at DFO5 (Table 2.7). Cluster b had a lower biomass than the spring-summer cluster, h, and the lowest copepod biomass of any cluster (Fig. 2.16). However, biomass of *Eucalanus bungii*, the taxon with the highest IndVal for this cluster (Fig. 2.15), increased from cluster h to b (Fig. 2.16). Biomass of *C. limacina*, polychaetes, siphonophores, also increased in cluster b as compared to cluster h (Fig. 2.16). Cluster b, as was the case with the abundance-based cluster h, occurred when the estuarine circulation was strongest (Fig. 2.4, Table 2.7).

As for the abundance-based cluster analysis, the highest spatial variability in biomass community composition occurred in 2008. More specifically the outer sites, DFO1 and DFO2, and DFO5 always differed from the common seasonal pattern defined by clusters g and h (Table 2.7). DFO1 in late March and early April 2008 was characterized by cluster f (Table 2.7). Cluster f showed the lowest overall biomass of any cluster and had lower biomass of *L. helicina*, winter non-feeding-summer herbivores copepods, and *M. okhotensis* than the winter-spring cluster g (Fig. 2.16). However, it showed higher abundance of chaetognaths, hydromedusae, *M. pacifica*, and *Paraeuchaeta elongata* (Fig. 2.16), the only taxon displaying a significant IndVal for this cluster (Fig. 2.15).
By contrast, early April 2008 at DFO2 was characterized by cluster a (Table 2.7). This cluster had a higher overall biomass than cluster g because of the increase in *C. limacina*, hydromedusae, *L. helicina*, *Thysanoessa longipes*, and *Thysanoessa raschii* indicator species for this cluster (Fig. 2.15 and Fig. 2.16), as well as *E. pacifica* (Fig. 2.16). As with cluster f, cluster a showed a higher biomass of hydromedusae and a lower biomass of winter non-feeding, summer herbivores than cluster g (Fig. 2.16). This may indicate that some mixing with inflowing water from DFO1 had occurred. Indeed an inflow of cooler water was observed at 25-75 m during this cruise (Fig. 2.2).

Cluster a transitioned to cluster e in late April 2008 at DFO2. Cluster e had the highest biomass of any cluster (Table 2.7). Biomass of *A. longiremis*, *Aetididae* spp., amphipods, appendicularians, *Candacia* spp., *Calanus marshallae*, *Cirripedia* nauplii, *E. pacifica*, its indicator species, hydromedusae, *L. helicina*, *M. pacifica*, ostracods, polychaetes, *Pseudocalanus* spp., siphonophores, *T. longipes*, and *T. raschii* increased as compared to cluster h, the spring-summer cluster (Fig. 2.16). By contrast, the biomass of *E. bungii* and *M. okhotensis* declined in cluster e as compared to cluster h (Fig. 2.16). *E. bungii* is more abundant in the inlet as compared to the shelf (unpublished data). Thus, its decrease is indicative of an inflow of shelf water at depth. Indeed, the temperature profile clearly shows that deep water renewal had started in late April 2008, marked by an inflow of cooler waters below 100 m (Fig. 2.2). Cluster e was also observed in late April 2010 at DFO3 when an inflow to DFO3 was occurring at 100 m (Fig 2.2, Table 2.7). By late May 2010 this community was observed at DFO5 (Table 2.7).

In May 2008 the cluster e community at DFO2 transitioned back to cluster a until early June (Table 2.7). As for cluster e, biomass of *C. limacina*, *E. pacifica*, hydromedusae, *T. longipes*, and *T. raschii* in cluster a were higher than in the spring-summer cluster, h, and
biomass of *E. bungii*, and *M. okhotensis* was lower (Fig. 2.16). However, as for cluster h, the biomass of *A. longiremis*, *C. marshallae*, and *L. helicina* in cluster a was lower compared to cluster e (Fig. 2.16). Cluster a likely arose from a mixing of cluster e and h zooplankton communities following an outflow of upper 25 m waters characterized by cluster h from DFO3 to DFO2 in early May (Fig. 2.2, Table 2.7).

The May to early June 2008 zooplankton biomass taxa composition also differed from the spring-summer community, cluster h, at DFO1, and was described by cluster i (Table 2.7). Cluster i was the cluster with the highest copepod biomass (Fig. 2.10). As compared to cluster h, there was an increase in the biomass of *A. longiremis*, its indicator species (Fig. 2.15), *C. marshallae*, *Candacia* spp., *L. helicina*, *M. pacifica*, and *Pseudocalanus* spp., but a decrease in the biomass of Aetidae spp., appendicularians, *E. bungii*, euphausiids, *M. okhotensis*, *N. plumchrus* and *P. elongata* (Fig. 2.10). As with the abundance-based cluster c, cluster i formed when an intrusion of shelf water reached the DFO1 station (Fig. 2.2, Table 2.7). In late June, cluster i developed into cluster g (Table 2.7). Biomass of appendicularians, Cirripedia nauplii, ostracods, siphonophores, and of all copepods but Aetidae spp., *E. bungii*, *M. okhotensis*, and *N. plumchrus* increased from cluster i to g (Fig. 2.16). However, the biomass of *L. helicina* decreased (Fig. 2.16). Density at 200-225 m increased in late June (Fig. 2.3), an indication that a deeper water mass moved from the shelf into DFO1, possibly generating the cluster i community. Cluster i also characterized the zooplankton community in late June 2010 at DFO1 (Table 2.7). Indeed, temperature between 50 and 150 m at DFO1 decreased from late May to late June 2010 (Fig. 2.2), an indication that an inflow of coastal waters may have occurred.

At DFO2, zooplankton composition in late June 2008 transitioned from cluster a to cluster l (Table 2.7). Cluster l was characterized by a higher Cirripedia nauplii biomass, its
indicator taxon (Fig. 2.15), as compared to cluster a (Fig. 2.16). The cluster l copepod biomass was the lowest of any cluster (Fig. 2.16). All copepod species except for *A. longiremis* decreased in biomass from cluster a to l (Fig. 2.16). The biomass of *L. helicina* also increased from a to l (Fig. 2.16). The late June temperature profiles showed evidence of an inflow of surface waters (75-25 m) from DFO1 to DFO2 (Fig. 2.2). Cluster l likely resulted from the inflow of surface waters from DFO1, characterized by cluster i and high numbers of *A. longiremis* and *L. helicina* (Fig. 2.16), into DFO2. Cluster l was also observed at DFO5 in late June 2008 (Table 2.7). It had a lower biomass of *A. longiremis* and *L. helicina* as compared to the spring-summer cluster, h (Fig. 2.16). The outflowing surface layer was large in late June 2008 (Fig. 2.4), and may have pushed the two taxa down inlet, reducing their biomass at DFO5.

The zooplankton community in late March 2009 and 2010 and early April 2009 was also characterized by cluster l (Table 2.7). Cluster l displayed a higher overall biomass than the winter-spring cluster, g, because of a higher biomass of Cirripedia nauplii and *L. helicina* (Fig. 2.16). However, copepod biomass remained low as compared to cluster g (Fig. 2.16). In late April 2009 the zooplankton composition transitioned from cluster l into cluster d at DFO4 and DFO5 (Table 2.7). Copepod biomass increased as compared to cluster l following a rise in the biomass of *E. bungii* (Fig. 2.16), the species with the highest IndVal for this cluster (Fig. 2.15). In late April 2009, at 130 m, an inflow of cooler waters was evident from DFO1 to DFO5 (Fig. 2.2). It is probable that this deep water inflow concentrated *E. bungii* at the head of the inlet. As in the winter-spring cluster, biomass of winter non-feeding summer herbivores, winter omnivores-summer herbivores, and carnivores in cluster d remained lower than in the spring-summer cluster, while biomass of winter-non feeding-summer herbivores was higher (Fig. 2.16).
As for the abundance-based cluster analysis, biomass-based taxa composition at DFO3 and DFO5 in late June 2010 differed from the spring-summer cluster and was characterized by cluster c (Table 2.3 and Table 2.7). However, unlike the abundance-based cluster h, which was common to all years, cluster c was only observed in 2010 (Table 2.3 and Table 2.7). Cluster c followed cluster e, which was found at DFO5 only in 2010 (Table 2.7), and, like cluster e, it showed a high biomass, the highest of any cluster, of *E. pacifica*, its indicator species (Fig. 2.15). Biomass of *Candacia* spp., *C. limacina, E. bungii, M. okhotensis, P. elongata*, and *T. longipes* rose as compared to cluster e, while biomass of *A. longiremis*, appendicularians, *C. marshallae, M. pacifica*, polychaetes, and siphonophores declined (Fig. 2.16). The strengthening of estuarine circulation in late June 2010 (Fig. 2.4) enhanced the landward flow of deeper dwelling taxa, increasing their biomass at DFO5 and decreased the abundance of more surface dwelling species.

Transitions among biomass clusters were driven by variations in the timing since the bloom (TSB) and 5 m salinity (5 day bin, S5) (Table 2.4). These variables explained 30% of the variance in zooplankton composition (Table 2.4) and were significantly correlated with MDS3 scores (Table 2.5). As for the abundance-based variables chosen by BIO-ENV, TSB and S5 are cruise-specific variables and therefore could not explain spatial variation in community composition. Generally, MDS3 separated clusters that occurred early in the sampling season from samples observed later in the season. Clusters b, e, h, and i displayed lower MDS3 scores, later TSB and lower S5 than clusters g, the winter- spring cluster (Table 2.8). Cluster c was also a late season cluster (Table 2.7) and displayed the latest TSB score (Table 2.8). However, its MDS3 scores overlapped that of both cluster g and h. Similarly, cluster f had one of the earliest TSB, only appearing in late March and early April 2008, but its MDS3 scores were comparable to both cluster g and h (Table 2.8). Thus, while a large part of the variation in MDS3 scores can
be explained by the two environmental variables, there remain some inconsistencies related to the aforementioned clusters.

2.4 Discussion

2.4.1 Pattern of zooplankton succession

One of the main aims of the present study was to understand whether patterns of zooplankton seasonal succession over the late winter-early summer period could be established. Both the abundance and biomass data show an annually recurring zooplankton successional pattern marked by a division between a winter-spring and a spring-summer community. The winter-spring zooplankton community was characterized by a lower abundance of non-copepod zooplankton and low overall biomass. Year-round omnivorous zooplankton, small copepods belonging to the genera *Oithona, Oncaea, Microcalanus* and *Microsetalla* and bryozoans, are more numerous in the winter-spring community. The relative biomass of the winter non-feeding-summer herbivores (*Calanus marshallae, Eucalanus bungii, and Neocalanus plumchrus*) and of *Thysanoessa spinifera* is also greater in the winter-spring community. By contrast, the spring-summer community is dominated by *Limacina helicina*, appendicularians, *Metridia pacifica*, euphausiids, *Acartia longiremis*, cladocerans, *Pseudocalanus* spp., *Clione limacina*, *Paraeuchaeta elongata*, Candacia spp., polychaetes, hydromedusae, siphonophores, and amphipods, all taxa belonging to the winter omnivores-summer herbivores, winter non-feeding-summer omnivores, or carnivores functional groups.
2.4.2 Environmental forcing of zooplankton succession

Both the biomass and abundance-based analyses indicated that the time since the bloom was the variable most highly correlated with changes in community composition, separating the winter-spring from the spring-summer zooplankton communities. It is well established that the spring bloom marks the beginning of zooplankton production in temperate marine systems (Kiorboe and Nielsen, 1994, Longhurst, 1995). Our study broadens this concept by showing not only an increase in zooplankton biomass with the arrival of the spring bloom, but also a change in the relative biomass of specific zooplankton taxa and functional groups, leading to the formation of two separate successional stages in zooplankton community composition.

Analysis of the seasonal patterns of the functional groups reveals how different taxa, best suited to specific trophic niches, dominate during different phases of the seasonal phytoplankton cycle. This conceptual model is summarized in Fig. 2.17. It has to be emphasized that the association between the arrival of the spring bloom and changes in zooplankton community composition remains correlative. Variation in zooplankton community patterns results from complex and species-specific processes such as shifts in zooplankton population dynamics driven by changes in vital rates as well as changes in emigration/immigration. We have shown that community-level succession dynamics are associated with spring bloom timing. However, different forcing variables, which are changing at the same temporal scale as chlorophyll, may be driving the population dynamics of each singular taxon.

Dynamics of the year-round omnivorous zooplankton are uncoupled from the spring bloom and they dominate in the winter-spring. These smaller copepod species belong to Atkinson’s (1998) type II strategy, having an omnivorous diet and an extended period of feeding and reproduction (Atkinson, 1998, Norrbin, 2001, Uye et al., 2002). Their dynamics have been
observed to be uncoupled from the spring bloom in western Greenland (Madsen et al., 2008) and they were also observed to dominate the winter-spring season in the Mediterranean Sea (Mazzocchi et al., 2011). Bryozoans were included in this group because they shared similar seasonal patterns to the small copepods, and also have an omnivorous diet (Barnes and Clarke, 1995). Bryozoans are observed to be an early spring species in Prince William Sound, Alaska (Cooney et al., 2001) and are not dependent on the spring bloom for recruitment (Barnes and Clarke, 1995, Boweden, 2005).

The linkage between the seasonality of the winter non-feeding summer herbivore group and phytoplankton dynamics is also less definitive. All these copepod species belong to Atkinson’s (1998) type I lifecycle strategy, diapausing as late stage copepodites over the winter, and having a short reproductive season. Molting of diapausing stage 5 copepodites into adults is supported largely by lipid stores and consequently does not require active feeding. It happens in late winter, prior to the start of our sampling season (Harrison et al., 1983, Smith and Vidal, 1986, Osgood and Frost, 1994, Mackas et al., 1998, Shoden et al., 2005, Takahashi and Ide, 2011). All three species have one major generation per year and diapause as stage 5 copepodites (Osgood and Frost, 1994, Mackas et al., 1998, Shoden et al. 2005), albeit a fraction of C. marshallae stage 5 may develop into adults and produce a second generation (Osgood and Frost, 1994). Classically, they have largely been considered herbivores (e.g. Harrison et al., 1983). However, recent dietary analysis has shown that both C. marshallae and N. plumchrus can feed omnivorously (El-Sabaawi et al., 2009). In this paper, we have retained the classical view as our study is centered over the spring bloom period when they would be expected to feed on high concentrations of phytoplankton. The biomass of the euphausiid T. spinifera was also higher in the winter-spring community. Unlike the copepods described above, it remains active in winter,
feeding omnivorously (Mauchline and Fisher, 1969). However, as with the winter non-feeding-summer herbivorous copepods, its reproduction starts in February (Feinberg and Peterson, 2003) and can be fuelled by stored lipids (Ju et al., 2009). Its spawning period starts earlier and the lipid stores are larger than those of *Euphausia pacifica* (Feinberg and Peterson, 2003, Ju et al., 2009), the euphausiid species dominating the spring-summer community. Having large lipid stores may allow winter non-feeding-summer herbivorous copepods and *T. spinifera* an earlier start of their annual reproductive cycle and result in their biomass being high in the winter-spring season.

By contrast, except for *T. spinifera*, taxa that are omnivorous in winter but switch to herbivory in spring-summer show an annual seasonal increase that is associated with the seasonal increase in phytoplankton biomass. The interannual variation in the abundance of *L. helicina antarctica*, a related species to *L. helicina*, has been linked to interannual changes in primary production (Seibel and Dierssen, 2003). Thus, their seasonal increase may be dependent on enhanced phytoplankton concentration. Similarly, food supply has been found to affect the developmental time and growth rate of *M. pacifica* (Liu and Hopcroft, 2006). Furthermore, *M. pacifica* stage 5 copepodites rely on the spring bloom to speed-up development and maturation (Padmavati et al., 2004). Thus, development rates of the overwintering stage 5 copepodites or of late winter eggs into adults may be dependent on high chlorophyll concentrations, leading to peak adult biomass in the spring-summer season. Food availability has also previously been observed to be a strong determinant of the appendicularians abundance (Li et al., 2010). Because of their fast growth rates, appendicularians can respond rapidly to increases in phytoplankton biomass (Hoover et al., 2006, Li et al., 2010). Finally, *E. pacifica* juvenile numbers peak in spring (Ross et al., 1982, Bollens et al., 1992) and are reduced when the April chlorophyll
concentration is low (Ross et al., 1982), suggesting *E. pacifica* growth and reproduction may also be strongly dependent on high phytoplankton concentrations. Nevertheless, we stress that the linkage between chlorophyll concentration and zooplankton community composition remains correlative. While we can hypothesize mechanism relating the abundance of these taxa to phytoplankton fluctuations, the uncovering of specific mechanism leading to a change in their population dynamics warrants a more in depth look at their stage-specific abundances, mortality rates, and life-history strategies. Such an analysis is the scope of a separate paper.

Dynamics of the carnivorous zooplankton functional group mirrored those of their spring-summer herbivorous prey, and their peak densities were also associated with the arrival of the phytoplankton bloom. Other studies have reported an increase in predator biomass in summer (Harrison et al., 1983, Bode and Ossorio, 2004). However, peak predator biomass lagged that of their herbivorous copepod prey, happening in summer rather than late spring (Harrison et al., 1983, Bode and Alvarez-Ossorio, 2004). We did not separate developmental stages of chaetognaths, polychaetes, and amphipods. Thus, it may be that the observed spring-summer increase in carnivorous zooplankton was caused by an increase in the biomass of juveniles, and was followed by an increase in adult biomass later in the summer, after the end of our sampling season, which we were unable to capture. The trophic position of juveniles may be different than that of adults, and this might have further enhanced the observed tight coupling between carnivores and their herbivorous prey.

Our analysis shows that the appearance of a third functional group, the winter non-feeding-summer omnivorous group, is also associated with the arrival of the spring bloom. However, we hypothesize that the dynamics of these small, omnivorous taxa may be less dependent on chlorophyll concentrations, with their seasonal abundance increase being only
indirectly associated with the spring bloom via another forcing variable that is changing at the same temporal scale. Cladocerans overwinter as resting eggs whose hatching is temperature dependent (Egloff et al., 1997). In all years, the switch to a spring-summer community occurred after the arrival of the bloom when surface water temperature was > 7.5°C. Thus, the appearance of cladocerans may have been indirectly related to chlorophyll concentrations through the change in temperature. The seasonal increase in *A. longiremis* abundance may also be more dependent on temperature than chlorophyll concentration. Many species belonging to the genus *Acartia* also produce resting eggs (Miller, 2004b). However, *A. longiremis* diapauses in low numbers as immature females (Norrbin, 2001), and the buildup of the population is dependent on the fast development of copepodites in spring (Norrbin, 2001, Debes and Eliaisen, 2006). *A. longiremis* ingestion rates are comparable between bloom and non-bloom phytoplankton concentrations (Debes et al., 2008). Thus, their growth rates may be more dependent on temperature changes. Indeed, both cladocerans and *Acartia* spp. biomass has been observed to be dependent on thermal conditions (Möllmann et al., 2000). Similarly, growth rates of *Pseudocalanus* spp. have been observed to be more temperature-dependent than food-dependent (Liu and Hopcroft, 2008). An assessment of the relative importance of temperature and chlorophyll on the population dynamics of this functional group is necessary.

While a similar zooplankton succession occurs in all years, the timing of the appearance of the spring-summer community varied, occurring a month later (abundance-based analysis) or one and a half months later (biomass-based analysis) in 2009 as compared to 2008 and 2010. The two weeks lag between the abundance and biomass-based succession timing may signify a slower response to environmental forcing of the larger taxa comprising the biomass-based community. The timing of the phytoplankton spring bloom, as the phenology of the zooplankton
community, was later in 2009. We hypothesize that the population increase of the winter omnivorous-summer herbivorous and carnivorous functional groups was delayed in 2009 following the change in phytoplankton phenology.

2.4.3 Spatial variation in zooplankton composition

Zooplankton composition along a fjord’s length is known to vary in response to changes in hydrographic circulation (Stone, 1977, Falkenhaug et al., 1997b). Spatial heterogeneity in community composition following shifts in water circulation was indeed evident in Rivers Inlet. More specifically, zooplankton composition at the inner and outer sites deviated from the rest of the inlet and from the general inlet succession pattern described above. In winter-early spring the head site was characterized by a lower biomass of large copepods, *C. marshallae*, *E. bungii*, *M. pacifica*, *M. okhotensis*, and *P. elongata* than the rest of the inlet. However, as for the winter-spring community, numbers of year-round omnivorous copepods remained higher than in the spring-summer community. Falkenhaug et al. (1997b) also reported that early in the season in Malagen fjord in northern Norway biomass of the dominant winter non-feeding-summer herbivorous copepod, *Calanus finmarchicus*, was higher at outer station than the inner part of the inlet. Kaartvedt and Svendsen (1995) related the different copepod composition at the head of a Norwegian fjord to shallower depths. Water depth may also explain the presence of the different copepod assemblage at head of Rivers Inlet. The head site is 196 m deep, e.g. 100-130 m shallower than the other stations. *C. marshallae*, *E. bungii*, *M. pacifica*, *M. okhotensis*, and *P. elongata* exploit deep water habitat during ontogenetic or daily vertical migrations (Evans, 1973, Osgood and Frost, 1994, Padmavati et al., 2004, Shoden et al., 2005) and may therefore not reside at the shallower head site in winter.
While the head site in winter-spring was always characterized by a higher abundance of year-round omnivores and lower abundance of large copepods than the rest of the inlet, between-year variation in the abundance of specific taxa in response to variation in wind pattern was also evident. Early in the season, river flow is low and the surface layer is thin, thus surface currents in a fjord can become subject to changes in local wind direction (Svendsen, 1981). Early 2008 displayed stronger inflowing winds, which were significantly related to the variation in zooplankton community composition. Wind-induced surface inflows are balanced by subsurface outflows (Baker and Pond, 1995). Such an outflow may have reduced abundance of *Microsetella* spp. *Oithona* spp., bryozoans, and bivalves at the head site in 2008 as compared to 2009. In 2010 the 25-50 m water column showed uniform temperatures across the length of the inlet, suggesting that a subsurface outflow may have had already occurred and waters may have been mixed across the length of the inlet. Abundances of *Microsetella* spp., *Oithona* spp., bryozoans, and bivalves remained lower than in 2009 and comparable to 2008.

Despite differences in community composition as compared to the rest of the inlet, the timing of seasonal succession at the head site corresponded to that of the other stations. Biomass-based community succession in spring 2009 was the only exception, with the change to a different community composition occurring in late April instead of early May as in the rest of the inlet. The shift in biomass-based community composition was due to a sharp increase in the biomass of *E. bungii* at the head sites. *E. bungii* migrates to the surface in response to high chlorophyll concentrations (Tsuda et al., 2006, Yamaguchi et al., 2010a). Thus, in 2009, when the bloom occurred in May, they may have still been at depth in late April and were displaced to the head sites following a mid-water inflow at outer sites.
In all years, biomass of *E. bungii* became higher at the head sites also at the time of the freshet. By contrast, numbers of surface dwelling cladocerans, Cirripedia nauplii, *A. longiremis*, *L. helicina* and appendicularians decreased. Such a reversal of the distribution pattern of deep dwelling zooplankton later in the season is common in many fjords, as increased river discharge carries zooplankton in surface waters downstream and accumulates those remaining in deeper water at the inlet head (Stone, 1977, Fosshagen, 1980, Falkenhaug et al., 1997b). It is interesting to note that daily migrating copepods such as *M. pacifica*, *M. okhotensis*, and *P. elongata* (Evans, 1973, Padmavati et al., 2004) (unpublished data), did not mirror the *E. bungii* distribution pattern, suggesting a degree of stasis due to the opposite actions of water mass movement at day and night depths. Also, no increase in the abundance of *C. marshallae* adults was observed at the head sites, likely as most of the population was characterized by C5 copepodites at the time of peak runoff.

Zooplankton composition at the outer sites also diverged from the common succession pattern, particularly in 2008. It is well known that changes in the circulation (upwelling and downwelling) in the coastal waters adjacent to fjords lead to water exchanges between fjords and outer waters (Fosshagen, 1980, Aksnes et al., 1989). Coastal downwelling has been shown to produce an inflow in the upper part of the fjord intermediate layer and an out-transport below (Aksnes et al., 1989). Such a pattern of in-transport of intermediate waters was evident in Rivers Inlet early in the season in all years. However, depth of inflow varied between years and was shallowest in 2008. *M. pacifica* and *P. elongata*, which remain active in winter (Evans, 1973, Padmavati et al., 2004) increased at the outer sites together with hydromedusae and siphonophores, which are also found in mid-water and remain active in winter (Hosia and Bamstedt, 2007) only in early 2008. This suggests that between years variation in the depth of
inflow, combined with seasonal specific depth distribution of dominant zooplankton taxa on the shelf, may lead to interannual differences in zooplankton composition and deviation from a “dominant” succession pattern at the outer sites.

Upwelling also leads to the appearance of a different zooplankton community at the outer sites (Aksnes et al., 1989, Flakenaugh et al., 1997b). Numbers of C. marshallae adults, the indicator species for this community, increase shoreward during upwelling (Peterson, 1998) and they are more abundant over the shelf than in Rivers Inlet (unpublished data). Thus it is not surprising that they characterized zooplankton composition of inflowing waters at the outer sites after the onset of deep water renewal. However, this late season inflow was only observed in 2008 and 2010 and not in 2009. C. marshallae has been observed to start reproducing in February (Osgood and Frost, 1994). Such early eggs have a high fitness value since reaching the first copepodite stage during the spring bloom enhances survival and recruitment to the next generation in May and June (Osgood and Frost, 1994, Baier and Napp, 2003). The lower biomass of C. marshallae in incoming waters in 2009 may be a consequence of poorer recruitment over the shelf when the bloom was later. Biomass of C. marshallae in the inlet was generally low. It was not an indicator species of any other cluster, thus, while changes in its abundance following a delayed bloom may also have occurred within the inlet population, they were not highlighted as similarity between inlet clusters was likely driven by other taxa.

Year 2009 also lacked the community characterized by high biomass of the euphausiids E. pacifica, T. longipes, and T. raschii. Both the temporal and spatial extent of this community was limited. It appeared only at mid inlet stations, DFO2 in 2008 and DFO3 in 2010, in late April, when zooplankton composition at the majority of the inlet sites shifted to a spring-summer community, as well as at head site in late May 2010. Euphausiids are known to aggregate in
fjords due to a combination of physical and behavioral processes (Zhou et al., 2005). Such an aggregation was absent in 2009. *E. pacifica* juvenile abundance in Puget Sound was greatly decreased when the spring bloom was in May instead of late March or early April (Ross et al., 1982). In 2009 the vernal increase in chlorophyll concentration in the inlet occurred later, and peak euphausiids juvenile numbers may have been reduced. The interplay between juvenile euphausiid concentrations, euphausiid reproduction, aggregation behavior, spring bloom timing, and water circulation in determining spatial and temporal distribution patterns of euphausiids in the inlet certainly warrants further investigation.

Spatial variability in zooplankton composition comprises a large fraction of the unexplained variability in zooplankton composition, particularly for the abundance-based assemblages. When between stations variability was reduced by averaging samples from each cruise across stations prior to analysis, the seasonal succession pattern was reinforced. Most of the change in zooplankton composition was described by the seasonal shift in community composition. Spearman rank correlation coefficients between biotic and abiotic similarity matrices increased from 0.42 to 0.78 for abundance and from 0.30 to 0.54 for biomass, with time since the bloom remaining the most highly correlated variables with changes in zooplankton composition. Spatial distribution of zooplankton in fjords is highly dependent on coastal circulation processes that influence fjord-shelf water exchanges (Aksnes et al., 1989). Our fjord specific environmental variables may not have entirely captured the physical forcing variables, such as density-fields of nearby coastal waters that may drive such exchange processes. Furthermore, recent evidence shows that top-down control may play an important role in controlling copepod variability (Ji et al., 2013). A differing distribution of zooplankton predators
between sites and years may have also led to some of the unexplained spatial variability in zooplankton composition.

2.4.4 Implications for higher trophic levels

El-Sabaawi et al. (2010), using stable isotope and fatty acids to assess the seasonality of copepod trophic dynamics in the Strait of Georgia, suggested that two different pathways of trophic transfer exist in winter and spring, the latter being shorter and more efficient than the first. Our results also indicate that seasonality in phytoplankton is associated with seasonality in zooplankton species composition and thus, with a seasonal change in the energy transfer pathways to higher trophic levels. Our results provide evidence for interannual variability in the timing of zooplankton succession. This phenological shift in zooplankton composition may affect the local food web, which has developed to take advantage of this seasonal biomass increase. Both the type and quantity of zooplankton available to higher trophic levels from March to June, when most fish larvae and juveniles, such as salmon or herring, reside in fjords, differed between years because of a change in the timing of zooplankton community succession, and in the characteristics of inflowing waters. The timing of the juvenile sockeye salmon migration through the inlet is consistent between years (Buchanan, 2007), and the potential for a trophic mismatch between juvenile salmon and its zooplankton prey needs to be investigated.

2.5 Conclusions

This study provides a baseline of zooplankton succession against which future changes in zooplankton community composition can be measured. Our results show that the March-June
zooplankton community composition of Rivers Inlet changed similarly between 2008 and 2010 following a seasonal cycle whose phenology was associated with the timing of the spring bloom. This analysis has been carried out from the perspective of the entire mesozooplankton community, rather than by studying the seasonal patterns of single species or taxonomic groups (e.g. calanoid copepods). Such an approach can be extended to other geographic areas, allowing for an assessment of commonalities in zooplankton succession and of those life history traits (e.g. feeding mode) that define an early species vs. a bloom dominant one. Definition of such functional groups will be essential to assess future scale of zooplankton seasonal variability under climate change, as we can expect different groups to respond differently to changes in the seasonality of environmental forcing. Indeed, our work shows that distinctive taxa responded differently to varying environmental conditions.

The results indicate that seasonal anomalies in the annual climate cycle may directly influence the development of the zooplankton community through changes in phytoplankton dynamics. Thus, we stress the importance of sampling frequently enough to describe the seasonal cycles of both zooplankton and phytoplankton. To be able to predict future changes in the timing of zooplankton succession, we highlight the importance of modeling studies such as that of Wolfe (2010) aimed at predicting the timing of spring bloom dynamics. Furthermore, our data demonstrates that intrusions of coastal waters enhance zooplankton biomass at the outer fjord stations. Therefore, the circulation processes resulting in exchanges between fjord and adjacent coastal waters, as well as the zooplankton dynamics of neighboring water bodies also need to be investigated to assess future zooplankton composition trends.
2.6 Figures

Figure 2.1 Map of Rivers Inlet showing sampling stations. The two insets show a regional map and a close up of the Florence Daily and Laska weather station locations.
Figure 2.2 Along inlet temperature depth profiles collected on each fortnightly (2008 and 2009) and monthly (2010) cruise.
Figure 2.3 Along inlet density depth profiles collected on each fortnightly (2008 and 2009) and monthly (2010) cruise.
Figure 2.4 Along inlet salinity depth profiles collected on each fortnightly (2008 and 2009) and monthly (2010) cruise.
Figure 2.5 Daily timeseries of Wannock River flow (daily average) from March 8 to June 18.
Figure 2.6 Feather plots of the daily mean wind velocity vectors with components $u$ (x component) and $v$ (y component) as arrows emanating from equally spaced points along a horizontal axis. Data shown is from March 8 to June 18 in 2008, 2009, and 2010. Shaded boxes indicate periods of missing data.
Figure 2.7 Along inlet chlorophyll $a$ depth profiles collected on each fortnightly (2008 and 2009) and monthly (2010) cruise.
Figure 2.8 Daily time series of integrated chlorophyll $a$ (0 to 20 m) at the Florence Daily station from March 8 to June 18.
Figure 2.9 Dendrogram of group-averaged clustering from similarities of abundance. Significantly different ($\alpha=0.05$) clusters are marked by a *.
Figure 2.10 Average zooplankton abundance by cluster showing major taxonomic group composition (left panel), and for copepod species only (right panel).
Figure 2.11 Representation of taxa with an IndVal of $\geq 25$ for each of the sample groupings at each hierarchical level of the abundance-based dendrogram. If a cluster did not have a taxon with an IndVal $\geq 25$, the taxon with the highest IndVal as compared to the other cluster at the same hierarchical level is presented. The highest IndVal across all clusters for each taxon is highlighted in bold.
Figure 2.12 Two-dimensional MDS of Bray-Curtis similarities of abundance. Each sample is labeled with the cluster it belongs to.
Figure 2.13 Dendrogram of group-averaged clustering from similarities of biomass. Significantly different ($\alpha=0.05$) clusters are marked by a *.
Figure 2.14 Two-dimensional MDS of Bray-Curtis similarities of biomass. Each sample is labeled with the cluster it belongs to.
Figure 2.15 Representation of taxa with an IndVal of ≥ 25 for each of the sample groupings at each hierarchical level of the biomass-based dendrogram. If a cluster did not have a taxon with an IndVal ≥ 25, the taxon with the highest IndVal as compared to the other cluster at the same hierarchical level is presented.

The highest IndVal across all clusters for each taxon is highlighted in bold.
Figure 2.16 Average zooplankton biomass by cluster showing major taxonomic group composition (left panel), and for copepod species only (right panel).
Figure 2.17 Conceptual model of zooplankton functional groups succession in Rivers Inlet.
### 2.7 Tables

<table>
<thead>
<tr>
<th>Functional Group</th>
<th>Indicator Species</th>
<th>Feeding Mode</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Winter non-feeding, summer herbivores</td>
<td><em>Calanus marshallae</em></td>
<td>Diapause in winter as C5(^1),(^2),(^3) Egg production commences prior to the bloom(^1),(^2) Herbivorous in spring-summer(^3)</td>
<td>(^1)Smith and Vidal, 1986 (^2)Osgood and Frost, 1994 (^3)Harrison et al., 1983</td>
</tr>
<tr>
<td></td>
<td><em>Eucalanus bungii</em></td>
<td>Diapause in winter as C3-C5(^4),(^5) Egg production commences prior to the bloom(^4),(^5) Herbivorous in spring-summer(^4),(^5),(^6)</td>
<td>(^4)Shoden et al., 2005 (^5)Takahashi and Ide, 2011 (^6)El-Sabaawi et al., 2009</td>
</tr>
<tr>
<td></td>
<td><em>Neocalanus plumchrus</em></td>
<td>Diapause in winter as C5(^7),(^8) Herbivorous in spring as C5-C6(^7)</td>
<td>(^7)Harrison et al., 1983 (^8)Mackas et al., 1998</td>
</tr>
<tr>
<td>Year-round omnivores</td>
<td><em>Oithona</em> spp.</td>
<td>Omnivore(^9) Active year-round(^9)</td>
<td>(^9)Lischka et al., 2007</td>
</tr>
<tr>
<td></td>
<td><em>Oncaeae</em> spp.</td>
<td>Omnivore(^10)</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Microsetella</em> spp.</td>
<td>Unknown, likely omnivore(^11)</td>
<td>(^11)Uye et al., 2002</td>
</tr>
<tr>
<td></td>
<td><em>Microcalanus</em> spp.</td>
<td>Omnivore(^12)</td>
<td>(^12)Michels and Schnack-Schiel, 2005</td>
</tr>
<tr>
<td></td>
<td>Bryozoans</td>
<td>Omnivore(^13) Recruitment does not coincide with the seasonal pulse in primary production(^13)</td>
<td>(^13)Barnes and Clarke, 1995</td>
</tr>
<tr>
<td>Winter non-feeding, summer omnivores</td>
<td><em>Acartia longiremis</em></td>
<td>Only a few, diapausing immature females overwinter(^14) Omnivore in summer(^14)</td>
<td>(^14)Norbin, 2001</td>
</tr>
<tr>
<td></td>
<td>Cladocerans</td>
<td>Overwinter as resting eggs(^15) Omnivore in summer(^15)</td>
<td>(^15)Katechakis and Stibor, 2004</td>
</tr>
<tr>
<td></td>
<td><em>Pseudocalanus</em> spp.</td>
<td>Overwinter as late stage copepodites(^16) Omnivore(^16)</td>
<td>(^16)Norbin et al., 1990</td>
</tr>
<tr>
<td>Winter omnivores, summer herbivore</td>
<td><em>Metridia pacifica</em></td>
<td>Overwinters as C5, which remain active and feed omnivorously(^17) Feeds herbivorously in spring(^17) Relies on spring bloom to speed-up development and maturation and induce spawning(^17)</td>
<td>(^17)Padmavati et al., 2004 (^18)El-Sabaawi et al., 2010</td>
</tr>
<tr>
<td></td>
<td>Appendicularians</td>
<td>Present year-round(^19),(^20) Higher biomass at higher Chl a concentrations(^18),(^20),(^21) Picoplankton represents a significant part of their diet only when it dominates biomass(^22)</td>
<td>(^18)Tomita et al., 2003 (^19)Li et al., 2010 (^20)Hoover et al., 2006 (^21)Fernández et al., 2004</td>
</tr>
<tr>
<td></td>
<td><em>Limacina helicina</em></td>
<td>Some adult females overwinter, but most individuals overwinter as veligers(^23) Omnivore over autumn and winter, herbivore in spring and summer(^23)</td>
<td>(^23)Gannefors et al., 2005</td>
</tr>
<tr>
<td></td>
<td><em>Thysanoessa spinifera</em></td>
<td>Can prey on smaller zooplankton, but primarily herbivorous when phytoplankton is abundant(^24)</td>
<td>(^24)Mauchline and Fisher, 1969</td>
</tr>
</tbody>
</table>
### Table 2.1 Division of indicator species by feeding mode.

<table>
<thead>
<tr>
<th>Functional Group</th>
<th>Indicator Species</th>
<th>Feeding Mode</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td><strong>Euphausia pacifica</strong></td>
<td>Can prey on smaller zooplankton, but primarily herbivorous when phytoplankton is abundant&lt;sup&gt;24&lt;/sup&gt;</td>
<td>24Mauchline and Fisher, 1969</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Most individuals overwinter as adult females stage II (immature eggs in ovaries) and mature in late winter&lt;sup&gt;25&lt;/sup&gt;</td>
<td>25Ross et al., 1982</td>
</tr>
<tr>
<td></td>
<td><strong>Thysanoessa raschii</strong></td>
<td>Can prey on smaller zooplankton, but primarily herbivorous when phytoplankton is abundant&lt;sup&gt;24&lt;/sup&gt;</td>
<td>24Mauchline and Fisher, 1969</td>
</tr>
<tr>
<td></td>
<td><strong>Thysanoessa longipes</strong></td>
<td>Can prey on smaller zooplankton, but primarily herbivorous when phytoplankton is abundant&lt;sup&gt;24&lt;/sup&gt;</td>
<td>24Mauchline and Fisher, 1969</td>
</tr>
<tr>
<td></td>
<td><strong>Chaetognaths</strong></td>
<td>Carnivore&lt;sup&gt;10&lt;/sup&gt;</td>
<td>10Miller, 2004a</td>
</tr>
<tr>
<td></td>
<td><strong>Polychaetes</strong></td>
<td>Carnivore&lt;sup&gt;10&lt;/sup&gt;</td>
<td>10Miller, 2004a</td>
</tr>
<tr>
<td></td>
<td><strong>Amphipods</strong></td>
<td>Carnivore&lt;sup&gt;10&lt;/sup&gt;</td>
<td>10Miller, 2004a</td>
</tr>
<tr>
<td></td>
<td><strong>Hydromedusae</strong></td>
<td>Carnivore&lt;sup&gt;10&lt;/sup&gt;</td>
<td>10Miller, 2004a</td>
</tr>
<tr>
<td></td>
<td><strong>Siphonophores</strong></td>
<td>Carnivore&lt;sup&gt;10&lt;/sup&gt;</td>
<td>10Miller, 2004a</td>
</tr>
<tr>
<td></td>
<td><strong>Ostracods</strong></td>
<td>Carnivore&lt;sup&gt;10&lt;/sup&gt;</td>
<td>10Miller, 2004a</td>
</tr>
<tr>
<td></td>
<td><strong>Clione limacina</strong></td>
<td>Feeds exclusively on Limacina helicina&lt;sup&gt;26&lt;/sup&gt;</td>
<td>26Conover and Lalli, 1974</td>
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<tr>
<td></td>
<td><strong>Paraeuchaeta elongata</strong></td>
<td>Carnivore&lt;sup&gt;27&lt;/sup&gt;</td>
<td>27Mauchline, 1998</td>
</tr>
<tr>
<td></td>
<td><strong>Candacia spp.</strong></td>
<td>Carnivore&lt;sup&gt;27&lt;/sup&gt;</td>
<td>27Mauchline, 1998</td>
</tr>
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</table>

### Table 2.2 List of environmental input variables used in the data analysis.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Units</th>
<th>Abbreviation</th>
<th>Sampling Frequency</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Integrated Chlorophyll &lt;i&gt;a&lt;/i&gt;</td>
<td>mg m&lt;sup&gt;-2&lt;/sup&gt;</td>
<td>IChl &lt;i&gt;a&lt;/i&gt;</td>
<td>Daily</td>
<td>Of 11 different moving averages, only the ones with the highest correlation to MDS1 or MDS2 scores from the abundance or biomass MDS analysis were selected</td>
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<tr>
<td>5 m Chlorophyll &lt;i&gt;a&lt;/i&gt;</td>
<td>mg m&lt;sup&gt;-3&lt;/sup&gt;</td>
<td>Chl &lt;i&gt;a&lt;/i&gt;</td>
<td></td>
<td></td>
</tr>
<tr>
<td>5 m Temperature</td>
<td>°C</td>
<td>T</td>
<td></td>
<td></td>
</tr>
<tr>
<td>5 m Salinity</td>
<td>PSU</td>
<td>S</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wind Speed</td>
<td>m s&lt;sup&gt;-1&lt;/sup&gt;</td>
<td>WS</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Inflow Wind Speed</td>
<td>m s&lt;sup&gt;-1&lt;/sup&gt;</td>
<td>IWS</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Outflow Wind Speed</td>
<td>m s&lt;sup&gt;-1&lt;/sup&gt;</td>
<td>OWS</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wannock River Flow</td>
<td>m&lt;sup&gt;3&lt;/sup&gt; day&lt;sup&gt;-1&lt;/sup&gt;</td>
<td>WRF</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intensity of incoming solar radiation</td>
<td></td>
<td>SR</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Distance from the date of the spring bloom</td>
<td></td>
<td>DSB</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Distance from the beginning of deep water renewal</td>
<td></td>
<td>DWR</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Integrated Chlorophyll &lt;i&gt;c&lt;/i&gt;</td>
<td>mg m&lt;sup&gt;-2&lt;/sup&gt;</td>
<td>IChl &lt;i&gt;c&lt;/i&gt;</td>
<td></td>
<td>Fortnightly (2008-2009), monthly (2010)</td>
</tr>
<tr>
<td>5 m Temperature</td>
<td>°C</td>
<td>T5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>50 m Temperature</td>
<td>°C</td>
<td>T50</td>
<td></td>
<td></td>
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<tr>
<td>75 m Temperature</td>
<td>°C</td>
<td>T75</td>
<td></td>
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<td>100 m Temperature</td>
<td>°C</td>
<td>T100</td>
<td></td>
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<tr>
<td>5 m Salinity</td>
<td>PSU</td>
<td>S3</td>
<td></td>
<td></td>
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<tr>
<td>50 m Salinity</td>
<td>PSU</td>
<td>S50</td>
<td></td>
<td></td>
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<tr>
<td>100 m Salinity</td>
<td>PSU</td>
<td>S100</td>
<td></td>
<td></td>
</tr>
<tr>
<td>150 m Density</td>
<td>kg m&lt;sup&gt;-3&lt;/sup&gt;</td>
<td>σ</td>
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Table 2.3 Distribution of abundance-based clusters over space and time. Empty cells were outliers not included in cluster analysis and no samples were collected during the site/cruise combinations marked by NA.

<table>
<thead>
<tr>
<th></th>
<th>DFO1</th>
<th>DFO2</th>
<th>DFO3</th>
<th>DFO4</th>
<th>DFO5</th>
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<tbody>
<tr>
<td>2008</td>
<td>Late March</td>
<td>h</td>
<td>NA</td>
<td>f</td>
<td>b</td>
</tr>
<tr>
<td></td>
<td>Early April</td>
<td>h</td>
<td>f</td>
<td>e</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Late April</td>
<td>g</td>
<td>e</td>
<td>f</td>
<td>NA</td>
</tr>
<tr>
<td></td>
<td>Early May</td>
<td>g</td>
<td>h</td>
<td>g</td>
<td>g</td>
</tr>
<tr>
<td></td>
<td>Late May</td>
<td>c</td>
<td>b</td>
<td>b</td>
<td>g</td>
</tr>
<tr>
<td></td>
<td>Early June</td>
<td>c</td>
<td>a</td>
<td>e</td>
<td>h</td>
</tr>
<tr>
<td></td>
<td>Late June</td>
<td>g</td>
<td>a</td>
<td>e</td>
<td>g</td>
</tr>
<tr>
<td></td>
<td>Late March</td>
<td>f</td>
<td>f</td>
<td>f</td>
<td>f</td>
</tr>
<tr>
<td></td>
<td>Early April</td>
<td>f</td>
<td>h</td>
<td>f</td>
<td>f</td>
</tr>
<tr>
<td></td>
<td>Late April</td>
<td>f</td>
<td>f</td>
<td>f</td>
<td>f</td>
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<td></td>
<td>Early May</td>
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<td>g</td>
<td>f</td>
<td>f</td>
</tr>
<tr>
<td></td>
<td>Late May</td>
<td>g</td>
<td>g</td>
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<tr>
<td></td>
<td>Early June</td>
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<td>g</td>
<td>NA</td>
<td>NA</td>
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<tr>
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<td></td>
<td>Late March</td>
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<td>Late April</td>
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<td></td>
<td>Late June</td>
<td>g</td>
<td>h</td>
<td>h</td>
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</tr>
</tbody>
</table>

Table 2.4 Combination of the environmental variables yielding the best match of biotic and abiotic similarity matrices as measured by Spearman rank correlation, r. IWS is the inflow wind speed, S is daily 5 m salinity, TSB is the time since the spring bloom, and WRF is the Wannock River flow.
### Abundance

<table>
<thead>
<tr>
<th></th>
<th>TSB</th>
<th>S2</th>
<th>IWS7</th>
<th>WRF9</th>
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<tr>
<td>a</td>
<td>68±8</td>
<td>28.0±0.6</td>
<td>1.9±1.1</td>
<td>494±66</td>
</tr>
<tr>
<td>b</td>
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</tr>
<tr>
<td>c</td>
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<td>29.0±0.6</td>
<td>2.9±1.5</td>
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</tr>
<tr>
<td>d</td>
<td>-25±8</td>
<td>30.0±0.3</td>
<td>3.8±1.2</td>
<td>126±50</td>
</tr>
<tr>
<td>e</td>
<td>35±20</td>
<td>28.9±0.6</td>
<td>11.1±6.7</td>
<td>294±119</td>
</tr>
<tr>
<td>f</td>
<td>-23±4</td>
<td>29.8±0.1</td>
<td>7.3±2.2</td>
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</tr>
<tr>
<td>g</td>
<td>27±4</td>
<td>29.4±0.1</td>
<td>2.7±0.6</td>
<td>323±38</td>
</tr>
<tr>
<td>h</td>
<td>35±10</td>
<td>29.1±0.3</td>
<td>6.8±3.9</td>
<td>400±69</td>
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</table>

Table 2.6 Abundance-based cluster means of each environmental variable selected by the abundance-based BIO-ENV analysis. IWS is the inflow wind speed, S is daily 5 m salinity, TSB is the time since the spring bloom, and WRF is the Wannock River flow. Cluster means for the binned variables (e.g. S2) were divided by the length of the bin (days) and are presented as average daily values.
<table>
<thead>
<tr>
<th></th>
<th>DFO1</th>
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<th>DFO3</th>
<th>DFO4</th>
<th>DFO5</th>
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<td>Late March</td>
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<td>g</td>
<td></td>
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<td>f</td>
<td>a</td>
<td>g</td>
<td>b</td>
<td></td>
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<tr>
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<td>e</td>
<td>h</td>
<td>h</td>
<td></td>
<td>NA</td>
</tr>
<tr>
<td>Early May</td>
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<td>h</td>
<td>g</td>
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<td>d</td>
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<td>h</td>
<td>e</td>
</tr>
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<td>Late June</td>
<td>i</td>
<td>h</td>
<td>c</td>
<td>b</td>
<td>c</td>
</tr>
</tbody>
</table>

Table 2.7 Distribution of biomass-based clusters over space and time. Empty cells were outliers not included in cluster analysis and no samples were collected during the site/cruise combinations marked by NA.

<table>
<thead>
<tr>
<th>Biomass Cluster</th>
<th>TSB</th>
<th>S5</th>
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</thead>
<tbody>
<tr>
<td>a</td>
<td>32±30</td>
<td>29.0±1.3</td>
</tr>
<tr>
<td>b</td>
<td>39±28</td>
<td>29.0±0.9</td>
</tr>
<tr>
<td>c</td>
<td>57±0</td>
<td>29.2±0</td>
</tr>
<tr>
<td>d</td>
<td>-13±10</td>
<td>29.9±0.6</td>
</tr>
<tr>
<td>e</td>
<td>14±13</td>
<td>29.6±0.2</td>
</tr>
<tr>
<td>f</td>
<td>-16±9</td>
<td>29.5±0.1</td>
</tr>
<tr>
<td>g</td>
<td>-18±33</td>
<td>29.9±0.8</td>
</tr>
<tr>
<td>h</td>
<td>26±25</td>
<td>29.4±0.5</td>
</tr>
<tr>
<td>i</td>
<td>49±13</td>
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</tr>
<tr>
<td>l</td>
<td>7±62</td>
<td>29.7±0.7</td>
</tr>
</tbody>
</table>

Table 2.8 Biomass-based cluster means of each environmental variable selected by the biomass-based BIO-ENV analysis. IWS is the inflow wind speed, S is daily 5 m salinity, TSB is the time since the spring bloom, and WRF is the Wannock River flow. Cluster means for the binned variables (e.g. S5) were divided by the length of the bin (days) and are presented as average daily values.
Chapter 3: Variability in the vertical distribution and advective transport of eight mesozooplankton taxa in Rivers Inlet, British Columbia, Canada, in spring.

Zooplankton vertical distribution data and velocity estimates from a hydrodynamic model were employed to determine zooplankton daily exchange rates from March to June 2010 in Rivers Inlet, a fjord in central British Columbia, Canada. Zooplankton transport rates varied seasonally, being fastest in March and April when water velocities were highest. The active vertical movement of the zooplankton interacted with the vertically sheared flow field to influence zooplankton advection. Surface dwelling plankton, such as copepod eggs and larvaceans experienced the highest advection losses, averaging -0.07 and -0.08 day$^{-1}$, respectively over the sampling season. By contrast, the mean exchange rate of *Paraeuchaeta elongata*, a deeper dwelling copepod, was 0.004 day$^{-1}$. Transport rates varied by stage, extent of diel vertical migration, and timing of ontogenetic migration. For all taxa, local biological processes dominated over advection in regulating zooplankton abundance over the sampling season. However, when local production was low, advection became an important determinant of population variability. We conclude that advection may be a significant driver of population dynamics in years with similar rates of population growth. We also stress the importance of determining advection rates to obtain accurate estimates of vital rates.
3.1 Introduction

Zooplankton, the most numerous multicellular animal group on earth (Schiminke, 2007), play a critical role in transferring energy to upper trophic levels as well as in the cycling of nutrients and carbon in biogeochemical cycles (e.g. Morales, 1999, Beaugrand et al., 2003, Ware and Thomson, 2005, Steinberg et al., 2012). Thus, to achieve an understanding of the structure and function of marine ecosystems, the mechanisms driving fluctuations in zooplankton populations should be determined and quantified. These fluctuations are produced by changes in vital life cycle rates such as birth, development, and mortality. Zooplankton ecologists have developed population growth models and fit them to in situ abundance data to obtain estimates of these vital rates (e.g. Batchelder and Miller, 1989, Neuheimer et al., 2010). Mortality rates, which cannot be easily obtained experimentally, are most often computed using such inverse methods. For many of these approaches, the validity of estimates of vital rates relies on the assumption that the samples collected represent the “true population” abundance unbiased by advection (e.g. Wood, 1994).

Zooplankton, derived from the Greek “planktos”, meaning drifter, are by definition influenced by advection as they are not large enough to swim against horizontal currents. Interannual changes in ocean circulation have been shown to determine zooplankton community composition and abundance at mesoscales (Davis, 1984a, Mackas et al., 2001, Edvardsen et al., 2003, Batten and Freeland, 2007, Keister, et al., 2011, Sydeman, et al. 2011). Circulation processes have also been shown to affect the abundance of mesozooplankton at smaller spatial scales, such as in the English Channel (Irigoien and Harris, 2003), the Gulf of St. Lawrence and Scotian Shelf (Zakardjian et al., 2003, Maps et al., 2011), bays (Ambler et al., 1985, Roman et al., 2001, Plourde et al., 2002, Marques et al., 2006, Hsieh et al., 2010), and fjords (Matthews
Zooplankton can, however, actively change their vertical position in the water column. Many species are known to undergo extensive vertical migrations from below the photic zone to productive surface waters on a daily basis (e.g. Hays, 1995). In areas of vertically sheared flow, this active vertical movement can actually serve as a mechanism to keep zooplankton in one place or move them in a specific direction. For example, in upwelling systems, diel vertical migration tends to retain zooplankton in the nearshore upwelling zone (Wroblewski, 1982, Mackas, 1992, Batchelder et al., 2002, Mackas and Coyle, 2005). In shallow, tidal estuaries, some zooplankton undertake short vertical migrations in synchrony with the tides to reduce outflow losses (Kimmerer and McKinnon, 1987). In fjords, taxa, such as cladocerans, that inhabit the fast flowing, brackish, surface layer, can be decimated by freshwater driven flushing (Kaartvedt and Svendsen, 1995). However, advection losses in a fjord may be insignificant for species such as *Metridia lucens*, that undergo diel vertical migration and spend the majority of their day below the surface layer (Lewis and Thomas, 1986).

In addition to diel vertical migration behaviour, zooplankton, such as copepods, undertake pronounced seasonal ontogenetic vertical migrations in spring as they exit the deep diapausing layer and move to the surface to reproduce (Mackas, 1992). Interaction of current shear with this active seasonal vertical movement may result in seasonally varying zooplankton advection rates. For example, Slagstad and Tande (1996) showed that seasonal vertical migration of *Calanus finmarchicus* adults enhances advection onto the Norwegian shelf during the ascent phase of their ontogenetic migration. Krause and Lewis (1979) reported that the timing of ontogenetic migration of *E. bungii* in the Strait of Georgia might influence advection into
adjoining fjord systems. Similarly, in upwelling systems, seasonal descent of stage five copepodites lengthens the reproductive season by enhancing on shore transport, leading to a high abundance of females in chlorophyll rich coastal waters (Peterson et al., 1979, Wroblewski, 1982). Clearly, the interaction of active zooplankton vertical movement and current shear can impact zooplankton advection at a variety at temporal scales, underlying the importance of resolving their seasonal and diel vertical movements when assessing advection patterns.

Despite transport processes being important in shaping zooplankton populations at a variety of spatial scales, there remains a need to assess more quantitatively how advection relates to biological rates and to what extent it controls temporal variability in zooplankton abundance. Aksnes et al. (1989) reported that in June and October advection of mesozooplankton in a fjord in western Norway could have exceeded local growth. Nielsen and Andersen (2002) showed that in a western Norwegian fjord July copepod biomass might be equally driven by advection and local production. The above examples indicate that advection can clearly control zooplankton biomass temporally. In temperate regions zooplankton seasonal production is known to appear in a specific time window (Longhurst, 1995). Thus, a seasonal comparison of the relative influence of advection and local biological processes on population dynamics, including the period of highest local production, has to be undertaken. Such a study was conducted by Edvardsen et al. (2003) on Calanus finnarchicus population dynamics in the western Barents Sea. This modeling study reported that increases in population size due to advection from March to October are four times higher than those due to local production. Conversely, biological rates dominate over advection rates in determining C. finnarchicus yearly dynamics in the Norwegian Sea (Aksnes and Blindheim, 1996) and on Georges Bank from January to June (Li et al., 2006). Even if transport may ultimately be a driver of zooplankton population dynamics in some regions,
estimates of zooplankton advection rates remain few and are restricted to a handful of species (e.g. *C. finmarchicus*), times of year, and geographic locations. In part, this is due to advection estimation being logistically challenging, requiring assessment of the vertical migration pattern of zooplankton species throughout their life cycle as well as concurrent estimates of water velocities.

It has previously been inferred that horizontal transport influences zooplankton abundance in British Columbia (Canada) fjords (Stone, 1977, Krause and Lewis, 1979, Gardner, 1982, Lewis and Thomas, 1986). However, in these studies zooplankton advection was addressed only qualitatively and neither estimates of transport rates nor a comparison of local biological rates vs. advection rates were undertaken. In this paper, we quantitatively estimate the interaction between zooplankton vertical distribution and migration and horizontal flows in Rivers Inlet, a British Columbia fjord, and its potential role in species population dynamics. We focus on the key copepod taxa driving the zooplankton community seasonal succession (Tommasi et al., 2013b): *Acartia longiremis, Metridia pacifica, Calanus marshallae, Eucalanus bungii, Paraeuchaeta elongata*, copepod eggs, cladocerans, and larvaceans. Specifically, we aimed to 1) determine the seasonal vertical distribution of the zooplankton taxa, 2) assess if the different vertical distribution of zooplankton taxa interacts with horizontal flows to produce taxon-specific advection rates, 3) evaluate if advection rates differ between various developmental stages, and ultimately 4) assess if advection is an important term in determining changes in the population size as compared to local biological processes.
3.2 Methods

For a description of the study area please refer to section 2.2.1.

3.2.1 Field sampling

Zooplankton vertical hauls with a Bongo net equipped with a 150 \( \mu \text{m} \) mesh net were conducted monthly in Rivers Inlet from March to the end of June 2010. All hauls were conducted during the day, from \(~5\) m above the bottom, or to a maximum depth of 300 m, to the surface across four sampling stations (DFO2-DFO5) equally spaced along the length of the inlet (Fig. 2.1). The Bongo net was harnessed with a General Oceanics mechanical flowmeter for volume filtered estimation from each haul. To determine the zooplankton vertical distribution additional zooplankton vertical hauls were carried out in the following depth intervals: 300-0, 100-0, 30-0, and 10-0 m at DFO2 both during the day and night on every cruise. A 2-0 m oblique tow was also obtained. After each haul the net was rinsed and the samples were preserved in a 5 \% formalin-seawater solution.

Prior to every Bongo net deployment, profiles of temperature (\( ^\circ \text{C} \)), salinity (S), and fluorescence were collected for entire water column with a SBE 25 CTD.

Daily averages of wind speed and direction for Rivers Inlet were obtained from the Laska weather station, located close to the daily sampling site (Fig. 2.1) (refer to Hodal, 2011 for details). M. Hodal also provided daily Wannock River flow (WRF) estimates, computed using Owikeno Lake water levels obtained from Environment Canada’s station 08FA007 (50° 41’ 26’’, 127° 09’ 43’’) and an empirical relationship between Owikeno Lake water levels and WRF. This empirical relationship was derived by M. Hodal from a table of both WRF and water levels obtained from Environment Canada (refer to Hodal, 2011 for details).
3.2.2 Zooplankton taxonomic analysis

Each sample was first examined for the presence of rare, large organisms such as hydromedusae, fish larvae, and euphausiids, which were counted and then removed from the full sample. The remaining sample was then split with a box plankton splitter to generate subsamples with approximately 100 individuals for the > 2 mm size fraction and 400 for the < 2 mm size fraction. Copepod adults and copepodites from stages 4 and 5 were identified to species. Copepodites 1 to 3 were identified to family for Calanidae copepods and to species for Metridia pacifica, Eucalanus bungii, Paraeuchaeta elongata, and Acartia longiremis. Because Calanus marshallae was the numerically dominant Calanidae copepod in this system, we assume that most of the Calanidae copepodites identified belong to this species and we refer to them as Calanus marshallae C1-C3 throughout this paper. Copepod eggs were counted but not identified to species. Cladocerans and larvaceans were identified to species whenever possible, but data are presented in these larger taxonomic categories as all species showed a similar vertical distribution. Zooplankton density was expressed on a unit volume basis (ind. m$^{-3}$). Moreover, zooplankton abundance on a unit area basis (ind. m$^{-2}$) was computed by multiplying the zooplankton density (ind. m$^{-3}$) by the water column sampled.

3.2.3 Data analysis

Zooplankton advection in and out of the inlet was estimated by computing zooplankton daily exchange rates, a measure of what fraction of the total zooplankton inlet population was transported in/out of the inlet for each day over the sampling season, using velocity depth profiles and depth resolved abundance data. Water velocities were acquired for DFO2 (Fig. 2.1),
see below. Zooplankton abundance vertical profiles were also sampled at this station. Therefore, DFO2 was considered as the inlet boundary.

3.2.3.1 Water velocities

Yeremy (2010) developed a 2-D circulation model of Rivers Inlet based on the 2-D numerical circulation model of Knight Inlet, British Columbia (Yeremy and Stacey, 1998). Wind, river flow, tides, and solar heating drive water circulation in the model. It consists of 175 center points aligned from DFO2 (taken as the inlet mouth) to the head of the inlet, 31 km landward. The vertical resolution of the model is represented in Fig. 3.2 and consists of a total of 40 vertical points. The model has a high vertical resolution in the first 10 m, with velocity estimates less than every meter to resolve the shallow freshwater layer at the surface.

Average hourly horizontal velocities (cm s\(^{-1}\)) at the DFO2 station from March to June 2010 were obtained from Yeremy’s 2-D circulation model described above. The CTD data collected on monthly cruises provided initial temperature and salinity fields as well as boundary data (i.e. depth profiles of temperature and salinity at the boundary, DFO2). Prior to computation of zooplankton advection rates, vertical velocities resolved at every meter for the entire water column were determined by linearly interpolating the velocity depth profiles outputted from the model.

The hourly velocities (cm s\(^{-1}\)), resolved at every meter, were converted to m hr\(^{-1}\) and summed over day and night hours to obtain day and night velocity estimates (m daytime\(^{-1}\) and m nighttime\(^{-1}\)) for each daytime and nighttime period during the sampling period. Length of daylight was computed from tables of standard times of solar rise/set for Port Hardy, British Columbia (127° 25’ W 50° 42’ N) downloaded from the National Research Council of Canada.

Fluxes of water (m$^3$ daytime$^{-1}$ and m$^3$ nighttime$^{-1}$) were computed by multiplying, at every meter, the day and night velocity estimates (m daytime$^{-1}$ and m nighttime$^{-1}$) by the inlet cross-sectional area (m$^2$) at DFO2 in each 1 m layer (height=1 m, width=inlet width at DFO2 at each depth). Depth resolved cross-sectional widths at DFO2 were extracted from a digital bathymetric map. Linear interpolation was used to obtain cross-sectional widths resolved at every 1 m depth.

### 3.2.3.2 Zooplankton vertical distribution

The vertical hauls conducted at DFO 2 were used to infer the vertical distribution of the zooplankton. They provided abundance data (ind. m$^{-2}$) in the following depth strata: 2-0 m, 10-0 m, 30-0 m, 100-0 m and 300-0 m during the day and the night. From these, the abundance (ind. m$^{-2}$) in each layer was computed by subtraction. For example, to obtain the number of individuals m$^{-2}$ from 2-10 m, the 2-0 m abundance estimate was subtracted from the 10-0 abundance. In those instances where the subtraction produced negative abundance values; the abundance was taken to be 0. These abundances were then transformed into relative abundance by comparing them to the total 0-300 m abundance (considered 100%).

Since depth stratified samples were not available for the other stations, their average depth layer abundance (ind. m$^{-2}$) was calculated by multiplying the frequency distribution estimates from DFO2 by the total station specific abundance (ind. m$^{-2}$). It was assumed that the zooplankton vertical distribution remained the same over the month and between stations. The abundances (ind. m$^{-2}$) were converted to densities (ind. m$^{-3}$) by dividing by the depth of the layer.
Bottom depth at the DFO2 station was 320 m. It was assumed the zooplankton density (ind. m\(^{-3}\)) in the bottom 20 m remained equal to the one in the 100-300 m layer. The same calculation was performed on the night samples.

Information on the vertical distribution of each taxa on each cruise and time of day was summarized by computing a weighted mean depth (WMD) as outlined in Andersen et al. (2001). The full vertical distribution profiles for each species and stage are also presented.

### 3.2.3.3 Zooplankton daily exchange rates

To obtain daily transport estimates past DFO2 given the vertical hauls monthly sampling frequency; we first had to assume that the zooplankton day and night vertical distribution remained constant over each month. Second, we applied a linear interpolation between consecutive cruises to attain daily estimates of zooplankton densities between cruises. Finally, to relate the vertical zooplankton density profiles to the velocity depth profile with a 1 m resolution by depth, we assumed that the zooplankton were evenly distributed in each of the zooplankton sampling layers to obtain zooplankton density estimates at every meter. The water flux in each 1 m layer (m\(^3\) daytime\(^{-1}\) and m\(^3\) nighttime\(^{-1}\)) was then multiplied by the zooplankton density (ind. m\(^{-3}\)) in each layer during the day and night to compute an estimate of the number of individuals transported past DFO2 (ind. daytime\(^{-1}\) and ind. nighttime\(^{-1}\)). These per layer estimates of transport were integrated over the entire water column to obtain the total number of individuals transported past DFO2 in the daytime and nighttime.

To compute the daily exchange rate, we had to also estimate the zooplankton density per layer during the day and night in the entire inlet. To do so, we multiplied the average inlet zooplankton concentration (ind. m\(^{-3}\)) during the day and night, by the total inlet volume in that
layer (m$^3$). Depth resolved inlet (DFO2 – head) volumes were computed by cumulative trapezoidal integration of 1 m resolved cross sectional center points widths along the inlet length.

The number of individuals in each layer (ind.) was summed over the entire water column to obtain a total number of individuals in the inlet per sampling cruise during the day and the night. Again, linear interpolation between consecutive cruises was employed to determine daily estimates of the total number of individuals in the inlet.

The daytime exchange rate (daytime$^{-1}$) was computed by dividing the total number of individuals transported past DFO2 during the day (ind. daytime$^{-1}$) by the total population in the inlet (ind.). The nighttime exchange rate was similarly computed using the night values. The two were added together to obtain an estimate of the daily exchange rate (DER) (day$^{-1}$).

The coarse resolution of the bottom zooplankton vertical sampling layer was a potential source of error to our DER estimates. To explore the sensitivity of the estimated DERs to different zooplankton distribution modes in the bottom layer, three test case models were developed. In the first, rather than assuming that zooplankton were evenly distributed in the bottom layer, zooplankton were considered as being concentrated between 100-120 m. In the second scenario, zooplankton were concentrated between 200-220 m, and in the third between 300-320 m.

### 3.2.3.4 Total advective transport

To assess the relative importance of advection in influencing population dynamics in comparison to local processes, such as birth, mortality and molting, we first estimated the population size of each taxa and stage on each day of the sampling period as if influenced only by advection according to the following equation:
\[ N_{t+1} = N_t + aN_t \]

Where \( N_t \) = total number of individuals in the inlet (At \( t = 0 \), \( N_t = N_o \) = total number of individuals in the inlet on cruise 1)

\( a \) = daily exchange rate (day\(^{-1}\))

\( t \) = sampling day (\( t = 0 \) is the date of cruise 1)

This calculation was carried out iteratively until the following cruise, on which day the abundance was re-seeded with the actual numbers observed in that cruise.

Second, we computed the total number of individuals of each taxa and stage lost or gained between consecutive cruises as the difference between the abundance on the day prior to the following cruise as calculated by our iterative model to the abundance on the initial cruise. This value was used to estimate the percentage of the initial population size that was lost/gained between cruises due to advection (A). Third, the actual percentage change in population size that was observed between cruises (T) was calculated. This was the ratio of the abundance on the initial cruise to the total number lost between cruises. The total number lost between cruises was computed as the difference in abundance between consecutive cruises. Finally, we estimated the change in population size due to local processes (L) as the difference between T and A. If advection is the dominant process in determining local population size, the ratio A/L > 1, but if A/L < 1 local processes dominate. Nielsen and Andersen (2002) similarly estimated the balance between local production rate and the advective rate as the ratio between experimentally derived production rates and advective rate. However, here our “production rate” represents “local processes” net gain/loss, as it also includes losses due to mortality and molting as well as production. Furthermore, any errors in the daily advection rate calculation will be included in this estimate of the change in population size due to local processes.
It has to be pointed out that because zooplankton samples were collected with a 150 μm mesh, small zooplankton may have been undersampled. The study of Nichols and Thompson (1991) has been widely accepted as a general guide on the effect of mesh size on zooplankton extrusion (Sameoto et al., 2000). They showed that almost all copepods (95%) would be captured by a net with a mesh size that is 75% of the copepods carapace width. Thus, in our study, we undersampled any zooplankton smaller than the mesh opening as well as those with a carapace width smaller than 113 μm, such as some copepod eggs, *A. longiremis* copepodites of stage 3 and below, *Metridia pacifica* copepodites of stage 2 and below, and Calanidae stage 1 copepodites. Since our estimates of zooplankton abundance are an underestimate relative to actual population numbers, we underestimated production for these taxa. Thus, comparison of advection losses vs. local process was not undertaken for these groups.

3.3 Results

3.3.1 Water velocities

Water velocities showed a clear pattern with depth and with season. They were always highest at the surface and were generally fastest in March (Fig. 3.1a and b). The surface velocity field was highly time-dependent (Fig. 3.1b), showing frequent directional changes driven by the fluctuating wind stress. These strong velocity events could extend 15 m into the water column in March and April (Fig. 3.1b). By contrast, high velocities were generally restricted to the top 2 m in May and June (Fig. 3.1b).

In May and June, the water circulation resembled that of a typical estuary, with a seaward flowing surface layer above ~5 m, and a persistent subsurface inflowing layer between 5-13 m. It has to be noted that flow direction in the top 2 m remained highly time-dependent and wind
driven. Earlier in the season the inflowing subsurface layer was more intermittent and deeper, extending to a depth of 150 m in March (Fig. 3.1a). It gradually decreased to a depth of 50 m in April and then to 13 m in May (Fig. 3.1a and b). Below this subsurface inflowing layer was an extensive (down to 250 m), persistent, slow moving outflowing layer. The layer from 250 m to the bottom was relatively stationary from the end of April onwards. In addition to this general flow pattern, we observed an intermediate inflowing layer at depth from ~125-200 m in late April to mid-May (Fig. 3.1).

As water velocities were highest at the surface, daily water exchange rates of the top 10 m (the ratio between the incoming/outgoing flux and the inlet volume in the first 10 m) were large, especially in March and April (Fig. 3.1c). At times, 80% of the top 10 m layer was washed out past DFO2 in a day (Fig. 3.1c). However, average exchange rates of the top 10 m over the entire sampling season were 0.05±0.2 (mean ± SD) day\(^{-1}\), corresponding to a retention time for the top 10 m of 20±5 days.

### 3.3.2 Zooplankton vertical distribution

Cladocerans were absent in March and showed the shallowest vertical distribution of all the zooplankton under study in April and May with an average weighted mean depth WMD of 5±2 m (WMD ± SD) across the time of day in this period (Fig. 3.2a). In June 40% and 10% of the population was also found below 100 m depth during the day and night, respectively (Fig. 3.2a).

Larvaceans showed a shallow, seasonally uniform vertical distribution with the majority of the population found above 40 m (Fig. 3.2b). However, in May their WMD was deeper, as
they showed a bimodal distribution with 30% of the larvacean population being found below 100 m (Fig. 3.2b).

Copepod eggs showed a shallow daytime vertical distribution from March to May with an average WMD of 15±22 m across the sampling season (Fig. 3.2c). By contrast, in June eggs were more numerous below 100 m (Fig. 3.2c). At night, eggs were always more numerous at depth except in April (Fig. 3.2c).

*Acartia longiremis* stage C1-C4 also showed a shallow daytime distribution, centered above 10 m (Fig. 3.3). Exceptions to this pattern occurred in June when 30% of the C2 population was found below 100 m. The C1-C4 night distribution was comparable to the daytime one with the exception for C1 and C2 in March, when 60% and 100 % of the population was found below 100 m, respectively (Fig. 3.3). Stage C5 in March, April, and June also showed a uniform shallow distribution during the day and night, with a mean WMD of 17±7 m (Fig. 3.3). However, in May stage C5 showed a bimodal distribution with 50% of the population also found below 100 m (Fig. 3.3). Adult females were on average distributed deeper in the water column and showed a larger seasonal variation in their WMD (Fig.3.3). They appeared to perform a reverse diel vertical migration in March and April, moving from a WMD of 42±42 m to 189±43 m in March and 4±2 m to 57±35 m in April (Fig. 3.3). In May, they had a daytime WMD of 76±37 m and 60% of the population performed a reverse DVM, moving below 100 m at night, while the rest of the population moved to the surface above 10 m (Fig. 3.3). In June, all were performing DVM with a day WMD of 41±16 m and 15±5 m at night (Fig. 3.3).

*Calanus marshallae* also presented its shallowest distribution for its youngest stage, C1 (Fig. 3.4). Stage C1 was absent in June and showed a uniform, shallow average daytime WMD of 31±23 m from March-May (Fig. 3.4). The night WMD was comparable in March and May,
27±14 m, but deeper, at 91±44 m, in April (Fig. 3.4). The vertical distribution of C2 was consistently shallow from April onwards, with an average WMD of 23±27 m across the day and night (Fig. 3.4). However, their March WMD was much deeper at 124±46 m (Fig. 3.4). C3 showed a similar seasonality in its vertical distribution with a broader distribution and a deeper WMD of 81±36 m across the day and night in March and a shallower WMD of 25±27 m in April and May (Fig. 3.4). While C1 and C2 were absent in June, C3 were present, but most remained below 100 m, possibly entering diapause (Fig. 3.4). C4 showed evidence of DVM and a bimodal distribution in March, with 40% of the population at the surface and 60% of the population staying at depth (Fig. 3.4). By April all moved to the surface layers and underwent DVM from a daytime WMD of 38±14 m to a nighttime WMD of 6±2 m. In May they again showed a bimodal distribution (Fig. 3.4). Like C3, their June distribution was deeper (Fig. 3.4). C5 showed a broader distribution generally centered at or below 100 m during the day and night and across the season and no evidence of DVM except for April at night when 25% of the population migrated to a WMD of 6±2 m (Fig. 3.4). By contrast, C6 showed evidence of DVM starting in March, moving from a daytime WMD of 194±43 m to a WMD of 29±16 m at night (Fig. 3.4). In April, 25% of the population continued to perform DVM from a WMD of 65±14 m to the surface layer (above 30 m), but the rest migrated down below 100 m at night (Fig. 3.4). In May, most of the population remained centered in the intermediate water column with a WMD of 65±14 m during the day and of 42±33 m at night. In June most C6 individuals remained at depth, showing an average WMD of 135±44 m across the day and night (Fig. 3.4).

Early stages, C1 and C2, of *Eucalanus bungii* also showed a shallow distribution, with an average daytime WMD of 15±6 m and 20±4 m, respectively across the season (Fig. 3.5). While the C1 distribution was consistent between months and time of day, C2 showed a seasonally
consistent WMD during the day, but not at night, with a deeper WMD of 65±14 m during the
night in March, but of 10±8 m during April and May (Fig. 3.5). All other stages showed a deeper
vertical distribution, a slight indication of DVM, and a greater seasonal variation in their vertical
distribution (Fig. 3.5). C3 individuals were likely still diapausing in March, when they were
found below 100 m both during the day and night (Fig. 3.5). They showed a shallower
distribution and underwent DVM for the rest of the sampling season with a WMD of 57±15 m
during the day and of 13±8 m during the night (Fig. 3.5). By contrast, C4 showed evidence of
DVM from March to May with a WMD of 49±20 m and 19±4 m during the day and night,
respectively, across this time period, but remained at below 100 m during both the day and night
in June (Fig. 3.5). It is likely that they entered diapause in June. Stages C5 and C6 always
showed a WMD deeper than 100 m except for April, when their WMD was of 65±14 m (Fig.
3.5). C5 performed DVM only in April and May, when their night WMD was of 18±8 m (Fig.
3.5). In March and June, they were below 100 m at night (Fig. 3.5). By contrast, C6 showed a
shallow distribution at night in March and April only, with a WMD of 21±8 m, remained below
100 m in May and were absent from the water column in June (Fig. 3.5).

All stages of *Metridia pacifica* showed a high seasonal variability in their vertical
distribution. Stage C1 had the deepest nighttime distribution of any stage, with an average WMD
of 158±51 m (Fig. 3.6). Their daytime distribution was less consistent. They displayed a daytime
WMD of 20±4 m in March, of 79±44 m in April, a bimodal distribution in May with 60% above
30 m and the rest below 100 m in May, and most were below 100 m in June (Fig. 3.6). Stage C2
were concentrated in the intermediate water column and exhibited a consistent vertical
distribution between the day and the night, with a WMD of 58±14 m across the day and night in
March and April and of 126±44 m in May and June (Fig. 3.6). C3 also presented a similar
vertical distribution during the day and night, with an average WMD over the day and night of 132±42 m from March to May and of 52±17 m in June (Fig. 3.6). Stage C4 were concentrated in the intermediate water column throughout the season, with a daytime WMD of 62±14 m in March and of 101±38 m from April onwards (Fig. 3.6). In March they performed DVM, reaching a nighttime WMD of 18±5 m (Fig. 3.6). They showed a similar distribution to the daytime in April and May and a bimodal distribution in June, with 70% of the individuals performing DVM and moving above 30 m at night (Fig. 3.6). Stage C5 showed a similar seasonality in vertical distribution to C4. They displayed a daytime WMD of 94±42 m in March and a deeper WMD of 168±40 m for the rest of the sampling season (Fig. 3.6). Like C4, they only performed DVM in March and in June, when their night distribution became shallower, with a WMD of 26±23 m. (Fig. 3.6). By contrast, C6 always performed DVM and showed no seasonal variation in their daytime vertical distribution, maintaining a daytime WMD of 198±21 m throughout the season (Fig. 3.6). At night, adults had an average WMD of 49±40 m from March to May and of 149±50 m in June (Fig. 3.6). In May 30% of the population remained in the deep layer also at night (Fig. 3.6).

*Paraeuchaeta elongata* individuals showed the deepest mean WMD across stages as well as evidence of DVM. There was little variation between stages and across season during the day (Fig. 3.7). The average WMD across stages was of 195±33 m during the day. Younger stages (C1-C4) were generally also at depth at night, except for C3 in April and C4 in April and May, when they were observed to perform short DVM to a WMD of 61±14 m, 43±14 m and 82±36 m, respectively. By contrast, C5 and C6 showed evidence of DVM from March to May, with a night WMD of 20±14 m and of 40±30 m, respectively.
3.3.3 Daily exchange rates

With the exception of *P. elongata*, all of the zooplankton species analyzed show an average negative daily exchange rate (DER) over the course of the sampling season (Fig. 3.8a). This implies that, for most species, advection acts more as a loss rather than a production term. The two deepest dwelling copepod species, *P. elongata* and *M. pacifica* exhibited the smallest range (min to max) in DERs, -0.1 to 0.2 and -0.2 to 0.2 day\(^{-1}\), respectively (Fig. 3.8b) and showed the least negative mean seasonal DER (Fig. 3.8a). Their mean seasonal DER was significantly more positive than *A. longiremis* (Wilcoxon test p-value <0.001 for both *P. elongata* and *M. pacifica*), copepod eggs (Wilcoxon test p-value <0.001 for both *P. elongata* and *M. pacifica*), and cladocerans (Wilcoxon test p-value <0.001 and =0.04 for *P. elongata* and *M. pacifica*, respectively). These are the taxa (cladocerans, copepod eggs, and *A. longiremis*), which experienced the highest advection losses over the season (Fig. 3.8a), and also exhibited a high variability in DERs, with ranges of -1.8 to 2.1, -1 to 0.9, and -2.7 to 3 day\(^{-1}\), respectively (Fig. 3.8b). *Calanus marshallae* displayed an intermediate level of seasonal variability in DERs, with a range of -0.4 to 0.5 day\(^{-1}\) (Fig. 3.8b), and its mean DER remained significantly higher than that of *A. longiremis* (Wilcoxon test p-value =0.021) and copepod eggs (Wilcoxon test p-value <0.001) but was significantly lower than that of *P. elongata* (Wilcoxon test p-value < 0.001) (Fig. 3.8a). *Eucalanus bungii* showed a higher seasonal variability in DERs than *C. marshallae*, with a range of -2.3 to 0.8 day\(^{-1}\) (Fig. 3.8b), and its mean DERs was only significantly lower than that of *P. elongata* (Wilcoxon test p-value <0.001) (Fig. 3.8a). Larvaceans had the widest range in DERs, -2.7 to 2.6 day\(^{-1}\) (Fig. 3.8b), and thus their mean seasonal DERs was not significantly different from any other taxa.
The high variability in DERs was generally a feature of the early part of the season (March-April) for most all taxa (Fig. 3.9). Cladocerans, copepod eggs, and larvaceans, being close to the surface, experienced the highest and most variable advection losses in this period (Fig. 3.9), when surface velocities were high and intensive velocity flow events extended deeper in the water column (Fig. 3.3).

DERs are however not only a function of flow velocities, but also of the relative abundance of the zooplankton at the boundary with the respect to the inlet. Since copepod eggs and larvaceans maintained a relatively constant concentration at the boundary in relation to the average inlet abundance (Table 3.1), their seasonal changes in DERs are solely a reflection of the lower water velocities over time. On the other hand, cladocerans showed a higher concentration at the boundary in the second cruise (Table 3.1) and this further magnified their early season DERs.

We observed a general trend for the seasonal mean DERs of A. longiremis to be more negative with decreasing stage (Fig. 3.10). Acartia longiremis early stages (C1 and C2) experienced higher advection losses (≥ 0.5 day⁻¹ over the season) than older stages (Fig. 3.10). Younger stages (C1-C4) were more consistently found closer to the surface throughout the season (Fig. 3.3), and thus were exposed to the high velocities in the surface layers (Fig. 3.1). While over the entire season older stages showed lower DERs, in March and early April C5 actually displayed the highest/lowest DERs observed for this species (3 and -2.7 day⁻¹). Their distribution was shallow at this time (Fig. 3.3) and all of the population was concentrated at the boundary (Table 3.1) for the first two cruises. This magnified the already high water exchange rate observed at 10 m in this period (Fig. 3.1c) and resulted in high DERs. Stage C6 females also showed a high fraction of their population at the boundary compared to other stages in cruise 1.
and their DERs were similarly magnified in March and early April. Stage C3 and C4 also showed their highest and most variable DERs in March and April, the period with the highest surface flow speeds (Fig. 3.1 and 3.9). Their DERs in this period are even lower than those of C1 and C2 (Fig. 3.9) as a result of their shallower night distribution in March (Fig. 3.3). By June most of the younger stages (C1-C3) were concentrated at the boundary (Table 3.1) and thus their DERs were magnified and remain relatively high (Fig. 3.9).

Unlike for *A. longiremis*, *C. marshallae* seasonal mean DER decreased with stage up to C4, the stage with the highest advection losses over the season, and increased again for stages C5 and C6 (Fig. 3.10). Unlike other early stages, stage C4 showed its most negative DER (-0.3 day$^{-1}$) in late April (Fig. 3.9), when they displayed their shallowest distribution (Fig. 3.4) and started to show a large fraction of the inlet population at the boundary (Table 3.1). Such extreme advection events may not have a lasting impact on the population size if infrequent. However, a sustained period of negative DERs may impact the population substantially, as will be further discussed in the next section. In April, C4 copepodites were shallower than 50 m both during the day and night (Fig. 3.4). Thus, they remained above the subsurface inflowing layer at all times, and experienced a period of mostly negative DERs until late April (Fig. 3.9), leading to low mean seasonal DER (Fig. 3.10). Other early stages showed a similar pattern of predominantly negative DERs in late April, but their magnitude was smaller as, either during the day or night, they were found deeper in the water column (Fig. 3.9 and 3.4). By contrast, adult females, with a daytime WMD of 65 m in both April and May, were in the inflowing subsurface layer until mid-April and experienced largely positive inflow in this period (Fig. 3.4). However, in late April and May, the inflowing subsurface layer deepened (Fig. 3.1) and adult females experience more
negative DERs (Fig. 3.4) as they are consequently found in the outflowing intermediate layer (Fig. 3.1 and 3.4).

Despite not showing the highest mean seasonal DER among C. marshallae stages, C1 copepodites displayed the highest and lowest overall DER, with almost 60% of the population flowing in during the strong, positive flow event on March 20\textsuperscript{th} and 45% of the population being lost on March 28\textsuperscript{th} (Fig. 3.9 and 3.10). Its distribution was the shallowest of any stage in this period (Fig. 3.4). Stage C2 showed their most negative DER (-0.25 day\textsuperscript{-1}) in early April (Fig. 3.9). At this time they were close to the surface (Fig. 3.4) and still maintained a large fraction of the inlet population at the boundary from cruise 1 (Table 3.1). Stage C3 also showed their most negative DER (-0.25 day\textsuperscript{-1}) in early April (Fig. 3.9), when at night they displayed a shallow vertical distribution (Fig. 3.4). It is notable that C3 DERs remained high late in the season compared to other young stages as a large fraction of the population was found at the boundary on cruise 4 (Table 3.1). Stage C5 had the lowest DERs (Fig. 3.9 and 3.10) as the majority of its population was below 100 m for the entire season (Fig. 3.4). By contrast, C6 were performing DVM March-May and showed higher DER than stage C5 in this period (Fig. 3.4 and 3.9). Interestingly, in March and April their DERs were comparable to those of stage C1, despite the vertical distribution of stage C6 being deeper (Fig. 3.4 and 3.9). This is because C6 were consistently more abundant at the boundary than in the inlet (Table 3.1) and their DERs were thus magnified.

Like A. longiremis, E. bungii also experienced its lowest and most variable DERs for its younger stages (C1-C4) (Fig. 3.10). However, stage C3 was an exception to this pattern, showing mean seasonal DERs only slightly lower than stage C5 and C6 (Fig. 3.10). This stage displayed the deepest March distribution, comparable to that of C5, than any other younger stage in March
Thus, they experienced lower DERs (generally smaller than ±0.25 day\(^{-1}\)) in this period of high surface flow rates (Fig. 3.9) and had low mean seasonal DERs (Fig. 3.10). Stage C5 had a much smaller fraction of its population at the boundary (Table 3.1) and displayed even smaller DERs early in the season (Fig. 3.9). Stage C6 females performed DVM (Fig. 3.5), thus their DERs were higher than C5, but remained smaller than those of C1 and C2 (Fig 3.9). In April, the adult female vertical distribution was shallower (Fig. 3.5), but few individuals were found at the boundary (Table 3.1) and thus their DERs were reduced as compared to March (Fig. 3.9). Stage C1 exhibited the highest DERs (0.7 day\(^{-1}\)) of any other stage in March (Fig. 3.9), when it displayed the shallowest March vertical distribution of any stage (Fig. 3.5) and most of its population was at the boundary (Table 3.1). In April C1 DERs were smaller (Fig. 3.9) since its distribution was slightly deeper (Fig. 3.5) and a lower fraction of the inlet population was at the boundary (Table 3.1). DERs in May remained comparable to those in April even if water flow was reduced because again most of the population was observed at the boundary (Table 3.1, Fig. 3.9). Stage C2 also maintained a shallow distribution throughout the season (Fig. 3.5) and displayed its highest and most variable DERs early in the season, however its DERs were slightly smaller than those of C1 as not a large fraction of the population was observed at the boundary (Table 3.1). Stage C2 had a shallower distribution than any other stage in May and its DERs remained quite variable in this period. Furthermore, both stages, like the early stages of *C. marshallae*, were shallower than 50 m during the day and night in April (Fig. 3.5). Thus, they remained above the subsurface inflowing layer at all times, and experienced a period of consistently mostly negative DERs until late April (Fig. 3.9). Once the subsurface inflow layer started to shallow in May (Fig. 3.1), C2 displayed a shallower distribution at night and remained above the inflowing layer (Fig. 3.5). Thus the pattern of sustained negative DERs was
maintained throughout May (Fig. 3.9). By contrast, the C1 distribution stayed comparable to the one in April, and coincided with the inflowing subsurface layer (Fig. 3.5). Hence, they experienced generally positive DERs in this period (Fig. 3.9). Adult females also showed consistently positive DERs in this period, as in May their distribution was deep both in the day and night, overlapping with intermediate inflowing layer (Fig. 3.1 and 3.5) Unlike other stages, C4 did not experience any positive DERs in March (Fig. 3.9), this is because, with a day WMD of 65±23 m and a night WMD of 20±7 m, it was found below the wind driven surface layer flow but still above the March intermediate inflowing layer (Fig. 3.1 and 3.5). However, in April most of the population was found above 30 m (Fig. 3.5) and all of the population was at the boundary, leading to the lowest DER (-1.2 day$^{-1}$) observed for this species over the entire sampling season. Furthermore, they experienced a prolonged period of negative DERs in this period, early April, as they were concentrated between 10 and 30 m, centered in the outflowing layer and exposed to deep outflowing wind events, but not high enough to be exposed to inflowing wind events (Fig. 3.1 and 3.5). Once the subsurface inflowing layer started to shallow in mid-April, their DERs became more positive (Fig. 3.1 and 3.9).

*Metridia pacifica* seasonal mean DERs of young stages (C1-C3) were only marginally lower than those of stage C5 and C6 (Fig. 3.10). Similarly to *C. marshallae*, stage C4 displayed the lowest mean seasonal DER (Fig. 3.10). Furthermore, unlike other species, in March *M. pacifica* experienced its highest and most variable DERs for its older stages (C4-C6) (Fig. 3.9). This was due to the different vertical distribution of young stages, which unlike those of the species considered so far, were generally found in the intermediate water column, below 50 m, rather than close to the surface (Fig. 3.6). The DERs of stage C1 to C3 were only rarely greater than ±0.1 day$^{-1}$. DERs of the older stages (C4-C6) showed a larger variability than early stages,
but remained less negative than the species considered so far, always less than -0.25 day$^{-1}$, except for a DER of almost 0.3 day$^{-1}$ for C4 during a strong outflow event on March 21st. Unlike the earlier stages, C4-C6 individuals showed some indication of DVM and at night they were observed above 50 m in March (Fig. 3.6). Their DERs were highest in this period, with C4 showing the largest DER since its daytime distribution was shallowest (Fig. 3.6 and 3.9). It is noteworthy that while C2, C3, C4 and C5 showed a consistent period of negative DER in late April and May, C1 and C6 displayed a period of consistent positive outflows (Fig. 3.9). This is because a large fraction of the C1 and C6 population was found in the subsurface inflowing layer (Fig. 3.1 and 3.6). However, C4 and C5, like C2 and C3, did not perform DVM in April and May and thus remained outside of the subsurface inflowing layer. Furthermore, the bulk of their distribution also remained above (C2, C3, C4) or below (C5) the intermediate, inflowing subsurface layer in both months (Fig. 3.1 and 3.6).

*Paraeuchaeta elongata* displayed the lowest range in DERs of any taxa, with most stages having DERs smaller than ±0.2 day$^{-1}$ (Fig. 3.9). It was also the only species that displays its most negative seasonal mean DERs for its older stages (Fig. 3.10). This is because stages C1 to C4 had a WMD of 200 m during the day and at night generally never migrate above 50 m (Fig. 3.7). By contrast, stage C5 and C6 performed DVM and were observed at the surface at night in March (C5) and May (C5 and C6) (Fig. 3.7). Indeed, stage C5 had its highest DERs of 0.3 day$^{-1}$ in March (Fig. 3.9). In May, C5 DERs were reduced as water velocities were slower and few individuals were found at the boundary (Fig. 3.1, Fig. 3.9, Table 3.1). Similarly, C6, even if also observed at the surface in May (Fig. 3.7), showed small DERs (Fig. 3.9) because their abundance at the boundary was low (Table 3.1). Stages C1-C4 all showed a period of consistently positive DERs in early May (Fig. 3.9), during a period of sustained intermediate inflow between 125-225
m (Fig. 3.1). Stage C4 showed the smallest positive DERs in this period (Fig. 3.9) as at night they were found just above this inflowing layer (Fig. 3.1 and 3.7). On the other hand, C1 showed the most positive DERs (Fig. 3.9) as a large part of the population was observed at the boundary at this time (Table 3.1).

3.3.3.1 Sensitivity to bottom layer depth distribution

When averaged over the entire sampling period, all the sensitivity analysis scenarios led to more negative DERs than those of the original analysis (Fig. 3.11). Both the 100-120 and 300-320 m distributions missed the late April-May mid water inflow (Fig. 3.1), leading to higher out transport rates than the base model. The 200-220 m distribution was also outside of the peak depth of inflow in late April and May (Fig. 3.1). However, the most negative transport values with this mid bottom layer distribution were observed in June, when water at this depth was outflowing faster than above or below (Fig. 3.1).

The magnitude of the decrease in DERs varied by taxon and its specific vertical and seasonal distribution. *Acartia longiremis*, cladocerans, copepod eggs, and larvaceans, whose population was concentrated in the upper water column, only displayed a small change in DER, less than 11% (Fig. 3.11). Cladocerans, which were only observed in the bottom layer in June (Fig. 3.2), displayed the highest change in DER with the 200-220 m layer distribution (Fig. 3.11). Copepod eggs, which were present in the bottom layer in all months except April (Fig. 3.2), experienced more negative DERs with both a top and mid distribution in the bottom layer (Fig. 3.11). Larvaceans were only found in the bottom layer in April and June and experienced the most negative change in DERs when they were concentrated in the top 20 m of the bottom layer (Fig. 3.11). *Acartia longiremis* showed a similar pattern, as its adult and C5 copepodites,
which had the deepest distribution of any stage, were most abundant in the bottom layer in May (Fig. 3.3). *Paraeuchaeta elongata*, which had the majority of their population for every stage distributed in the bottom layer (Fig. 3.7), saw more substantial decreases in DERs than any other taxa if distributed in a 20 m layer (Fig. 3.11). A distribution in the topmost 20 m of the bottom layer resulted in a 6 fold reduction in DERs (Fig. 3.11). This was a result of more negative DERs in late April and May resulting from the lack of inflowing water velocities at this depth (Fig. 3.1). *Metridia pacifica*, *Calanus marshallae*, and *Eucalanus bungii* also showed the highest decrease in DERs with a topmost distribution, albeit the reduction was not as substantial as for *P. elongata* (Fig. 3.11), given their ontogenetic and daily vertical migration behavior and shallower distribution of juvenile stages (Fig. 3.5 and 3.6). Furthermore, the highest abundance of these copepods in the bottom layer occurred in May and June rather than April and May and thus, unlike *P. elongata*, a distribution in the 300-320 m layer led to a comparable decrease in DERs as one between 200-220 m (Fig. 3.11).

### 3.3.4 Potential importance of advection to population size

For most species, stages and sampling times, the potential change in population size between cruises caused by advection was small compared to that brought about by local processes. We present in Fig. 3.12 the plot of *M. pacifica* adult females as an example. It is clear that the change in population size between cruises could not be explained by changes brought about by advection and that changes due to local population growth processes were of a higher importance in determining variability in population size over time (Fig. 3.12). The remaining plots in Fig. 3.12 are of those stages and species for which advection was an important controlling variable at some time during the season (Fig. 3.12). As described in the Methods
section, it was determined that advection was important in producing changes in population size between any two cruises if the ratio of the percentage change in population size due to advection over the change due to local processes (A/L) was greater than one. We call A relative advection losses/gains and L relative net local production.

Advection dominated population dynamics of species living in the shallow surface layers later in the spring season, when net changes in population size due to local processes were low. For example, the cladocerans decreased in population size by 70% between cruise 3-4, with most losses being accounted for by advection (Fig. 3.12). The relative losses due to advection were comparable from cruise 2 to 3, but local growth processes dominated and exceeded any changes brought about by advection (Fig. 3.12). Similarly, larvaceans were able to increase in population size only from cruise 1 to 2, when relative net local production was high (Fig. 3.12). Relative advection losses were actually a lot lower from cruise 2 onwards, but relative net local production was even lower and thus variation in population size was largely influenced by advection (Fig. 3.12). Likewise, advection caused a large part of the variation in the population size of A. longiremis C4, C5, and C6 in the latter part of the spring season, between cruises 3 and 4, with losses due to advection of 70%, 47%, and 46%, respectively dominating the total change in population size (Fig. 3.12). Relative advection losses were actually highest between cruise 1 and 2, but were balanced by local growth processes and no large change in population size was observed (Fig. 3.12).

Advection was an important determinant of population change also for C. marshallae stages C2 to C4, and C6, which, unlike stage C5, were found near the surface, at times when net growth rates were low. In particular, advection dominated changes in population size from cruise 1 to cruise 2 (Fig. 3.12). Stage C2 and C6 inlet net production was low in this period, but
advection caused a 54% and a 32% decrease, respectively in population size (Fig. 3.12). In the same time period, stage C4 and C3 experienced declines of 83% and 93% in population size, respectively due to advection (Fig. 3.12). However, these losses were only slightly higher than net local production gains of 66% and 79%, respectively, and thus the decline in population size was not as large as for C2 and C6 (Fig. 3.12). Advection losses for stages C2 and C4 drastically decreased between cruise 2 and 3 and the observed changes in population size were driven by mortality/molting (stage C2) or production (stage C4) (Fig. 3.12). By contrast, in the same period, changes in stage C3 population size remained dominated by advection (23% change) since relative local net production was low (11%), likely because many C3 copepodites were moulting into stage C4 (Fig. 3.12). Unlike other stages, C6 experienced the highest relative advection losses between cruise 2 and 3. Nevertheless, they experienced the largest net production in this period (Fig. 3.12) and thus population dynamics were governed by local biological processes. Advection dominated again for stages C4 and C6 from cruise 3 to 4 when relative net local production was small and negative, likely because of high mortality and/or molting (Fig. 3.12).

For *E. bungii*, the largest contribution of advection to population dynamics occurred for stages C4 and C5, from cruise 1 to 2. In this period, the 85% decrease in stage C4 was largely generated by advection (Fig. 3.12). Stage C5 experienced lower relative advection losses of 18% but these were still higher than the 12% decrease due to local processes (Fig. 3.12). By contrast, local biological processes governed population dynamics during cruise 2 to 3, when both stages experienced high net production (Fig. 3.12). Local biological processes remained the controlling mechanism of changes in population size between cruises 3 and 4, but the stage C5 population increased, while C4 decreased in numbers, likely as a consequence of high moulting and/or
mortality rates (Fig. 3.12). Stage C2 also experienced highest relative advection losses in March and April (Fig. 3.12). However, relative net production was even higher and thus local biological processes dominated changes in population dynamics between cruise 1 and 2 (Fig. 3.12). In the same time period, relative advection losses were also lower than relative net production for stage C6, but its population declined, likely because mortality dominated local biological processes (Fig. 3.12). Advection was instead a large determinant of change in the population size of stages C6 and C2 from cruise 2 to 3. Stage C2 experienced relative advection losses of 66% in this time period, which contributed to most of the 71% decline in population size observed between cruises (Fig. 3.12). By contrast, advection caused a concurrent increase in the numbers of stage C6, just slightly higher than the local loss rates of 88% (Fig. 3.12). Likewise, for both stages, local biological processes controlled changes in population dynamics between cruise 3 and 4 (Fig. 3.12).

Advection was at times more important than local biological processes for the population dynamics of *M. pacifica* stages C4 and C5 (Fig. 3.12). Advection contributed 33% to the 52% decrease in C4 population size from cruise 1 to 2 (Fig. 3.12). By contrast, most of the change in population size caused by advection for stage C5 occurred from cruise 2 to 3 (Fig. 3.12). At this time, C5 relative advection losses (22%) were not particularly high, but remained higher than relative net local production (18%) (Fig. 3.12).

Finally, while generally vital rates caused the largest changes in *P. elongata* population size for most stages, advection produced a 43% increase in the population size of C2 from cruise 2 to 3. This dampened the 25% decrease in population size caused by local processes, such as mortality and molting (Fig. 3.12). Stage C1-C4 also experienced immigration due to advection in this period, but the change in population size due to advection remained lower than that brought
about by local processes. Even if *P. elongata* relative advection losses were very low, they became important when relative net local production was low. This occurred for stage C6 from cruise 2 to 3 when they experienced losses of 7% between cruises at a time when local processes were dominated by losses (3%) and for C4 between cruise 3 and 4 when advection losses were low (5%), but still higher than the 4% losses due to mortality or molting (Fig. 3.12).

### 3.4 Discussion

#### 3.4.1 Water velocities

Our estimated zooplankton exchange rates depend on accurate model outputs of flow velocities. Although it was not the aim of this paper to assess the accuracy of model estimates, a comparison of model outputs to flow velocities from similar estuaries increases our confidence in the model results. For example, our estimated velocities correspond to those obtained in Knight Inlet by Baker and Pond (1995), who reported velocities on the order of $\pm 50$ cm s\(^{-1}\) for the top 2 m. Moreover, the general flow of the model corresponds with what is generally known as the typical fjord flow pattern of estuarine flow near the surface paired with a subsurface inflow (Pickard, 1961). Furthermore, the model estimates of average residence time for the top 10 m (20±5 days) are fairly comparable with the 7 days retention time during high river discharge (May and June) and 15 days during low discharge (March and April) estimated by Hodal (2011) for 2008 and 2009. Hodal’s calculations were first-order estimates of estuarine circulation and did not include the effect of wind or tides, thus some discrepancy is expected. It is also notable that oxygen and density measures did not give any indication of deep water renewal for Rivers Inlet until late June (Hodal, personal communication). Likewise, the model used in this study gave no indication of deep water renewals, with bottom layers remaining
stationary for the entire sampling season. However, we did observe mid depth renewals in late May. Such renewals have also been observed in Knight Inlet (Baker and Pond, 1995) and in Norwegian fjords (Aksnes et al., 1989).

3.4.2 Zooplankton vertical distribution

Cladocerans are a known coastal neritic species (Peterson et al., 1979, Nielsen and Andersen, 2002). Indeed, they exhibited a shallow, seasonally uniform vertical distribution throughout our sampling period. Larvaceans also showed a shallow vertical distribution. These results are in agreement with observations from a Norwegian fjord (Nielsen and Andersen, 2002), the Canada Basin in the Arctic Ocean (Kosobokova and Hopcroft, 2010), and coastal waters in southeast Brazil (Miyashita and Lopes, 2011).

The vertical distribution of copepod eggs was less uniform over the season and 24-hour cycle likely reflecting diverse spawning strategies employed by different copepod species. Our results clearly show that from March to May the bulk of copepod eggs were at the surface during the daytime and at depth during the nighttime except in April, when the majority of eggs were at the surface around the clock. Calanus marshallae eggs are known to be at depths < 10 m (Peterson et al., 1979), Eucalanus bungii is also assumed to reproduce at the surface during the phytoplankton bloom (Yamaguchi et al., 2010b). From their vertical distribution it was apparent that their reproductive peak during our sampling season occurred in March and April. Thus, it is likely that a large contribution to the presence of eggs at the surface during April is due to their combined reproductive output.

Acartia longiremis, a well known neritic copepod (e.g. Peterson et al., 1979) had the most seasonally consistent and shallowest distribution of all the copepod species under study. While
Stages C1-C4 were generally always distributed in the surface layer, stages C5 and C6 showed a broader and more seasonally and diurnally variable vertical distribution. According to Holliland et al. (2012) and Peterson et al. (1979), C5 and C6 individuals are stronger vertical migrants than younger stages. Predator evasion has been shown to be the main cause of DVM in some copepod species (Hays, 1995). We hypothesize that the *A. longiremis* females may vary their vertical distribution seasonally to lay their eggs in a more favourable depth strata with respect to predation pressure. This genus is under strong predation pressure from both planktivorous fish (Bollens and Frost, 1989a) as well as other copepods such as *Calanus* spp. (Irigoien and Harris, 2006, Holliland et al. 2012). *Acartia longiremis* females performed reverse DVM in March and April, when two of the largest copepods in the system, *Eucalanus bungii* and *Calanus marshallae*, were at the surface, and DVM when visual predators, such as juvenile salmonids and herring, increased in abundance (personal observation). Studies on the feeding rates of these two copepod species on *Acartia* spp. eggs and juveniles as well as of *A. longiremis* vertical migration behavior under different predation regimes should be carried out to verify this hypothesis.

Seasonal variation in the vertical distribution of *E. bungii* was much higher than for *A. longiremis*. Only *E. bungii* juvenile stages C1 and C2 were in surface waters throughout the season. All other stages were at the surface only at night, and only for part of the sampling season. For example, *E. bungii* adult females were present in surface waters only in March and April at night. In April they remained above 100 m also during the day. Thus, it appears that *E. bungii* adult females had left their resting stage and were possibly already reproducing at the start of the sampling season. Yamaguchi et al. (2010b) and Krause and Lewis (1979) noted *E. bungii* as undergoing an ontogenetic migration to reproduce at the surface at the onset of the spring bloom. Chlorophyll levels in Rivers Inlet were already relatively high (> 50 mg m\(^{-2}\)) in March
(Tommasi et al., 2013b), thus it is likely that *E. bungii* females had already begun spawning. While stage C4 were also already actively performing DVM, C3 and C5 remained at depth in March. A similar delayed seasonal upward migration of stage C3 with respect to adult females has been reported in the Oyashio region (Yamaguchi et al., 2010a). Our findings support the suggestion that *E. bungii* overwinters at stages C3-C5 with C5 beginning to molt into C6 at depth in late winter, prior to the bloom (Shoden et al., 2005, Yamaguchi et al., 2010a, Sato et al., 2011). By May all adult females had left surface waters and none were present in June. Stages C4 and C5 stopped DVM and were all at depth by June. In the Strait of Georgia, *E. bungii* females are also present in surface waters only in March and April, and the first C4-C5 individuals also descend to deeper waters in June (Krause and Lewis, 1979).

Similarly, *C. marshallae* displays a high seasonal and between stage variability in its vertical distribution in Rivers Inlet. Like *E. bungii*, C6 females were already undergoing DVM in March, implying that reproduction had already started. Indeed, some C1 copepodites were already present in shallow water in March. Osgood and Frost (1994) observed that overwintering *C. marshallae* C5 individuals in Dabob Bay, Washington, started molting to adults in January, with the first copepodites appearing in February. An initiation of spawning in January would agree with the stage composition observed in Rivers Inlet in March. Reproduction continued through to April when 25% of females were still present in shallow waters at night. Stage C5 were always in deep waters except for a small fraction that underwent DVM in April, during the chlorophyll biomass peak (Tommasi et al., 2013b). From May onwards all stage C5 were at depth while stages C1-C4 were at the surface. By June, stage C3 and C4 were also at depth, implying they might molt to stage C5 at depth or undergo diapause. In Dabob Bay, the majority of the *C. marshallae* spawned in March also arrested development and moved to deep waters in
May as stage C5 (Osgood and Frost, 1994). However, a small fraction turned into adults and produced a small second generation (Osgood and Frost, 1994). Perhaps it was only those C5 molting to C6 that needed access to further energy sources for gonad development and migrated to surface waters in April.

The vertical distribution of *Metridia pacifica* copepodites showed a reduced seasonal variation as compared to that of *E. bungii* and *C. marshallae*. The majority of *M. pacifica* stages C1-C3 remained in the intermediate water column for the entire season. A similar distribution of C1-C3 in the intermediate water column has been observed in other regions: between 50-100 m in Dabob Bay (Osgood and Frost, 1994), and between 0-250 m in the Oyashio region (Padmavati et al., 2004, Yamaguchi et al., 2010a). The *Metridia* genus is a well known diel vertical migrator from stage C4 onwards (Hays, 1995, Padmavati et al., 2004, Takahashi et al., 2009, Yamaguchi et al., 2010a). Indeed, the majority of *M. pacifica* adult females underwent DVM throughout the season in this study. However, C4 and C5 stopped DVM in April and May, the period with the highest chlorophyll concentration (Tommasi et al., 2013b). Yamaguchi et al. (2010a) followed the variation in *M. pacifica* in the Oyashio region in March and April and observed cessation of C4 and C5 DVM in late April. They hypothesized that in this period the vertical flux of phytoplankton from the surface may have provided sufficient food at depth (Yamaguchi et al., 2010a). It is plausible that the same mechanism stopped the occurrence of DVM for *M. pacifica* stage C4 and C5 in Rivers Inlet.

*Paraeuchaeta elongata* also showed a reduced seasonal variation in its vertical distribution compared to *C. marshallae* and *E. bungii*, and its juvenile stages C1-C2 displayed the deepest distribution of the copepod species recorded at the same developmental stage. This is not surprising since *P. elongata* egg clusters hatch in deep waters (Evans, 1973). Stages C3 and
C4 remained deep in the water column for most of the sampling season, except for C3 performing DVM up to 60 m in April, and C4 up to 40 m and 80 m in April and May, respectively. Evans (1973) also noted that *P. elongata* may undergo DVM from stage C3 onwards. Stage C5 and C6 females performed DVM throughout the season.

### 3.4.3 Daily exchange rates

To our knowledge, this study represents the first seasonal estimates of daily, and stage specific zooplankton advection losses and gains in a fjord for all the taxa under study. Our estimates of daily exchange rates (DER) are generally in agreement with those determined by Aknses et al. (1989) in a fjord in western Norway for the bulk mesozooplankton community during one day in June and a day in October as 0.2 day$^{-1}$ and 0.04 day$^{-1}$, respectively. However, we did observe occurrences of higher advection rates (> 1 day$^{-1}$) for surface dwelling species early during the sampling the season in March and April. This discrepancy may be due to our longer sampling season, which spanned months, such as March, of high wind velocities, as well as to our species-specific advection rates. Osgood and Frost (1996) deduced that between September and October advection may have removed 50% of the *C. marshallae* inlet population in Dabob Bay. This was an approximation computed using only the residence time of bottom water and comparing the abundance of all stages of *C. marshallae* outside and inside of Dabob Bay (Osgood and Frost, 1996). Nevertheless, it is comparable to the estimated between cruises loss determined for some *C. marshallae* stages in Rivers Inlet.

Furthermore, the present investigation clearly demonstrated that the active vertical movement of zooplankton interacts with the vertically sheared flow field to affect net horizontal advection of zooplankton. Water velocities were fastest at the surface, thus, *A. longiremis*
copepodites, which displayed the shallowest vertical distribution of the copepod species under study, experienced the highest daily exchange rates (DERs), whereas *P. elongata* copepodites, with the deepest vertical distribution of any other copepod species, experienced the lowest. *M. pacifica* copepodites also had generally low DERs because of their distribution in the intermediate water column rather than surface layers. The majority of *C. marshallae* C5 was always below 100 m and also displayed low DERs. Aksnes et al. (1989) similarly notes that zooplankton found above the sill level in a fjord in western Norway are 3 times more influenced by advection than deeper dwelling plankton.

Since the fastest flow rates are at the surface, any behavior, such as diel vertical migration (DVM), that minimizes time spent at the surface, minimizes advection losses. Indeed, our data show that daily exchange rates of *M. pacifica*, *A. longiremis*, *E. bungii*, and *C. marshallae* adult females were reduced as compared to their copepodites because of DVM. On the other hand, *P. elongata* adult females had higher advection losses than earlier stages because their DVM behavior brought them to the surface, whereas their copepodites were generally always below 100 m. Lewis and Thomas (1986) also showed that vertical distribution and vertical migration behavior reduced the influence of tidal driven advection on *M. lucens* (*pacific*) individuals in Indian Arm, a shallow-silled fjord in southern British Columbia, compared to surface dwelling species.

It is clear that even consecutive stages belonging to the same species exhibit a different advective history, which is dependent on their vertical distribution and DVM behaviour, particularly in a system with large vertical gradients in flow velocities such as a fjord. For *A. longiremis* advection losses were decreased with developmental stage, reflecting the deeper distribution and DVM behavior of older stages. The opposite was true for *P. elongata*, with deep
dwelling C1-C4 being less exposed to advection losses than vertically migrating adults. *M. pacifica* also tended to follow this pattern, but the differences between stages were not as marked as its copepodites were distributed further up in the water column.

On the other hand, advection of *C. marshallae* and *E. bungii* copepodites was not only dependent on DVM, but also on the timing of the seasonal ontogenetic migration of each stage. Water velocities changed not only with depth but also seasonally, being highest in March and April. Thus, the timing of seasonal ontogenetic migration into surface layers also influenced advection rates. Copepod eggs for example, that were numerous early in the sampling season and shallow in the water column, experienced high advection losses. *Eucalanus bungii* C3, which were still at depth in March, experienced lower advection than *C. marshallae* C3, which were already above 100 m in March. Slagstad and Tande (1996) and Krause and Lewis (1979) have also shown that copepods’ seasonal vertical migration affects the magnitude and direction of copepods’ transport rates.

The precision of our DER estimates relies on the correctness of the assumption that the zooplankton under study were evenly distributed in the vertical sampling layers. This assumption may have been reasonable for the more finely sampled upper 100 m, but is less certain for the bottom, 200 m deep, sampling layer. Falkenhaug et al. (1997a) sampled a 350 m deep fjord in Northern Norway in 50 m intervals and observed a broad distribution of *C. finmarchicus* in the bottom 200 m. By contrast, distribution of *M. lucens* was concentrated in the upper 100 m of the bottom layer (Falkenhaug et al., 1997a). Skarra and Kaartvedt (2003) determined that *P. norvegica* in a southern Norwegian fjord inhabited the bottom 50 m of a 200 m deep water column. Thus, while our assumption may have held for *C. marshallae*, it may have not for *M. pacifica* and *P. elongata*. Sensitivity analysis revealed that the estimated DERs of the deepest
dwelling species, *P. elongata* and *M. pacifica*, are quite sensitive to the depth distribution parameterization in the bottom layer. However, as a result of the slower velocities of the bottom layer, even the largest change in the original DER estimates, resulting from a distribution in the upper 20 m of the bottom layer, does maintain both *P. elongata* and *M. pacifica* as one of the species with the least negative DERs. Nevertheless, we recommend implementing a finer vertical sampling frequency in the bottom layer in future studies to reduce the error in the DER estimates of deep dwelling taxa.

### 3.4.4 Importance of advection relative to local processes

Even if advection losses can at times be quite high (up to -3 day\(^{-1}\)), for all taxa under study maximum relative net production was higher than maximum relative advection losses or deliveries. Thus, our results illustrate that advection is not the major contributor to changes in the population size for most species and stages over the entire spring season in Rivers Inlet. Indeed, average daily exchange rates over the entire sampling season were less than 10% day\(^{-1}\) for every taxa and stage. Evidence from a modeling study of *Calanus finmarchicus* on Georges Bank also determined that physical transport was generally small compared to biological processes from January to June (Li et al., 2006). Another modeling study concluded that advection was equally important to in-fjord production in determining in-fjord total copepod biomass in a Norwegian fjord in July (Nielsen and Andersen, 2002). However, they did not consider the copepod community residing below sill depth (110 m), thus actual advection loss estimates may have been overestimated.

Over the sampling season, the abundance of the overwintering stage of diapausing copepod species, stage C5 for *E. bungii*, *C. marshallae*, *M. pacifica* and C6 for *A. longiremis*
of the year-round active copepod *Paraeuchaeta elongata*, increased in numbers over the sampling season, implying that recruitment to the next generation was not impaired by advection. Considering the high rates of egg production of copepods, it is not surprising that advection rates were lower than production rates over the spring season, the period of highest zooplankton productivity in temperate waters. More specifically, maximum egg production rates obtained from the literature for the copepod species analyzed in this study are: 8 eggs female\(^{-1}\) day\(^{-1}\) for *A. longiremis* (Peterson et al., 1991), 13 eggs female\(^{-1}\) day\(^{-1}\) for *P. elongata* (Tonnesson et al., 2006), 40 eggs female\(^{-1}\) day\(^{-1}\) for *M. pacifica* (Hopcroft et al., 2005), 60 eggs female\(^{-1}\) day\(^{-1}\) for *C. marshallae* (Peterson, 1988) and 150 eggs female\(^{-1}\) day\(^{-1}\) for *E. bungii* (Yamaguchi et al., 2010b).

However, the advection rates we presented are comparable to the few estimates of mortality rates available in the literature for *Calanus* spp. copepodites, which range from 0.1 to 0.5 day\(^{-1}\) (Eiane et al., 2002, Li et al., 2006, Hirst et al., 2007, Plourde et al., 2009). Thus, even in a relatively enclosed system like a fjord, it is necessary to estimate advection losses prior to computing mortality rates via horizontal life table methods. This is necessary even for species that show low DERs like *P. elongata* copepodites, since their highest DERs can be still as much as half (0.05 day\(^{-1}\)) of the lowest maximum mortality rate obtained from the literature. *Calanus* spp. maximum egg mortality rates, 6 day\(^{-1}\) (Hirst et al., 2007), on the other hand, are higher than the maximum daily exchange rate for copepod eggs, 1.2 day\(^{-1}\) computed in this study. However, mortality would still be substantially over estimated if advection were not taken into account.

Notwithstanding that advection may be of lower importance relative to local biological processes over the entire spring period, our results demonstrate that advection does play an
important role at specific times of year, when local relative net production is limited. As such it may become important in determining differences in zooplankton population size in years with similar egg production rates. For example, in April-May, production of cladocerans more than balanced advection losses. This is consistent with what Nielsen and Andersen (2002) showed for a Norwegian fjord, where even if found in the fast flowing surface layer, the production rate of cladocerans, a parthenogenetic zooplankton, more than compensated for its advection losses. However, here we show that when mortality dominated over growth in late June, advection became an important loss term for cladocerans. The same was true for larvaceans, whose population size was in part dictated by advection from mid-April onwards, after a highly productive period in March-April. Evidence from a modeling study of *C. finmarchicus* in the Barents Sea also shows that the balance between local growth and advection is seasonally variable (Edvardsen et al., 2003). There, advection was the main driver of *C. finmarchicus* population dynamics except during the May–June, the period of highest local growth (Edvardsen et al., 2003).

Likewise, copepods population dynamics in this system can potentially be governed by advection during periods of low net production. Copepods, which have many different developmental stages, and accumulate individuals in longer lived stages, display, for each stage, periods of no substantial productive inputs when a large cohort of young of the year develops into the following stage and is not replaced by a new cohort of incoming individuals. We show that during these instances of low production, population dynamics can possibly be controlled by advection. For example, *C. marshallae* C2 experienced high advection losses in March and April, at a time when most of the C1 and C2 were developing into C3 and C4 and not many eggs were recruited into new C1 individuals (either because the main spawning event had passed
and/or mortality was high). Thus, between cruise changes in population size were driven by advection. By contrast, in the same period, advection losses for C3 and C4 were partly balanced by production and the decline in population size was not as large.

It is evident that for copepods, the timing of the period when advection becomes the main determinant of population dynamics depends on the species phenology and development time. For example, it appears that the phenology of *E. bungii* was later than for *C. marshallae*, with *E. bungii* C2 still experiencing high relative net production at the beginning of the sampling season. This resulted in advection controlling *E. bungii* stage C2 dynamics only between cruise 2 and 3, rather than from cruise 1 as for *C. marshallae* stage C2. Mackas et al. (2012) reported an earlier timing of seasonal ontogenetic migration for some copepod species in years of warmer spring temperatures. It remains to be assessed how changing zooplankton phenologies may impact zooplankton variability and species success in fjord-like systems through interaction with seasonally changing water velocities.

Our results also demonstrated that advection could potentially influence zooplankton seasonal succession in the fjord. For example, surface dwelling taxa like cladocerans, and *A. longiremis* all experienced advection rates > 1day$^{-1}$ in March and April. Clearly these species necessitate high growth rates to be able to maintain in-fjord populations early in the season. High advection rates in early spring may maintain a community dominated by deeper dwelling taxa if the cool temperatures and low food concentrations prevent surface dwelling taxa from achieving the highest growth rates required to prevent flushing. Indeed, Tommasi et al. (2013b) have shown that cladocerans and *A. longiremis* are a late successional species dominating the fjord in May and June.
It is notable that while generally being a loss term for most species and stages, advection acted as an input of individuals between certain cruises. We show that in late April to mid-May, *E. bungii* females and C5, *M. Pacifica* females, and *P. elongata* copepodes C1-C4 experienced advection deliveries. These taxa were all distributed between 100-300 m in May, centered within the inflowing subsurface layer that was observed in the intermediate water column from 125-225 m from late April to mid-May. Moreover, those species, such as *M. pacifica* C6 and *E. bungii* C5, that were performing DVM migrated to a depth of 13-15 m at night, which, as we saw, corresponded with the inflowing subsurface layer and acted to further increase advective deliveries. Such mid-depth intrusions have been observed in other fjords (Baker and Pond, 1995, Aksnes et al., 1989) and occur when upwelled, denser water from the shelf flows over the sill but is not dense enough to completely renew the fjord bottom waters. Given the importance of such renewal events on the advection of some of the zooplankton species discussed, it raises the need of assessing what would be the consequence of changes in the timing and variability of such events in the future.

### 3.5 Conclusions

Here we have presented the vertical distribution of key mesozooplankton species in the region over the spring period, and assessed the existence of diel and seasonal vertical migration for each stage and species. By incorporating the vertical distribution data with water velocity profiles, the first seasonal estimates of daily exchange rates for the species discussed have been determined.

Our findings echo the recommendation of Aksnes et al., (1997) and Gentleman et al., (2012) that studies of zooplankton population dynamics, particularly in regions of high vertical
velocity shear, need to include a careful examination of zooplankton advective rates to avoid producing biased mortality estimates. This also applies to vertical life table inverse methods (e.g. Aksnes and Ohman, 1996), as we show that even consecutive stages within a species may have different advective histories given their different vertical migration behavior and vertical distributions. As Ohman (2012) suggests, these advective fluxes should be explicitly incorporated into population models.

We show that over the scale of the sampling period all the taxa examined can sustain populations within the fjord because of high inlet production. However, in critical times of the year, when production rates are low (or mortality and moulting rates high), advection can become one of the main forcing on population dynamics, particularly for those stages and species in the upper layer of the fjord. Therefore, to compare population dynamics processes and predict future population sizes, one has to take into consideration advection, as it is at times a key influence on zooplankton population dynamics.
3.6 Figures

Figure 3.1 Contours of daily profiles of water velocities at DFO2 from March 20 to June 28 2010 in the entire water column (a) and the top 30 m only (b). Red indicates an inflow, blue an outflow. The vertical resolution of the daily outputted model velocities is depicted by the column of *. (c) Average water daily exchange rates (flow at DFO 2/inlet volume) for the top 10 m.
Figure 3.2 Grey bars represent the vertical distribution of cladocerans (a), larvaceans (b) and copepod eggs (c) by cruise and time of day. Weighted mean depth (WMD) ±SE is shown as a solid red line bounded by two dotted red lines.

Figure 3.3 Grey bars represent the vertical distribution of *Acartia longiremis* by cruise and time of day for different stages. Weighted mean depth (WMD) ±SE is shown as a solid red line bounded by two dotted red lines.
Figure 3.4 Grey bars represent the vertical distribution of *Calanus* spp. by cruise and time of day for different stages. Weighted mean depth (WMD) ±SE is shown as a solid red line bounded by two dotted red lines.
Figure 3.5 Grey bars represent the vertical distribution of *Eucalanus bungii* by cruise and time of day for different stages. Weighted mean depth (WMD) ±SE is shown as a solid red line bounded by two dotted red lines.
Figure 3.6 Grey bars represent the vertical distribution of *Metridia pacifica* by cruise and time of day for different stages. Weighted mean depth (WMD) ±SE is shown as a solid red line bounded by two dotted red lines.
Figure 3.7 Grey bars represent the vertical distribution of *Paraeuchaeta elongata* by cruise and time of day for different stages. Weighted mean depth (WMD) ±SE is shown as a solid red line bounded by two dotted red lines.
Figure 3.8 a) Mean daily exchange rate (DER) per taxa. Error bars represent standard errors. b) Boxplot of DER per taxa showing the median (horizontal line) and the 25th (upper hinge) and 75th (lower hinge) percentiles. The upper whisker extends from the hinge to the highest value that is within 1.5 * inter-quartile range (IQR) of the hinge. The lower whisker extends from the hinge to the lowest value within 1.5 * IQR of the hinge. AL=Acartia longiremis, MP=Metridia pacifica, CM=Calanus marshallae, EB=Eucalanus bungii, PE=Paraeuchaeta elongata, CL=Cladocers, EG=Copepod eggs, LR=Larvaceans.
Figure 3.9 Daily exchange rate (DER) per taxa and stage. Positive DERs (grey) are inflows, negative (black) outflows. 0 DERs are also coloured in grey. Note that *Calanus marshallae* C1-C3 are Calanidae C1-C3 individuals.
Figure 3.10 Seasonal mean (March to June) daily exchange rate (DER) per taxa and stage. Error bars represent standard errors.
Figure 3.11 Percent change in the seasonal mean daily exchange rate (DER) per taxa relative to the seasonal mean DER computed for each of the sensitivity analysis model runs. Top refers to a distribution in the bottom layer from 100-120 m, mid to a distribution from 200 to 220 and bottom to a distribution between 300-320 m.
Figure 3.12 Inlet population size over time for those taxa most affected by advection. Grey dots represent estimates of total inlet population size obtained from an average of field data among sites on each cruise multiplied by the inlet volume. Black dots represent the population size after advection (size of population on the previous day + size of population on the previous day*daily exchange rate). Note that *Calanus marshallae* C2-C3 are Calanidae C2-C3 individuals.
### 3.7 Tables

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Table 3.1 Ratio of abundance at DFO2 over the average inlet abundance for each cruise, taxa, and stage. A ratio of 4.0 implies that all the observed individuals were found at DFO2.
Chapter 4: Differential response of distinct copepod life history types to spring environmental forcing

The temporal dynamics of five copepod species common to coastal waters of the Pacific Northwest were examined in relation to variability in spring temperature and phytoplankton dynamics in 2008, 2009, and 2010 in Rivers Inlet, British Columbia, Canada. The five species were differentiated by life history strategies. *Acartia longiremis, Metridia pacifica,* and *Paraeuchaeta elongata* remained active over most of the year. By contrast, the reproductive effort of *Eucalanus bungii* and *Calanus marshallae* was concentrated over the spring period and they spent most of the year in diapause as C5 copepodites. A delay in the timing of the spring bloom resulted in a shift in the phenology of all species. However, following the delay in spring bloom timing, recruitment to the G1 cohort was reduced only for *E. bungii* and *C. marshallae.* Recruitment successes of *E. bungii* and *C. marshallae* was also drastically reduced in 2010, an El Niño year, when spring temperatures were highest. Reasons for the observed differential response to spring environmental forcing, and its effect on upper trophic levels, are discussed.

4.1 Introduction

Organisms have evolved diverse life history strategies to maximize their fitness in different environments (Hairston and Bohonak, 1998). Because resources in the environment are limited, each individual, in allocating resources to maximize fitness, has to make choices in regards to growth, maintenance, and reproduction (Hairston and Bohonak, 1998). Differences in such life history decisions are particularly evident in the overwintering adaptations of temperate
and polar marine zooplankton. Temperate and polar systems are characterized by strongly seasonal physical and biological cycles. Most of the yearly phytoplankton production is focused in the spring or fall blooms (Longhurst, 1995), leading to a short feeding season and long periods of limited resources. Zooplankton have evolved different strategies to contend with the long intervals of diminished food availability in these environments. Atkinson (1998) describes two life history strategies adopted by different copepods to survive the winter period and exploit the short, but productive feeding season. One group, Type I, diapauses in winter as late stage copepodites and focuses reproduction in the spring period (Atkinson, 1998). They possess large lipids stores that are used for metabolic maintenance during diapause, maturation to the adult stage, and, for some species, initiation of egg production prior to the onset of the spring phytoplankton bloom. Thus, for Type I copepods, capital breeding, which is reproduction focused on stored resources (Varpe et al., 2009), may contribute to the yearly total reproductive effort. Type II copepods have a longer reproductive season, a broader diet, and less reliance on diapause to overwinter (Atkinson, 1998). These copepods are more likely to rely solely on income breeding, with most of their reproductive effort dependent on concurrent feeding (Varpe et al., 2009). Given the distinctive life history strategies of these two copepod groups, they may respond differently to changes in the seasonal timing of the spring bloom.

In high latitude systems, the onset of the productive spring period occurs when an increase in stratification, due to the seasonal warming of surface waters and a decrease in wind speeds, shallows the mixed layer depth, allowing for an increase in phytoplankton growth rates (Sverdrup, 1953). The timing of such physical spring forcing events varies interannually and is shifting following climate change. For example, the arrival of spring-like sea surface temperature (SST) is advancing in the North Sea (Edwards and Richardson, 2004) and in the Northeast
Pacific (Mackas et al., 2007, Mackas et al., 2012). Furthermore, the onset of upwelling winds in
the California Current System and along the British Columbia shelf is occurring later (Bograd et

The timing of the onset of the productive spring period is expected to vary under climate
change following such changes in its forcing variables (Ji et al., 2010). For instance, on the
British Columbia shelf, a later start of upwelling has been correlated with a delayed onset of the
spring phytoplankton bloom (Borstad et al., 2011). In the Bering Sea, absence of ice in years of
higher spring temperatures is associated with a late phytoplankton bloom (Stabeno et al., 2001).
It remains to be assessed if a specific type of zooplankton overwintering strategy will be more
successful under the observed shifts in the spring timing of physical forcing events and
phytoplankton phenology. Will Type I and Type II copepods experience different phenological
changes and will one type be more resilient to forecasted future changes in the spring
environment?

Zooplankton provide the trophic link between primary producers and upper trophic
levels, and therefore knowledge of their life cycles and phenological variability is of interest to
marine conservation and fisheries management issues. Changes in their phenology may result in
the de-coupling of trophic linkages and declines in the annual reproductive success of upper
trophic levels (Sydeman and Bograd, 2009). Phenological shifts in the timing of spring plankton
production have been correlated with reduced recruitment of their gadoid fish predators in the
North Sea (Cushing, 1984, Ellersten, 1987, Kristiansen et al., 2011), in the North Atlantic (Platt
et al., 2003, Kristiansen et al., 2011), and on the Bering Sea Shelf (Coyle et al., 2011). Similar
phenologically driven changes in upper trophic levels have been observed in North Sea herring
(Clupea harengus L.) (Cushing, 1990b), British Columbia Pacific sand lance (Ammodytes
hexapterus) and rhinocerous auklets (Cerorhinca monocerata) (Borstad et al., 2011), California Current sablefish (Anoplopoma fimbria) and Pacific ocean perch (Sebastes alutus) (Holt and Mantua, 2009), and Gulf of Alaska murres (Uria aalge) and kittiwakes (Rissa tridactyla) (Shultz et al., 2009). However, as zooplankton data are more difficult to obtain than environmental variables such as wind and phytoplankton biomass, many of these studies have assumed rather than demonstrated (Cushing et al., 1984, Ellersten, 1987, Shultz et al., 2009, Coyle et al., 2011 are exceptions) that the observed variation in upper trophic level recruitment following changes in timing of spring forcing events is a result of a disruption of the trophic coupling between their zooplankton prey and spring environmental conditions.

The mechanisms relating phenological changes in zooplankton to variation in spring environmental conditions are not completely understood and may be region specific. Globally, the seasonal timing of many zooplankton taxa has been observed to occur earlier when spring temperature is warmer (Mackas et al., 2012). Zooplankton phenological data from the offshore Northeast Pacific, focused solely on the Type I copepod Neocalanus plumchrus, also point to an earlier biomass peak in association with warmer spring SST (Mackas et al., 2007, Mackas et al., 2012). However, on the Northeast Pacific shelf, the response of zooplankton to climate change may be more complex than the “earlier when warmer” global trend. In the Bering Sea shelf ecosystem, recruitment of Calanus marshallae, the dominant copepod in the area, is highest in years of an early spring bloom (Baier and Napp, 2003). Over the British Columbia shelf, variation in the recruitment of upper trophic levels, believed to be driven by changes in zooplankton phenology, appear to be more strongly related to the onset of upwelling winds and phytoplankton spring bloom timing than spring SST (Borstad et al., 2011). However, zooplankton phenological studies have yet to be conducted in the region to verify which signal,
warmer spring temperatures or a later onset of the feeding season following a delayed arrival of upwelling winds, is the most important determinant of zooplankton phenological changes.

Copepods are the most abundant metazoans on earth (Hardy, 1970) and generally dominate the mesozooplankton both by abundance and biomass in all the world oceans (Miller, 2004a). Copepods are indeed the dominant zooplankton by biomass in the open North Pacific, comprising 80-90% of the total zooplankton biomass (Miller et al., 1984, Vidal and Smith, 1986). They also constitute a large fraction (20-50%) of the biomass in coastal shelf regions (Vidal and Smith, 1986, Mackas et al., 2004) and fjords (Cooney et al., 2001, Tommasi et al., 2013b). In turn, their biomass is dominated by only a few species. *Eucalanus bungii*, *Neocalanus plumchrus*, *Neocalanus cristatus*, and *Metridia pacifica* constitute 95% of the total copepod biomass in the open North Pacific and *C. marshallae* 92% of the total copepod biomass over the shelf (Vidal and Smith, 1986). Therefore, it is possible to gain insights into phenologically driven ecosystem shifts by analyzing trends in the abundance of only a few copepod species.

Here we examine the seasonal cycle of five copepods species in the coastal environment of the Northeast Pacific: *Acartia longiremis*, *C. marshallae*, *E. bungii*, *M. pacifica*, and *Paraeuchaeta elongata*. These five species constitute the majority of copepod biomass in the study area, Rivers Inlet, British Columbia (Tommasi et al., 2013b). Amongst them, *C. marshallae* and *E. bungii* display a Type I overwintering strategy (Osgood and Frost, 1994, Shoden et al., 2005). *Calanus marshallae* descends to overwintering depths in early summer and diapause mainly as C5 copepodites (Harrison et al., 1983, Smith and Vidal, 1986, Osgood and Frost, 1994). Exit of diapause and molting from C5 copepodites to adults occurs in early winter, prior to the spring bloom (Smith and Vidal, 1986, Osgood and Frost, 1994, Peterson, 1998, Baier and Napp, 2003). Spawning starts before the spring bloom (Smith and Vidal, 1986, Osgood and
likely using lipid reserves (Osgood and Frost, 1994), and continues over the spring period, peaking at high food concentrations (Osgood and Frost, 1994, Peterson, 1998). In the case of *E. bungii*, the majority overwinter as C5 copepodites, but a minority do so as C3 or C4 (Krause and Lewis, 1979, Shoden et al., 2005, Yamaguchi et al., 2010b). Molting to the adult stage starts prior to the bloom, in February. However, unlike *C. marshallae*, final gonad maturation and spawning are associated with the onset of the spring bloom (Shoden et al., 2005, Yamaguchi et al., 2010b, Takahashi and Ide, 2011). Thus, *E. bungii* may rely more on income breeding than *C. marshallae*.

By contrast, *A. longiremis, M. pacifica*, and *P. elongata* display a Type II strategy. The majority of the *M. pacifica* population overwinters as adult females, which remain active and feed omnivorously (El-Sabaawi et al., 2009). All copepodite stages appear year-round and reproduction is thought to occur throughout the year (Batchelder 1985, Osgood and Frost, 1994, Padmavati et al., 2004). *Paraeuchaeta elongata* reproduces year-round and remains active during the winter (Evans 1973, Ikeda and Hirakawa 1996). Similarly, *A. longiremis* has a long reproductive season, from March to September (Norrbin, 1994). However, only adult females overwinter, and they do so in very low numbers (Norrbin, 1994, Norrbin, 2001).

Specific aims for this study were to 1) present the seasonal cycle of these species in the region; 2) assess if the phenology of these copepods varied following interannual differences in spring bloom timing and spring temperature; 3) determine how the interaction between overwintering strategy and spring bloom timing affects recruitment success. We focused our analysis on the spring season as juveniles of upper trophic levels that depend on zooplankton for successful recruitment appear during this period (Borstad et al., 2011, Coyle et al., 2011).
4.2 Methods

Refer to Chapter 2 for a detailed description of the study area and field sampling methodologies. Briefly, zooplankton hauls from ~5 m above the bottom (to a maximum depth of 300 m) to the surface were conducted fortnightly (2008 and 2009) or monthly (2010) from March to June across five sampling stations equally spaced along the length of the inlet (Fig. 2.1) with a 150 µm mesh bongo net from the MV Western Bounty. During the early June 2009 cruise only a sample at DFO2 was collected. Samples from the remaining stations were collected from the MV CCGS J. P. Tully using a 236 µm bongo net during a routine biannual cruise of the Department of Fisheries and Oceans Canada.

At the DFO2 station zooplankton sampling was continued through to September in 2008. In 2009, at DFO2, sampling commenced in late February and lasted until August. In 2010, at DFO2, sampling continued over the fall and winter to February 2011. Additional samples from the DFO2 station for February 2008, September 2009, and September 2010 were collected from the MV CCGS J. P. Tully using a 236 µm bongo net during routine biannual cruises of the Department of Fisheries and Oceans Canada. Prior to every bongo net deployment, profiles of temperature, salinity, and fluorescence were collected for entire water column with a SBE 25 CTD. Profiles of temperature, salinity, and fluorescence were also taken every morning to a depth of 30 m from the Florence Daily site (Fig. 2.1).

4.2.1 Zooplankton taxonomic analysis

Each sample was first examined for the presence of rare, large organisms such as hydromedusae, fish larvae, and euphausiids, which were counted and then removed from the full
sample. The remaining sample was then split with a box plankton splitter to generate subsamples with approximately 100 individuals for the > 2 mm size fraction and 400 for the < 2 mm size fraction. Copepod adults and copepodites from stages C4 and C5 were identified to species. Copepodites C1 to C3 were identified to family for Calanidae copepods and to species for *M. pacifica*, *E. bungii*, *P. elongata*, and *A. longiremis*. Because *C. marshallae* was the numerically dominant Calanidae copepod in this system, we assume that most of the Calanidae copepodites identified belong to this species and we refer to them as *C. marshallae* C1-C3 throughout this paper. Zooplankton density was expressed on a unit volume basis (ind. m\(^{-3}\)). Moreover, zooplankton abundance on a unit area basis (ind. m\(^{-2}\)) was computed by multiplying the zooplankton density (ind. m\(^{-3}\)) by the depth of the water column sampled.

*Acartia longiremis* copepodites stage 3 and below, *M. pacifica* copepodites stage C2 and below, and Calanidae stage C1 copepodites were likely undersampled by the 150 µm mesh net (Nichols and Thompson, 1991). However, as the same undersampling bias was present across years we believe that comparison of seasonal and interannual dynamics are warranted even if absolute values of abundance need to be treated with care.

### 4.2.2 Determination of development times

Birth dates of the C1 spring cohort and adult (*A. longiremis* and *M. pacifica*) or C5 cohort (*C. marshallae* and *E. bungii*) were backcalculated using development times. No clear cohort could be distinguished for *P. elongata* and no birth date estimates were computed for this species. Copepod development time is temperature dependent and is generally modeled as a Belehrádek-type temperature dependent function (Corkett et al., 1986):

\[
D = a(T + \alpha)^\beta
\]
where $a$ and $\alpha$ are species and stage specific parameters. Corkett et al. (1986) showed that $\beta$ remained constant, at -2.05, for 11 copepod species. Thus, in our development rate parameterization we assumed a constant $\beta$ of -2.05 for all species and stages.

The $a$ and $\alpha$ parameters were estimated by fitting the Belehrádek equation to experimentally derived development times obtained from the literature using maximum likelihood in R. We assumed that the data were normally distributed with uniform variance. 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). Table 4.1 lists the studies employed and the fitted parameters. Development times were derived from stage C1 onwards. For $E. bungii$, the only experimental investigation of development time was conducted at a single temperature (5 °C, Takahashi and Ide, 2011). Therefore, using a $Q_{10}$ of 2.2 for development rate (development rate = reciprocal of development time) (Hirst and Bunker, 2003), we computed development time at 10 °C before fitting the Belehrádek curve. For $C. marshallae$ we used $a$ and $\alpha$ parameters computed by Campbell et al. (2001) for $C. finmarchicus$, as was done by Ji et al. (2012) and Baier and Napp (2003) in their estimates of $C. marshallae$ development. $Calanus finmarchicus$ has a similar length, 2.4 to 4.2 mm, as $C. marshallae$, 2.9 to 4.5 mm (Frost, 1974).

Vertical frequency distribution data in the day and night for zooplankton were available for 2010 at DFO2 in the following layers: 0-2, 0-10, 10-30, 30-100, and 100-300 m. Mean temperature in each zooplankton sampling layer for each cruise/year/site/time of day combination was computed. These temperature data were then input into the Belehrádek function with the fitted stage and species specific $a$ and $\alpha$ parameters to determine development times in Rivers Inlet for each depth layer/cruise/year/site/species/stage combination. The development
time for the entire water column was then computed as an average weighted by the relative abundance of each stage and species in each layer. It was assumed that the zooplankton maintained the same vertical distribution between sites and years. For each cruise/year/site combination the weighted average by length of daylight of the day and night development times estimates was computed. Length of daylight was obtained from tables of standard times of solar rise/set for Port Hardy, British Columbia (127° 25’ W 50° 42’ N) downloaded from the National Research Council of Canada sunrise/sunset calculator (http://www.nrc-cnrc.gc.ca/eng/services/sunrise/advanced.html, accessed January 2013).

4.2.3 Determination of egg production rates

To assess if the copepod species under study behaved more like income or capital breeders we compared seasonality in egg production rate (EPR) and numbers of egg produced to the back-calculated birthdate of the $G_1$ cohort. We searched the published literature for equations relating egg production rate (EPR) (eggs female$^{-1}$ day$^{-1}$) to chlorophyll concentration (mg m$^{-3}$) (Table 4.2). Gómez-Guttiérez and Peterson (1999) present a linearly increasing EPR with chlorophyll concentration for *Calanus marshallae*. However, for the related species *C. finmarchicus*, the maximum EPR has been reported as 50 eggs female$^{-1}$ day$^{-1}$ (Plourde and Runge, 1993). Nevertheless, at Rivers Inlet chlorophyll concentrations, no EPR greater than 50 eggs female$^{-1}$ day$^{-1}$ was ever estimated. The *Eucalanus bungii* relationship between EPR and chlorophyll was derived from a logarithmic regression of the EPR and chlorophyll concentrations reported in Smith and Lane (1991) for *E. californicus* (Appendix E). For *Metridia pacifica*, Hopcroft et al. (2005) reported a relationship between specific egg production (SEP) (d$^{-1}$) rather than EPR and chlorophyll. To estimate EPR from SEP, SEP estimates were multiplied
by the ratio of the dry weight (DW) of Rivers Inlet *M. pacifica* adult females, 136 µg, and the *M. pacifica* egg DW, 0.62 µg. Egg DW was estimated from egg carbon weight derived from the egg diameter, 145 µm, (Hopcroft et al. 2005), and egg density, 0.14 × 10⁻⁶ µg C µm⁻³ (Kiorboe and Sabatini, 1994). Egg carbon weight was then converted to ash free dry weight (AFDW) assuming a 0.4 ratio of carbon to AFDW (Hopcroft et al., 2005) and finally to DW assuming a 0.9 ratio of AFDW to DW (Hirst and Bunker, 2003). Egg production rates estimates were corrected to in situ temperature using a Q₁₀ of 2.7 (Bunker and Hirst, 2004).

The equations in Table 4.2 were used to determine EPR for each cruise/year/site/species combination from in situ chlorophyll concentrations as follows. Chlorophyll concentration depth profiles for each cruise/year/site/time of day combination were averaged over each of the vertical stratified zooplankton sampling layers and species specific EPR were obtained for each depth layer/cruise/year/site/time of day combination. The EPR of each layer was then multiplied by the abundance of adult females in each layer to estimates the number of egg produced. These estimates were summed to compute the total number of eggs produced over the entire water column. For each cruise/year/site combination the weighted average by length of daylight of the number of eggs computed during the day and night was computed. Length of daylight was obtained from tables of standard times of solar rise/set for Port Hardy, British Columbia (127° 25’ W 50° 42’ N) downloaded from the National Research Council of Canada sunrise/sunset calculator (http://www.nrc-cnrc.gc.ca/eng/services/sunrise/advanced.html, accessed January 2013).

Phytoplankton growth rates are fast and chlorophyll can fluctuate widely over the course of two weeks. Therefore, to better assess the seasonal fluctuations in EPR we also determined EPR from the daily chlorophyll time series. Daily chlorophyll depth profiles were only taken
down to 30 m, thus EPR for the daily station is an estimate for the first 30 m of the water column. However, as chlorophyll below 30 m is very low (Fig. 4.1), EPR down to 30 m was a good approximation of total EPR (Appendix F).

*Paraeuchaeta elongata* is a carnivorous copepod and as such it was felt that chlorophyll would not be an adequate proxy of food consumption and no EPR was computed for this species.

### 4.3 Results

#### 4.3.1 Hydrography

Hydrography data have been presented in detail elsewhere (Chapter 2). Briefly, the spring bloom occurred from early April to early May in both 2010 and 2008 (Fig. 4.1 and 4.2). In 2009 it started later, in early May, and was less prolonged (Fig. 4.1 and 4.2), even if in February chlorophyll concentration at DFO2 was comparable between 2008 and 2009 (Fig. 4.3). Temperature in 2010, an El Niño year, was consistently higher than 2008 or 2009 (Fig. 4.1 and 4.2). Daily mean 0-30 m temperature did not show a large variation between 2008 and 2009 over most of the sampling season (Fig. 4.2). Nevertheless, upper 50 m temperatures in March 2008 temperatures were warmer than 2009 (Fig. 4.1). DFO2 February temperature profiles revealed that the temperature difference between 2008 and 2009 observed in March was already present in February, and was particularly significant in the intermediate water column (Fig. 4.3).

#### 4.3.2 Modeled development times

Our estimated, seasonally averaged development times are in agreement with data from the literature. McLaren (1978) observed a 42 days generation time for *Acartia clausi* at 8.5 °C, which is comparable to our 48 days generation time estimates for *A. longiremis* computed using
parameterization for *A. clausi* (Table 4.3). Similarly, a generation time for *E. bungii* of 129 days (Table 4.3) is comparable, given a $Q_{10}$ of 2.2 for development rate (Hirst and Bunker, 2003) and an average temperature of 8 °C, to the 160 days generation time estimate at 5 °C by Takahashi and Ide (2011). *Metridia pacifica* generation time in the Gulf of Alaska computed by adding stage durations of egg-nauplii (Pinchuck and Paul, 1998) and C1-C6 (Liu and Hopcroft, 2006) at 5 °C was 158 days, comparable, using a $Q_{10}$ of 2.2 for development rate (Hirst and Bunker, 2003) and an average temperature of 8 °C, to our 125 days estimate. Our estimated generation time of 49 days for *Calanus marshallae* development time (Table 4.3), considering a $Q_{10}$ of 2.2 for development rate (Hirst and Bunker, 2003) and an average temperature of 8 °C, is consistent with a generation time of 84 days at 1.7 °C reported by Baier and Napp (2003). The 259 days generation time of *Paraeuchaeta elongata* is comparable to the 321 days estimated by Ikeda and Hirakawa (1996) for the Japan Sea at a temperature of 4.5 °C (range of temperatures experienced over a lifecycle is 0.5 to 8 °C) assuming a $Q_{10}$ of 2.2 and a temperature of 7 °C.

The between year temperature variation did not result in large differences in development times between years or across the sampling season (Fig. 4.4). One exception was the species *A. longiremis*, which showed longer development times in March of all years and in early April 2009 as compared to the rest of the sampling season (Fig. 4.4). *A. longiremis* showed the shallowest distribution of the copepod considered (Chapter 3), and thus was exposed to the larger seasonal temperature variation of surface waters (Fig. 4.2). *A. longiremis*, the smallest copepod studied, also showed the shortest generation time, of 48 days (Table 4.3, Fig. 4.4), while *P. elongata*, one of the largest and the deepest living copepod examined, showed the longest generation time, of 259 days (Table 4.3, Fig. 4.4). Type I copepods, *E. bungii* and *C. marshallae*, showed a shorter generation time relative to size than the other species (Table 4.3).
4.3.3 Phenology and population structure

4.3.3.1 Paraeuchaeta elongata

There was no distinct seasonal or interannual trend in the abundance of adult female *P. elongata*, with no clearly discernible cohort of adult females (Fig. 4.5). However, abundance of C1 varied seasonally and a shift between years in the timing of C1 copepodites peak abundance was observed (Fig. 4.5). Highest densities of C1 copepodites occurred in late April in 2008 and 2010, but in early May and June in 2009 (Fig. 4.5). This resulted in the total population size peaking in April 2008 and 2010 and in June in 2009 (Fig. 4.5). Given a 3 months development time to C1 (Table 4.3), birth dates of this C1 cohort were back calculated to late January in 2008 and 2010 and to early February in 2009.

Stage C1 copepodites were always present over the spring-early summer season, implying that reproduction occurred continuously, as is typical of a Type II overwintering strategy copepod (Fig. 4.5). Abundance data from DFO2 shows that young copepodites (stage C1-C4) were present in the summer as well as in February of all years (Fig. 4.5). Furthermore, winter data from 2010-2011 demonstrates that young copepodites also occurred in late November (Fig. 4.5). Thus, reproduction likely occurred throughout the year.

4.3.3.2 Metridia pacifica

The timing of the appearance of the first cohort of *M. pacifica* adult females (G1) shifted between years. G1 abundance peaked in late April in 2008, but in early June in 2009 (Fig. 4.6). However, the phenology change was not associated with differences in the size of the cohort, which remained comparable between 2008 and 2009 (Fig. 4.6). Assuming a 4 months
development time to the adult stage (Table 4.3), the $G_1$ cohort birthdate was in late December in 2008 and in early February in 2009 (Fig. 4.7). In 2010, adult female abundance was highest in late May, albeit abundances started increasing in late April (Fig. 4.6). Numbers of adult females in 2010 were less than in 2008 and 2009 (Fig. 4.6). However, total population size was highest in 2010 and lowest in 2008 (Fig. 4.6). Peak female abundances in 2008 and 2009 were short lived (less than two weeks) (Fig. 4.6), thus the monthly sampling frequency of 2010 may have missed peak 2010 female abundances.

The seasonal timing of the first C1 copepodite cohort also differed between years. In 2009, densities of stage C1 copepoides first increased in early April (Fig. 4.6). The development time from stage C1 to C6 is calculated as a range, with the maximum as the difference in development time between stage C1 and C6 and the minimum as the difference in development time between stage C2 and C6. For *M. pacifica*, this results in a range of 79-90 days. Thus, considering our two-week sampling frequency, the early April 2009 stage C1 abundance peak (Fig. 4.6), likely resulted in the June 2009 cohort of $G_1$ females (Fig. 4.7). Since adult females numbers peaked in late April 2008 and in late May in 2010 (Fig. 4.6) and since the development time between stage C1 copepodites and adults is 79-90 days, the first peak in stage C1 copepodites in 2008 likely occurred in late January-early February, and in 2010 in early to late March (Fig. 4.7). Indeed, in 2008 the first peak in stage C1 copepodites happened at or prior to the start of sampling season (Fig. 4.6). And in late March 2010 abundance was dominated by stage C3 (Fig. 4.6), suggesting that the first C1 cohort occurred in early March. No between year variability in the appearance of the second cohort of stage C1 copepodites was observed. It occurred in late May in all years (Fig. 4.6).
As copepods with a Type II overwintering strategy, *M. pacifica* appeared to have a long reproductive season, lasting from January to October. Data from DFO2 showed that stage C1 and C2 copepodites were already present in February of all years (Fig. 4.6), implying that reproduction had already started in late December or January. Reproductive activity lasted throughout the summer, with juvenile stages (C1-C3) present throughout the spring-early summer across inlet stations (Fig. 4.6), and at DFO2 until September (Fig. 4.6). Winter sampling from 2010 indicated that stage C1 copepodites were present until late October (Fig. 4.6).

### 4.3.3.3 *Eucalanus bungii*

The phenology of *E. bungii* shifted between years. Peak abundance of stage C1 copepodites occurred in late April in both 2008 and 2010 but in early June in 2009 (Fig. 4.8). Similarly, the G1 stage C5 cohort abundance appeared in early May 2008 and late May 2010, but only in late June 2009 (Fig. 4.8). This timing is consistent with a development time of 25-41 days from stage C1 to C5 (Table 4.3). The back calculated birth date of the G1 C1 cohort was late March for 2008 and 2010, and early May for 2009 (Fig. 4.9). Abundance of the C5 cohort was higher in 2008 as compared to 2009 and 2010 (Fig. 4.8), implying that recruitment success to the diapausing cohort may have been more successful in 2008.

*E. bungii* behaved as a Type I overwintering strategy copepod, showing a short reproductive season and diapausing over the winter months. Its reproductive activity, when *E. bungii* non-diapausing stage C1 and C2 were present, was focused between March-May in 2008 and 2010, and in June in 2009 (Fig. 4.8). By July of all years the population was dominated by C5 copepodites, presumably in diapause (Fig. 4.8). A second reproductive event appears to have occurred in the late summer of each year. We observed an increase in the relative abundance of
adult females as compared to stage C5 copepodites in late July 2008 and 2009, and in September 2010 (Fig. 4.8). This spawning activity may have resulted in the August and September 2009 increase in C3 and C4 copepodites abundance and in the November 2010 rise in numbers of C4 copepodites (Fig. 4.8). Winter data from 2010-2011 showed that the population diapaused mainly as stage C5 copepodites from October-January (Fig. 4.8). In February of all years some stage C5 copepodites had already started molting into adults (Fig. 4.8). The fraction of adults in the population in February 2008 was higher than in 2009 (Fig. 4.8), but by late March of both years most of the C5 had molted into adults (Fig. 4.8).

4.3.3.4 *Calanus marshallae*

*Calanus marshallae* displayed a distinct change in phenology between years. Maximum abundances of stage C5 copepodites occurred in early May 2008 and late May 2010, but in early June in 2009 (Fig. 4.10). Assuming a 15-18 days development time from stage C1 to C5 (Table 4.3), the early June 2009 C5 G₁ cohort would have developed from stage C1 copepodites present in late May, while the early May 2008 stage C5 G₁ copepodites would have developed from late April stage C1 copepodites, and the 2010 May G₁ stage C5 cohort would have resulted from late April stage C1 copepodites (Fig. 4.11). Even considering the fortnightly sampling frequency in 2008 and 2009, there is a discrepancy, especially marked in 2009, between the appearance of maximum C1 copepodites abundance and the back-calculated timing of appearance of the G₁ C1 cohort (Fig. 4.11). It appears that early season copepodite mortality is high, and that only the C1 cohort whose appearance was timed with the spring bloom recruited successfully to stage C5. As for *E. bungii*, abundance of the C5 cohort of *C. marshallae* was higher in 2008 as compared to
2009 and 2010 (Fig. 4.10), implying that recruitment success to the diapasing cohort may have been more successful in 2008.

As typical of a Type I overwintering strategist, *C. marshallae* reproductive activity was focused in the spring period and by June most of the population was composed of stage C5 copepodites, presumably in diapause (Fig. 4.10). However, it appears that a fraction of the population did not enter diapause but continued to spawn. For example, a fraction of the stage C5 cohort of 2008 molted into adult females in early June (Fig. 4.10). This continued reproductive activity did not result in large cohorts of juvenile stages over the summer (Fig. 4.10). A second, major, reproductive event was apparent in August 2008 and 2009, when the majority of C5 copepodites molted into adult females (Fig. 4.10). No sampling was conducted in August 2010, but a similar pattern was observed in October 2010, albeit the fraction of C5 molting into females was less than in August (Fig. 4.10). The population was again diapausing as stage C5 copepodites from November to January (Fig. 4.10). Molting from stage C5 to C6 started in February in all years (Fig. 4.10).

### 4.3.3.5 *Acartia longiremis*

A phenological shift in the timing of the *G₁* adult female population was also apparent for *A. longiremis*. Female abundance peaked in late May in 2008 and 2010 and in early June in 2009 (Fig. 4.12). Maximum numbers of C1 copepodites occurred late April in 2008 and in late May in 2009 (Fig. 4.12). Assuming a development time of 23-26 days from stage C1 to C6 (Table 4.3), it is probable that these C1 cohorts developed into the observed *G₁* adult populations (Fig. 4.13). The sampling resolution in 2010 was too coarse to resolve a peak in juvenile stages, but, using the observed *G₁* adult female abundances, the estimated date of appearance of the C1 cohort was
assessed as late April (Fig. 4.13). Abundance of *A. longiremis* G<sub>1</sub> adult females were comparable between years (Fig. 4.12). *A. longiremis*, as a Type II overwintering strategy copepod, displayed a long reproductive season. Stage C1 and C2 were present since the start of the sampling season in March of all years (Fig. 4.12), and data from DFO2 showed that reproduction was prominent at least until September in 2009 and until November in 2010 (Fig. 4.12). In January and February, the population consisted only of females (Fig. 4.12). Surprisingly, no juvenile stages were observed over the summer of 2008 (Fig. 4.12). This may have resulted from the fact that DFO2 is a single station and that as such it is affected by patchiness noise and between year changes in the inlet circulation.

### 4.3.4 Modeled egg production rates

*Metridia pacifica* egg production rate (EPR) was relatively high already at the start of the sampling season in 2008 and 2010. In 2009, it only reached comparable values in early May (Fig. 4.14). Sustained high maximum EPR was observed from early April to late May in 2008 and 2010 and from early to late May in 2009 (Fig. 4.14). The number of eggs started to increase from the low early spring values in late April in 2008 and 2010 and in early May in 2009 (Fig. 4.15). Given the 35 days development time from egg to stage C1, these spawning events likely produced the second cohort of stage C1 copepodites observed in late May of all years (Fig. 4.14). However, the birthdate of G<sub>1</sub> cohort was over the winter, in late December 2008, early February 2009, or late January 2010, a full 3-3.5 months before the bloom (Fig. 4.7). Thus, the *M. pacifica* G<sub>1</sub> cohort did not result from income breeding of concurrent chlorophyll resources, but from capital breeding using stored lipids or income breeding with a feeding source other than chlorophyll.
*Eucalanus bungii* EPR was already quite high at the start of the 2008 and 2010 season, and reached comparable levels only in early May in 2009 (Fig. 4.14). The late April peak in stage C1 copepodites of 2008 and 2010 was a result of a spawning event in late March (Fig. 4.9), at the onset of the spring bloom (Fig. 4.2) and of increased EPR rates (Fig. 4.14), and high egg production (Fig. 4.15). By contrast, in 2009, while the number of eggs produced was highest in late March (Fig. 4.15) as there were more females at the surface at the start of the season (Fig. 4.8), the estimated birthdate of the observed G1 C1 cohort occurred in early May at the onset of the 2009 spring bloom (Fig. 4.9) and of high EPR (Fig. 4.14). This suggests *E. bungii* may rely on income breeding for spawning.

*Calanus marshallae* EPR, similarly to the other copepod species, was higher in 2008 and 2010 at the beginning of the sampling season, and only reached comparable levels in late April and in early May in 2009 (Fig. 4.14). Since the *C. marshallae* development time from eggs to stage C1 is 17 days (Table 4.3), the observed G1 C5 cohort developed from eggs produced in April in 2008 and 2010 and in early May in 2009 (Fig. 4.11) at the onset of the bloom when EPR was highest (Fig. 4.14). The observed early April stage C1 cohort in 2009 would have instead developed from eggs spawned in late March 2009, when numbers of egg produced were highest (Fig. 4.15). Similarly, the observed late March stage C1 copepodites of 2008 and 2010 would have resulted from an early spawning event in early March. However, these pre-bloom C1 cohorts did not successfully develop into C5 (Fig. 4.10). *C. marshallae* appears to have a long reproductive period, but copepodites were recruited to the diapausing cohort only after the bloom.

*Acartia longiremis* EPR peaked earlier, in early April, in both 2008 and 2010 as compared to 2009 (Fig. 4.14). There is a 22 day development time from egg to stage C1, thus,
given our 15 days sampling frequency, the peak in C1 copepodites observed in late April 2008
and late May 2009 may have resulted from a the increase in egg production rate in early April
2008 and early May 2009 (Fig. 4.13). The number of eggs produced was maximal later in the
season (Fig. 4.15), when higher densities of adult females were present (Fig. 4.12). *Acartia
longiremis* behaved as an income breeder, with the entire G1 population developing from eggs
spawned during the bloom. When the bloom was a month later (Fig. 4.2), the appearance of the
G1 cohort occurred a month later (Fig. 4.12).

4.4 Discussion

4.4.1 Life history strategies

*Paraeuchaeta elongata, Metridia pacifica,* and *Acartia longiremis* displayed life history
traits characteristic of a Type II overwintering strategy. All three species had an extended
reproductive period: *P. elongata*’s lasted from February to November, *M. pacifica*’s from
January to October, and *A. longiremis*’s from March to November.

Our results confirmed the observations of Evans (1973) and Ikeda and Hirakawa (1996)
on the continuous reproduction of *P. elongata*. The *Paraeuchaeta* genus is carnivorous
(Mauchline, 1998), and continues to feed over the winter (Bamstedt, 1979, Oresland, 1995).
Thus, the observed late winter reproduction may have been sustained by concurrent predation.
Alonzo et al. (2000) and Auel and Hagen (2005) suggest winter reproduction of *P. antarctica* is
fuelled by a combination of stored lipids and concurrent carnivorous feeding.

In this study, we show that *Metridia pacifica* also has a long reproductive season,
confirming observations from other regions (Koeller et al., 1979, Batchelder, 1985, Osgood and
Frost, 1994). In Rivers Inlet, the first major cohort of the year was spawned in winter, when
chlorophyll concentrations were low, and may have been fuelled either by stored lipids or concurrent omnivorous feeding. Indeed, *M. pacifica* females were observed to remain active and to rely on an omnivorous diet during winter (El-Sabaawi et al., 2009). Lipid and isotopic composition data for *M. gerlachei* and *M. longa* have also shown these two polar *Metridia* species to have an omnivorous feeding behavior in winter and to be less dependent on lipid reserves as compared to other co-occurring calanoid copepods (Schnack-Shiel and Hagen, 1995, Sato et al., 2002, Stevens et al., 2004, Pasternak et al., 2009).

In agreement with the findings of Davis (1976) and Norrbin (1994), *A. longiremis* was observed to have a prolonged reproductive period in Rivers Inlet. Its population built up over the spring and reached maximum abundances in May and June. *Acartia longiremis* overwinters as fertilized females in a state of active diapause, still feeding, but with considerably reduced metabolism (Norrbin, 1994). Of the three Type II copepods examined, *A. longiremis* was the only one which did not spawn over the winter and whose reproduction appeared most tightly related to the chlorophyll bloom. The birthdate of the *G*₁ cohort was during the phytoplankton bloom, when egg production rates were highest. *Acartia longiremis*, therefore, is a classic income breeder. It should be noted that while chlorophyll appears to be a good proxy for *A. longiremis* egg production, this copepod is omnivorous (Norrbin, 2001) and heterotrophic feeding has been observed to contribute to the reproductive effort of this species (Dam et al., 1994).

As a Type I copepod, seasonality in reproduction and stage composition of *Eucalanus bungii* was more pronounced than for the Type II species above. Its spawning period was focused over the spring months. However, unlike many Type I copepods, none of the reproductive effort of *E. bungii* appeared to be a result of capital breeding. As a classical income
breeder, most of its reproduction seemed to be supplemented by concurrent feeding, with the birthdate of the $G_1$ cohort corresponding to the onset of the spring phytoplankton bloom, when egg production rates were highest. Dependence on spring bloom initiation for *E. bungii* spawning has also been proposed by Shoden et al. (2005), Kobari et al. (2010), and Yamaguchi et al. (2010b). Vertical distribution data collected over March to June 2010 in Rivers Inlet revealed that *E. bungii* females were migrating to the surface only in March and April (Chapter 3), further supporting the conclusion that reproduction occurs at the onset of the spring bloom.

Similarly to other Type I copepods, *E. bungii* in Rivers Inlet relied on diapause to overwinter. The population spent the summer largely as diapausing stage C5 copepodites. Indeed, Tommasi et al. (Chapter 3) have shown that stage C5 copepodites stopped diel vertical migration in June, an indication that they may have entered diapause. In the Strait of Georgia, *E. bungii* females are also present in surface waters only in March and April, and the first C5 individuals descend to deeper waters in June (Krause and Lewis, 1979). Another minor reproductive event occurred in late summer-early fall, but by October the population was again in diapause as stage C5 copepodites, which started molting into adults in February of the following year. Our findings are consistent with the *E. bungii* life-cycle proposed for the Oyashio region; where *E. bungii* stage C5 copepodites start their terminal moult into adults in February, develop from stage C1-C5 over the spring-early summer and diapause as C5, with a second reproductive event in August/September (Shoden et al., 2005).

The life cycle of *C. marshallae* was also characteristic of a Type I life history strategy. Our results showed that its reproductive activity was focused over the spring period, from February to May. Vertical distribution data collected March-June 2010, demonstrated that adult females were at the surface only in March and April (Chapter 3), implying spawning was
restricted to the early spring period. The reproductive period of *C. marshallae* was longer than that of *E. bungii*, with spawning starting well before the bloom. Egg production has been observed to start prior to the spring bloom in other systems (Smith and Vidal, 1986, Osgood and Frost, 1994, Baier and Napp, 2003). Indeed, Osgood and Frost (1994) demonstrate that *C. marshallae* can produce eggs solely with lipid reserves, albeit egg production rates do increase at higher food concentration. In Rivers Inlet, however, this capital breeding effort had a low reproductive value. Only those eggs spawned at the onset of the bloom were successfully recruited to the diapausing pre-adult stage.

As other Type I copepod species, *C. marshallae* spent a large part of the year in diapause. By June the population was largely comprised of stage C5 copepodites, which in 2010 were at depth, presumably in diapause (Chapter 3). However, a small fraction of the population molted to adults and continued to reproduce over the summer. A second, major reproductive event took place in late summer. From September to January most of the population consisted of stage C5 copepodites, which started molting to adults in February. Terminal moult from stage C5 to adults occurs in late winter also in the Bering Sea (Smith and Vidal, 1986, Baier and Napp, 2003), in Dabob Bay (Osgood and Frost, 1994), and in the California current upwelling system (Peterson, 1998).

### 4.4.2 Relationship between phenology, overwintering strategy, and spring environmental forcing

Phenology of all the copepod species under study was delayed when the spring bloom occurred later. Thus, even the seasonality of omnivorous and carnivorous Type II copepods must be indirectly linked to the seasonality in phytoplankton production. Indeed, even when the timing
of seasonal succession in zooplankton community composition was delayed in years of a later bloom, the same community composition characterized the Rivers Inlet zooplankton seasonal cycle in each year (Tommasi et al., 2013b).

For *Paraeuchaeta elongata*, the phenology shift only applied to its early life stages, with adult densities remaining constant over the spring period. Alonzo et al. (2000) and Auel and Hagen (2005) observed that *P. antarctica* reproduction increased in spring, possibly as a result of improved feeding conditions following the ontogenetic ascent and reproduction of overwintering copepods. In the Skagerrak, *P. norvegica* consumes 6-14% of copepod population spring production (Tonnesson et al., 2006). The observed increase of *P. elongata* C1 copepodites in early spring in Rivers Inlet is consistent with enhanced feeding conditions in late winter and early spring, when *M. pacifica* and later *C. marshallae* exited diapause and commenced reproduction. Indeed, stage C5 and C6 were already undergoing diel vertical migration in March, possibly exploiting the improved early spring feeding conditions in surface waters (Chapter 3).

*Metridia pacifica* displayed the earliest cohort timing of any species. The appearance of the first annual cohort of stage C1 copepodites always occurred approximately 45 days prior to the bloom and its birthdate was consistently 3 months before the bloom. For a continuously reproducing copepod species, appearance of a distinct cohort may be a result of an increase in bottom-up driven rates, such as egg production, or of a decrease in top-down processes, such as mortality. In all years, the second cohort of *M. pacifica* may have been an example of an increase in egg production rate following an increase in chlorophyll. However, the *M. pacifica* G1 cohort was spawned in winter, when egg production was at its lowest, suggesting that survival may have controlled the appearance of this cohort. Cohort development of *M. lucens* in the North Atlantic was negatively related with *C. finmarchicus* abundance through intraguild predation of
C. finmarchicus on the early stages of M. lucens (Irigoien and Harris, 2006). The birthdate of the M. pacifica G₁ cohort occurred prior to the ontogenetic migration of C. marshallae in every year, suggesting that a similar mechanism may have been at play in Rivers Inlet. Unlike P. elongata, M. pacifica is a surface spawner (Padmavati et al., 2004) and thus its eggs may be vulnerable to predation from newly molted C. marshallae females. A careful assessment of M. pacifica winter and early spring mortality rates, predation pressure, and feeding history in relation to the spring phytoplankton bloom should be undertaken to determine the potential mechanism of the observed M. pacifica phenological variation.

A later onset of the spring bloom was associated with a delay in A. longiremis peak egg production rates, and resulted in a phenological shift in the appearance of its G₁ cohort. Adult A. longiremis abundance peaked at the end of the spring bloom, when dinoflagellates dominated the phytoplankton community composition (Margalef, 1978). A later Acartia spp. biomass peak following a later dinoflagellate phenology was also observed in the North Sea (see review by Mackas et al., 2012). Since the observed differences in development times resulting from the interannual variation in spring temperature cannot account for the one month interannual difference in the timing of appearance of peak stage C₁ densities and since phenology of A. longiremis was comparable in 2008 and 2010, two years of differing spring temperatures, we conclude that in Rivers Inlet an earlier buildup of the population is more dependent on an earlier timing of the spring bloom, and the associated high egg production rates, than on temperature. However, Acartia spp. phenology in other regions of the North Atlantic and in the Mediterranean appears to be more strongly associated with SST than phytoplankton phenology (see review by Mackas et al., 2012). Such regional differences may arise from variation in the overwintering strategy of the dominant Acartia species. Most Acartia species overwinter as resting eggs, whose
hatching is temperature dependent (Miller, 2004b). By contrast, *A. longiremis* diapauses in low numbers as immature females (Norrbin, 2001).

As for *A. longiremis*, the dependence of *E. bungii* on spring bloom initiation for spawning resulted in a phenology shift in the timing of *G₁* copepodites following a shift in spring bloom timing. However, while in 2008 and 2010 the egg production pattern coincided with the timing of high egg production rate and cohort timing, in 2009 it did not. The estimated egg numbers were actually highest in late March 2009 because of high female abundance. The discrepancy between egg production estimates and the timing of appearance of the C1 cohort suggests that egg mortality was extremely high or that females were immature pre-bloom. In the Oyashio region significant numbers of mature *E. bungii* females only appeared at the onset of the spring bloom (Shoden et al., 2005, Yamaguchi et al., 2010b), suggesting that *E. bungii* females may indeed have been immature prior to the bloom.

A shift in *E. bungii* cohort timing may also have resulted from a later emergence from diapause. Indeed, a larger fraction of the population comprised adult females in February 2008 as compared to 2009, suggesting that moulting from *C₅* to adults occurred earlier in 2008 than 2009. The cue to exit diapause and initiate moulting in *E. bungii* is unknown. However, temperature has been proposed as an environmental control of diapause emergence and maturation in other copepod species (Mackas et al., 2012). Thus, the later maturation in 2009 may be related to the lower temperatures of the deep layers in late winter 2009. By late March water temperatures below 50 m were comparable between years, and most of the population had molted into adult females also in 2009. Nevertheless, no stage C1 copepodites were observed until early June 2009, thus a temperature-driven shift in the timing of emergence was not a likely driver of the observed changes in cohort timing.
Phenology of *C. marshallae* was driven by differences in survival rather than changes in egg production. Reproduction started before the bloom, but recruitment was successful only for the cohort that developed into early copepodites during the spring bloom. These results are in agreement with observations from the Norwegian Sea demonstrating that *C. finmarchicus* copepodites do not develop beyond the early copepodites stages until the spring bloom (Hirche et al., 2001), and with observations from the Bering Sea indicating that fitness is highest for those *C. marshallae* C1 copepodites appearing at the onset of the bloom (Baier and Napp, 2003). Thus, in Rivers Inlet, like in the Bering Sea, *C. marshallae* phenology appears to be controlled by differential survival of early copepodites rather than production and is dependent on the timing of the spring bloom.

As for *E. bungii*, a delay in phenology may also have been driven by interannual changes in temperature. However, the timing of the terminal molt of *C. marshallae* was not later when water temperatures were colder in 2009; the fraction of adult females relative to stage C5 copepodites was actually higher in February 2009 as compared to February 2008. Therefore, internal controls of timing of diapause emergence such as accumulated lipid reserves may be more important than direct temperature control in determining the timing of emergence of *C. marshallae* C5 copepodites, as was concluded by Johnson et al. (2008) for *C. finmarchicus*. This suggests that temperature was not a direct driver the observed variation in *C. marshallae* phenology. Nevertheless, these results are in disagreement with data from the North Sea (see review by Mackas et al., 2012), showing that sea surface temperature may be a more important forcing of *C. finmarchicus* phenology than phytoplankton bloom timing. This may be due to site-specific differences in the seasonality of phytoplankton dynamics, the seasonality of predation pressure, or the relative importance of advection as a driver of population dynamics. In Rivers
Inlet, advection was not the main driver of *C. marshallae* population dynamics as compared to local demographic processes (Chapter 3).

### 4.4.3 Relationship between recruitment success, overwintering strategy and spring environmental forcing

In terms of recruitment success, the response of the copepods under study was specific to each type of overwintering strategy. While the phenology of all copepod species was delayed following a later bloom, a delay in bloom timing was only associated with poorer recruitment success of Type I copepods. Reduction in recruitment of *E. bungii* and *C. marshallae* following a delay in spring bloom timing has also been observed elsewhere (Baier and Napp, 2003, Kobari et al., 2007). Furthermore, only Type I copepods displayed declines in $G_1$ cohort size at high temperatures, during the El Niño year. It appears that continuous reproduction and omnivorous feeding strategy allows Type II copepods to exploit seasonally variable food resources and to build their populations to a comparable size during years of varying spring environmental forcing and spring bloom timing. By contrast, species that focus their reproductive effort over the spring period appear more vulnerable to interannual variation in spring forcing.

Differential response of copepods to environmental forcing has long been recognized in the Northern California Current system, where Northern copepods dominate over Southern types in relation to ocean transport (Hooff and Peterson, 2006, Mackas et al., 2007, Keister et al., 2011). However, most of the species considered here belong to the Northern group. More specifically, *E. bungii* and *M. pacifica* are subarctic oceanic copepods and *C. marshallae* and *A. longiremis* are boreal shelf copepods (Mackas et al., 2007). *P. elongata* has generally not been associated with either Northern or Southern copepods. Our results are the first to demonstrate
that further changes in community composition may be superimposed over the observed transport-driven variation following shifts in environmental forcing. This pattern may be particularly important for northern regions, which are presumably sources of these copepods, as well as for coastal embayments, such as fjords or inland seas, whose zooplankton community may not be as impacted by the circulation over the shelf break.

While it was not an aim of this study to assess the mechanisms for the observed variation in recruitment, some generalizations on the potential drivers of the observed pattern can be made. The 2009 spring bloom was less prolonged. Earlier termination of the bloom may have reduced growth rates of both *E. bungii* and *C. marshallae* copepodites (Campbell et al., 2001, Takahashi and Ide, 2011), and have resulted in a smaller diapausing cohort. However, the 2010 bloom was similar in duration to 2008, suggesting that top-down processes, rather than bottom-up processes played a role in determining the size of the diapausing C5 cohort. Recent studies have shown that mortality may be an important driver of copepod recruitment (Li et al., 2006, Plourde et al., 2009, Ji et al., 2013). Thus, overall recruitment of both *E. bungii* and *C. marshallae* may have been lower when the bloom was later because of higher cumulative mortality of adult females from the time of diapause emergence to the time of successful copepodite recruitment during the bloom. Higher mortality of copepodites with a later birthdate may also explain the lower recruitment when the bloom was late. The substantial decrease in Type I recruitment during the El Niño year provide further support for the hypothesis of higher mortality of Type I copepods at higher temperatures. The number of invertebrate predators increases over the season (Sullivan and Meise, 1996, Tommasi et al., 2013b), predation rate increases with temperature (Davis 1984b, Ji et al. 2009), and the mortality of stage C5 and adults of *C. finmarchicus* is maximum in May and June (Li et al. 2006), suggesting that mortality of Type I copepods may have indeed
been higher at higher temperatures. Indeed, the short reproductive period of Type I copepods may well have evolved as a response to higher predatory rates over the summer period. Since summer plankton appears to respond more strongly to changes in sea surface temperature than copepods dominating the spring community (Edwards and Richardson 2004), an assessment of the potential for an increase in the overlap of high predation and Type I copepod at high spring temperatures is warranted. Future research should also assess seasonal and interannual variation in predator densities in relation to temperature and phytoplankton dynamics to assess the potential for top-down control of *E. bungii* and *C. marshallae*.

4.4.4 Implications for upper trophic levels

Our results provided further confirmation that zooplankton phenology is affected by seasonality in primary production. This mechanistic link has often been implied in the studies that have shown declines in upper trophic level recruitment following changes in spring bloom timing (e.g. Platt et al. 1993, Borstad et al. 2011), and forms the basis of the Hjort-Cushing match-mismatch hypothesis. This hypothesis states that the variation in fish year-class strength is a result of change in the duration of overlap of peak larval abundance with the period of high food variability (Hjort 1914, Cushing 1969, 1990a). Evidence in support of the match-mismatch hypothesis (Cushing 1969, 1990b, Ellersten, 1987, Platt et al., 2003, Holt and Mantua, 2009, Shultz et al., 2009, Borstad et al., 2011, Kristiansen et al., 2011) demonstrates that variation in spring forcing and plankton dynamics can significantly impact higher trophic levels. Our results confirmed the potential for a match-mismatch between fish larvae/juveniles and zooplankton when the bloom is delayed.
According to our results, instances of trophic decoupling between zooplankton and upper trophic levels may become more common in this region under projected climate change scenarios. Spring bloom timing is driven by wind conditions in late winter/early spring (Wolfe, 2010, Borstad et al., 2011). The timing of arrival of upwelling winds is occurring later and this trend might persist in the future with continued climate change (Foreman et al., 2011). Such wind patterns would lead to a later phytoplankton bloom timing in the future, and a potential shift in the phenology of the major copepod species in the region to later periods. Such changes may have important repercussions for the recruitment of upper trophic levels whose phenology is driven by other factors or may not be as flexible as that of their zooplankton prey.

Furthermore, our results showed that in years of a late spring bloom, upper trophic levels not only have to contend with a later appearance of high food resources, but also with reduced abundances of Type I copepod prey. The life history characteristics of Type I copepods, such as their ontogenetic surface migration and large lipid stores, may make them an easily accessible, high quality prey for upper trophic levels (Mackas et al., 2007, Trudel et al., 2007, Hunt et al., 2011). Indeed, Mackas et al. (2007) show that a lower biomass of “subarctic” copepods, which includes *E. bungii*, and of “boreal shelf” copepods, which includes *C. marshallae*, is correlated with declines in the salmon, sablefish, and seabird recruitment. Clearly, the impact of shifts in spring bloom timing on upper trophic levels appears likely to be further magnified by the reduction in Type I copepod biomass. As Type I copepods were reduced also in the El Niño year, we may expect a reduction of trophic level recruitment also in years of high temperatures.
4.5 Conclusions

We have shown that changes in the phenology of dominant North Pacific shelf copepod species are associated with changed in phytoplankton bloom timing. We suggest that for *C. marshallae* such an association was caused by a direct effect of phytoplankton bloom timing on copepodite survival. For income breeders, such as *A. longiremis* and *E. bungii*, the timing of the bloom delayed the timing of peak egg production. For the winter omnivorous *M. pacifica* and carnivorous *P. elongata*, the phytoplankton effect may have been indirect via co-variation of another un-tested variable such as prey availability that affected egg production, copepodite survival, or both.

The observed phenological changes also affected relative zooplankton species composition due to differential response to changes in spring forcing. The recruitment of *P. elongata, M. pacifica,* and *A. longiremis* was not impacted by the change in phytoplankton phenology or by high spring temperatures. These species have a varied diet and a long reproductive season and thus are able to adapt to variable spring forcing. By contrast, recruitment of the two Type I copepod species in the system, *E. bungii* and *C. marshallae*, was reduced following the change in phenology and in the year of high spring temperatures, possibly because of reduced survival of adults and/or copepodites. These two species are herbivorous and concentrate their reproductive effort in the spring, with most of the population diapausing over the summer. They are therefore strongly dependent on the spring phytoplankton bloom and on low predation rates in spring for successful recruitment. Nevertheless, both species had a second major spawning event in late summer/early fall. It remains to be assessed how phenology of fall spawning events changes interannually and how important fall spawning events are to recruitment in the following spring. If the successful recruitment window of Type I copepods in
spring, marked by high chlorophyll concentrations and low mortality, will be reduced under future climate change scenarios, fall recruitment events may become essential to the maintenance of the annual reproductive success of these species.

Since recruitment success of fish larvae relies on synchronization with peaks of their zooplankton prey (Hjort, 1914, Cushing, 1969, 1990a), the observed phenological variation in zooplankton dynamics may result in phenologically driven ecosystem shifts. Recruitment success of upper trophic levels may be further impaired in years of a delayed spring bloom or high spring temperatures by declines in Type I copepods, an energy rich prey (Mackas et al., 2007, Trudel et al., 2007). Future studies should evaluate direction of climate driven changes in spring forcing events and their effect on both zooplankton phenology and that of upper trophic levels to assess the potential for a significant mismatch between upper trophic levels and their zooplankton prey in the future.
4.6 Figures

Figure 4.1 Seasonal depth profiles of chlorophyll (mg m$^{-3}$) and temperature ($^\circ$C) averaged across inlet stations for the three years of observations. Note that in 2010 depth profiles were taken monthly rather than fortnightly.
Figure 4.2 Average upper 30 m chlorophyll (panel A) and temperature (panel B) from March to June at the Florence Daily station for the three years of observations.
Figure 4.3 February depth profiles of chlorophyll (mg m$^{-3}$) and temperature (°C) at DFO2 for 2008 and 2009.
Figure 4.4 Species and stage-specific estimates of development times averaged across inlet stations computed for each sampling cruise and sampling year. Error bars represent standard errors.
Figure 4.5 Left panel: stage-specific variation in abundance of *Paraeuchaeta elongata* averaged across inlet stations over the spring period (March to June). Right panel: stage-specific relative abundance at DFO2 over the winter, summer, and fall.
Figure 4.6 Left panel: stage-specific variation in abundance of *Metridia pacifica* averaged across inlet stations over the spring period (March to June). Right panel: stage-specific relative abundance at DFO2 over the winter, summer, and fall.
Figure 4.7 Late December (LD) to late June (LJ) cohort development of *Metridia pacifica*. Solid boxes represent actual observations. Dotted boxes are back-calculated estimates using development times. In each box, the central black line represents the actual timing of sampling. Boxes were extended two weeks (2008 and 2009) or a month (2010) from this date to represent the uncertainty in the cohort appearance resulting from our fortnightly (2008 and 2009) or monthly (2010) sampling resolution. The C1 cohort has two potential timings because of the almost two-week duration of the C1 stage. See text for more details. The rectangle on the time axis represents the timing and duration of the spring bloom. Note that the C1 G1 cohort was not sampled within the sampling season timeframe in 2008 and 2010 and hence no observed C1 G1 cohort is shown.
Figure 4.8 Left panel: stage-specific variation in abundance of *Eucalanus bungii* averaged across inlet stations over the spring period (March to June). Right panel: stage-specific relative abundance at DFO2 over the winter, summer, and fall.
**Eucalanus bungii**

- Light gray box = Birth of $G_1$
- Brown box = C1 $G_1$ cohort
- Gray box = C5 $G_1$ cohort
- Dark gray box = Modeled
- White box = Observed

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Figure 4.9 Late December (LD) to late June (LJ) cohort development of *Eucalanus bungii*. Solid boxes represent actual observations. Dotted boxes are back-calculated estimates using development times. In each box, the central black line represents the actual timing of sampling. Boxes were extended two weeks (2008 and 2009) or a month (2010) from this date to represent the uncertainty in the cohort appearance resulting from our fortnightly (2008 and 2009) or monthly (2010) sampling resolution. The rectangle on the time axis represents the timing and duration of the spring bloom.
Figure 4.10 Left panel: stage-specific variation in abundance of *Calanus marshallae* averaged across inlet stations over the spring period (March to June). Right panel: stage-specific relative abundance at DFO2 over the winter, summer, and fall.
Figure 4.11 Late December (LD) to late June (LJ) cohort development of *Calanus marshallae*. Solid boxes represent actual observations. Dotted boxes are back-calculated estimates using development times. In each box, the central black line represents the actual timing of sampling. Boxes were extended two weeks (2008 and 2009) or a month (2010) from this date to represent the uncertainty in the cohort appearance resulting from our fortnightly (2008 and 2009) or monthly (2010) sampling resolution. The rectangle on the time axis represents the timing and duration of the spring bloom.
Figure 4.12 Left panel: stage-specific variation in abundance of *Acartia longiremis* averaged across inlet stations over the spring period (March to June). Right panel: stage-specific relative abundance at DFO2 over the winter, summer, and fall.
Figure 4.13 Late December (LD) to late June (LJ) cohort development of *Acartia longiremis*. Solid boxes represent actual observations. Dotted boxes are back-calculated estimates using development times. In each box, the central black line represents the actual timing of sampling. Boxes were extended two weeks (2008 and 2009) or a month (2010) from this date to represent the uncertainty in the cohort appearance resulting from our fortnightly (2008 and 2009) or monthly (2010) sampling resolution. The rectangle on the time axis represents the timing and duration of the spring bloom.
Figure 4.14 Seasonal variation in species-specific egg production rate estimates (egg female$^{-1}$ day$^{-1}$) at the Florence daily station (top panel).
Table 4.15 Average of egg abundance estimates (# m$^{-2}$ day$^{-1}$) across inlet stations ± standard error.

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</tr>
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<tr>
<td></td>
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<td></td>
<td>2009</td>
<td>2010</td>
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<tr>
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</tr>
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<td>2008</td>
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<td>2008</td>
<td>2009</td>
</tr>
<tr>
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</tr>
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Figure 4.15 Average of egg abundance estimates (# m$^{-2}$ day$^{-1}$) across inlet stations ± standard error.
### 4.7 Tables

<table>
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Table 4.1 Species and stage specific Belehrádek parameters used in the calculation of development times.

Literature sources of the experimental data employed to derive the parameters are highlighted.
Table 4.2 Egg production rate equations derived from the literature.

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<td>( EPR = 54.01 \times (1-e^{0.29*\text{Chl}-0.17}) )</td>
<td>Dam et al., 2004 (for <em>Acartia tonsa</em>)</td>
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| *Calanus marshallae* | \( EPR = 2.7021 \times \text{Chl}+1.3116 \)
If \( EPR > 50 \), \( EPR = 50 \) | Gómez-Gutierrez and Peterson, 1999                                                      |
| *Eucalanus bungii*  | \( EPR = 19.874 \times \ln(\text{Chl})+65.414 \)                           | Smith and Lane, 1991 (for *Eucalanus californicus*)                                       |
| *Metridia pacifica* | \( EPR = 0.18 \times \text{Chl}^{1.95}/(1.02^{1.95}+\text{Chl}^{1.95}) \) | Hopcroft et al., 2005                                                                  |

Table 4.3 Species and stage specific development times and stage durations. Development times represent the days taken to develop to the specified stage and were computed from the species and stage-specific Belehrádek parameters listed in Table 4.1. Stage durations were computed from the difference of two consecutive development times.
Chapter 5: Investigating the environmental drivers of *Calanus marshallae*
and *Eucalanus bungii* population dynamics: a modeling approach

A stage structured population model was used to simulate the population dynamics of the copepods *Calanus marshallae* and *Eucalanus bungii* over the spring period. Simulations successfully reproduced the interannual and seasonal variability in the abundance of the two species in three different years of observations. The copepods displayed different reproductive strategies. *Calanus marshallae* started reproduction in late winter and spawned over a long period. By contrast, the reproductive effort of *E. bungii* was focused at the onset of the spring bloom. Variation in mortality was the main driver of the observed interannual differences in the size of the new diapausing cohort. When the bloom was late more of *C. marshallae* reproductive effort was lost to mortality. *E. bungii* experienced lower recruitment when the bloom was late because of a reduction in the numbers of females and of an increase in the mortality of copepodites with a later birth date. For both copepods, high mortality was associated with low chlorophyll concentrations and high temperatures. The biomass of the diapausing cohort of both species was reduced during an El Niño year.

5.1 Introduction

*Eucalanus bungii* is a large (adult total length 5-7 mm (Shoden et al., 2005)), subarctic oceanic copepod (Mackas et al., 2007). It is a major component of the zooplankton biomass in the Subarctic Pacific Ocean and adjacent inland seas (Miller et al., 1984) and also constitutes a large fraction of the copepod biomass of North Pacific fjords (Krause and Lewis, 1979). *Calanus*
*C. marshallae*, a medium sized (3-4.5 mm (Frost, 1974)), boreal shelf copepod (Mackas et al., 2007), spans a similar latitude range, from the Northern California Current system to the coastal Gulf of Alaska and the Bering Sea, but favors a more neritic habitat, and is a dominant member of the zooplankton community on the continental shelf (Smith and Vidal, 1986, Peterson, 1998, Mackas et al., 2004, Mackas et al., 2007).

Both copepod species demonstrate a Type I overwintering strategy (sensu Atkinson, 1998; see Chapter 4). They survive the winter period of low food availability by diapausing as lipid-rich stage C5 copepodites (Smith and Vidal, 1986, Shoden et al., 2005) with a minority of *E. bungii* copepodites also diapausing as stage C3 or C4 (Krause and Lewis, 1979, Shoden et al., 2005, Yamaguchi et al., 2010b).

Molting from diapausing stage C5 copepodites to females occurs in late winter, prior to the spring bloom (Smith and Vidal, 1986, Baier and Napp, 2003, Shoden et al., 2005, Yamaguchi et al., 2010b) and females dominate the biomass of the pre-bloom zooplankton community (Tommasi et al., 2013b). It is widely acknowledged that *E. bungii* depends on the spring phytoplankton production for final gonad maturation and spawning (Shoden et al., 2005, Yamaguchi et al., 2010b). Since *E. bungii* reproduction relies on concurrent food intake, it may be considered an income breeder (Varpe et al., 2009). By contrast, dependence of *C. marshallae* on the spring bloom for reproduction is unclear and may be region specific. For example, the main spring cohort in the Bering Sea develops from eggs hatched prior to the bloom (Baier and Napp, 2003), and it has been suggested that *C. marshallae* may have a reproductive strategy similar to *C. glacialis*, which is a capital breeder whose spawning is independent of the bloom (Baier and Napp, 2003). Pre-bloom egg production was observed to be responsible for the bulk of *C. marshallae* recruitment in spring in Dabob Bay (Osgood and Frost, 1994) and in Rivers
Inlet (Chapter 4). By contrast, in the Oregon upwelling system, the main reproductive period of
_C. marshallae_ is associated with the spring bloom (Peterson, 1998) as has been observed for _C. finmarchicus_ in the North Atlantic (Niehoff et al., 1999).

Since both species accumulate lipids prior to entering diapause (Smith and Vidal, 1986, Shoden et al., 2005) they may provide a high energy, good quality prey for upper trophic levels (Mackas et al., 2007, Trudel et al., 2007). Indeed, both species have been shown to play a critical role in transferring energy to upper trophic levels. _Eucalanus bungii_ is predated upon by a variety of fish species (Irie et al., 1979, Seki and Shimizu, 1998, Beamish et al., 1999, Yamamura et al., 2002) and seabirds (Hunt and Harrison, 1990, Russell et al., 1999) while _C. marshallae_ constitutes a major prey species for larval and juvenile fish (Grover, 1991, Coyle et al., 2011), seabirds (Springer et al., 2008), and whales (Tyan et al., 2001).

Given their importance in oceanic and coastal food webs of the North Pacific Ocean, fluctuations in their abundance may have significant consequences for upper trophic levels. Declines in salmon survival (Mackas et al., 2007, Bi et al., 2011), sablefish recruitment (Mackas et al., 2007), and seabird reproduction (Mackas et al., 2007) have been linked to reduced dominance of subarctic and boreal copepod groups, that include _E. bungii_ and _C. marshallae_, highlighting their importance to ecosystem function.

Substantial interannual and decadal fluctuations in the abundance and seasonal timing of both copepod species are thought to reflect variation in physical forcing (Baier and Napp, 2003, Kobari et al., 2007, Coyle et al., 2008, Coyle et al., 2011). Unlike omnivorous copepod species, demonstrating a Type II life history strategy (Atkinson, 1998), the abundance of _C. marshallae_ and _E. bungii_ can be greatly reduced in years of warm spring temperatures or of a delayed spring phytoplankton bloom (Chapter 4). In the Bering Sea, declines of _C. marshallae_ during warm
years have also been associated with a shift towards dominance of more omnivorous species (Coyle et al., 2008). Since such changes in zooplankton community structure are known to have repercussions for upper trophic levels (Beaugrand et al., 2003, Mackas et al., 2007, Coyle et al., 2011), it is important to assess what life history traits make Type I copepods more vulnerable to variation in spring environmental forcing. It has been hypothesized that the success of the spring cohort of *C. marshallae* is dependent on a match between the onset of the spring bloom and the appearance of early stage copepodites (Baier and Napp, 2003, Chapter 4). Physiological changes, such as earlier diapause exit, brought about by warming of overwintering bottom waters, have been suggested to further aggravate the mismatch between *C. marshallae* copepodites and the timing of the bloom, which in the Bering Sea is later when ice extent is low and waters are warm (Coyle et al., 2011). Similarly, Kobari et al. (2007) have proposed that changes in *E. bungii* biomass and seasonal timing are related to variation in phytoplankton dynamics, with recruitment being more successful under conditions of an early, prolonged spring bloom. Reductions in egg production and lower copepodite survival have been put forward as possible mechanistic explanations of the observed association between primary production and successful recruitment of these two copepod species (Baier and Napp, 2003, Kobari et al., 2007, Takahashi and Ide, 2011).

Analysis of field data has been essential to determining the potential drivers of changes in the population dynamics of *E. bungii* and *C. marshallae*. However, numerical models are needed to test the validity of the proposed mechanistic explanations and to assess the relative importance of co-varying forcing variables whose effect on population dynamics may not be easily separated in the field. Such models can be used not only to assess our conceptual framework of the drivers
of *C. marshallae* and *E. bungii* recruitment, but also to highlight gaps that may exist in our present knowledge of these species’ life histories and point to future research needs.

Here we build a simple, 0 dimensional model of *E. bungii* and *C. marshallae* population dynamics and test its ability to resolve the observed seasonal and interannual variation of their abundance by validating simulated densities against field observations collected from March to June in 2008, 2009, and 2010 in Rivers Inlet, a fjord in central British Columbia. We have chosen to focus on this data set as the seasonal cycle of both species in this system is well understood from extensive analysis of both hydrographic and biological field data (Tommasi et al., 2013b). Furthermore, the three years of available observations span large fluctuations in the seasonal cycle of primary production, with the phytoplankton bloom occurring a month later in 2009, as well as in temperature, with 2010 being an El Niño year (Tommasi et al., 2013b).

Whilst this interannual variation in the physical environment has been associated with changes in both the seasonal timing and biomass of both *E. bungii* and *C. marshallae*, the main processes controlling their recruitment remain uncertain (Chapter 4). Finally, since Rivers Inlet is a fjord, zooplankton can emigrate/immigrate only via one exchange boundary and the effect of advection on the local zooplankton population can be adequately addressed in the 0 dimensional model by computation of zooplankton daily exchange rates between the fjord and the outer shelf area (Chapter 3). The aims of this study were to 1) build a population model that could successfully simulate the observed seasonal and interannual variability in the abundance of *E. bungii* and *C. marshallae* over the spring period, 2) test the hypothesis that *C. marshallae* recruitment is reduced when the spring bloom is delayed because of lower copepodite survival, 3) test the hypothesis that *E. bungii* recruitment is reduced when the spring bloom is delayed because of higher female and copepodite mortality, 4) use the model to identify the environmental factors
driving the observed interannual variability in both the phenology and size of the main spring cohort, 5) assess what knowledge gaps in our understanding of the life history of these two copepod species may need to be addressed in future studies.

5.2 Methods

Details of the collection of the zooplankton and hydrographical field data have been described at length in Chapter 2 and 3. Briefly, zooplankton hauls and CTD casts were conducted fortnightly in 2008 and 2009 and monthly in 2010 from mid March until late June at 5 inlet stations (Fig. 2.1) between the surface to the bottom. In 2010, stratified vertical net hauls were conducted at the DFO2 station in the following depth strata: 0-300, 0-100, 0-30, 0-10, 0-2 m, both during the day and night.

Population dynamics of both copepods were simulated using a 0 dimension, time varying only, 7-stage (egg and nauplii, C1, C2, C3, C4, C5, C6) mean-age model. This model was first developed by Hu et al. (2008) in a 4-stage (egg, nauplii, copepodite, adult), 0-dimension configuration and has been shown to effectively remove the numerical diffusion problem of abundance based copepod models and to reproduce observed development times without requiring a computationally intensive age within stage structure (Hu et al., 2008). This model was also coupled to a 3D circulation model of the Gulf of Maine-Georges Bank region to successfully simulate the seasonal dynamics of Pseudocalanus spp. and Centropages sp. (Ji et al., 2009, Stegert et al., 2012, Ji et al., 2013).

A basic population dynamics equation governs the model as specified below. For each stage (i), the number of individuals (N) in the next time step is computed as:
\[ N_i(t+H) = N_i(t) + \text{RN}_i(t) - M_iN_i(t) - m_iN_i(t) + a_iN_i(t) \quad \text{for } i = 1 \]
\[ N_i(t+H) = N_i(t) + M_{i-1}N_{i-1}(t) - M_iN_i(t) - m_iN_i(t) + a_iN_i(t) \quad \text{for } 1 < i < S \]
\[ N_i(t+H) = N_i(t) + M_{i-1}N_{i-1}(t) - m_iN_i(t) + a_iN_i(t) \quad \text{for } i = S \]

Where \( H=1 \) day, \( S \) is the number of stages, \( R \) is the reproduction rate, \( m \) is the mortality rate, and \( M \) is the molting rate. Here we modified the model to also include an advection rate, \( a \).

The reproduction rate depends on the egg production rate (epr) of mature females and the fraction of females that are mature and spawning (f). The empirically derived equation relating egg production rate to the upper 30 m mean chlorophyll concentration for each species has been described in Chapter 4. At each time step, a new epr was calculated according to the chlorophyll concentration and temperature of that time step. The fraction of spawning, mature females was initially set as being equal to the fraction of females in the upper 30 m estimated at a monthly frequency at DFO2 in 2010. It was assumed that the vertical distribution would remain constant over each month and between years. This initial parameterization was refined further as described in the results section to improve the fit between observed and simulated data.

The molting rate was derived from the molting probability function (Hu et al., 2008). The probability of molting is dependent on the mean age of each stage and the stage duration (Hu et al., 2008). As in Stegert et al. (2012), the molting probability function \( (p) \) was described by a normal distribution with a mean equal to the stage duration (SD) and a gradient parameter of 0.4. As outlined in eq. 5 of Hu et al. (2008), the molting rate \( (M) \) of each stage \( (i) \) at mean age \( (k) \), is defined as:

\[ M_i(k) = \frac{p_i (k)dt}{(1 - P_i (k))} \]
If, at the specified mean age, the probability of growing older in that stage is high (i.e. mean age is less than SD), the probability of molting will be low. At each time step, the mean age of each stage is computed as outlined in eq. 4a of Hu et al. (2008) for the egg/nauplii stage and as eq. 4b for the remaining stages.

The stage duration was modeled as a Belehrádek-type temperature dependent function (Ji et al., 2009)

\[ SD = a(T + \alpha)\beta \]

where \(a\) and \(\alpha\) are species and stage specific parameters. Corkett et al. (1986) showed that \(\beta\) remained constant, at -2.05, for different copepod species. Thus, we assumed a constant \(\beta\) of -2.05 for each species and stage. The \(a\) and \(\alpha\) parameters were estimated by fitting the Belehrádek equation to experimentally derived stage durations obtained from the literature using maximum likelihood in R. We assumed that the data were normally distributed with uniform variance. 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). The same studies listed in Table 4.1 used to compute development times were employed here.

Instead of estimating mortality using the general temperature dependent formulation described in Ji et al. (2009), temporally dynamic and stage dependent daily mortality rates over the sampling period were computed from field observations of abundance with the population surface method (PSM) developed by Wood (1994) using the posum 2 R package. This method solves the McKendrick-von Foerster equation by fitting a smooth population surface to the observed population data using spline functions and requires estimates of the abundance of each stage at a series of times and independent estimates of the development time of each stage at the
same series of times (Wood, 1994). Development times during each cruise were a function of temperature. Details of the computation of development times for each cruise are found in Chapter 4.

Eiane et al. (2002) showed that a monthly sampling resolution was adequate for resolving mortality of each stage of *Calanus* spp. when egg and all nauplii stages were aggregated into one stage. Thus, we assumed that the fortnightly 2008 and 2009, and monthly sampling frequency in 2010 were adequate to resolve mortality for *E. bungii*, which has a longer development time than *Calanus* spp., and for *C. marshalli* as here egg and nauplii were aggregated into one stage.

However, it should be noted that the abundance of egg/nauplii was not sampled directly from field observations. The numbers of eggs produced on each cruise, computed using empirical relationships between egg production rate and chlorophyll concentrations, as described in Chapter 4, served as estimates of the number of egg and nauplii on each cruise. Even if all the females were considered to be mature and spawning, and hatching success was set at 1, the estimated number of eggs/nauplii may be an underestimate, as it does not take into account numbers of eggs/nauplii that may have already been present.

The PSM method requires the observed population data to be an estimate of the true population, unaffected by advection. Stage specific daily exchange rates (a) between the inlet and outer waters (boundary set at DFO2) were computed for each year, as described in Chapter 3, and the losses due to advection between cruises were calculated (see Chapter 3 for more details). The true population abundance was then computed as the sum of the observed abundance and the number advected between cruises. Wind data were missing from April 24 to May 9 in 2008 and from April 10 to June 1 in 2009 and no advection rates could be computed during these periods. The missing advection rates were estimated by linear interpolation. Since
eggs were not identified to species the total egg advection rate as computed in Chapter 3, was taken as the estimate of advection rate for the egg/nauplii stage of each species. This appears to be a reasonable assumption since both *E. bungii* and *C. marshallae* have been observed to spawn at the surface.

The model was run over the sampling period of March 20 to June 19 in each year. It was initiated with the mean inlet (DFO2-DFO5) abundance of each stage in the first cruise (March 19) of each year. The model was forced with daily mean upper 30 m chlorophyll and temperature, daily advection rates, and daily mortality rates. A conceptual framework of the model is presented in Fig. 5.1.

5.3 Results
5.3.1 *Eucalanus bungii*
5.3.1.1 Refined parameterization of the fraction of mature, spawning females

When the initial model was run for all the years and compared to the observations, some inconsistencies were observed (Fig. 5.2). In 2008, peak abundances of every stage but stage C6 and C1 were delayed and abundances of all stages but C6 were overestimated (Fig. 5.2). In 2009, the model simulated a peak in the abundance of C1 that was absent in the data (Fig. 5.2). This resulted in the simulated peak in abundance of every stage but adults to occur too early as compared to the observations (Fig. 5.2). Abundances of all stages but C6 were overestimated (Fig. 5.2). The simulated peaks in abundance of all stages in 2010 were also too high and, possibly, too late (Fig. 5.2). However, the monthly sampling frequency of 2010 rendered the comparison of estimated and observed dynamics more difficult.
Results from these preliminary runs suggested that the model erroneously estimated the timing of peak reproduction, leading to an erroneous timing of appearance of the first major cohort. According to our parameterization, the reproduction rate depends on the egg production rate, which depends on the chlorophyll concentration, and, to a lesser extent, temperature, in the upper 30 m of the water column (Fig. 5.3).

However, the reproduction rate is also dependent on the fraction of spawning mature females. This parameter was modeled according to the vertical distribution data of 2010, which demonstrated that the fraction of females in the upper 30 m varied from 40% and 50% in March and April, respectively, to 0% in May and June. All females at the surface were assumed to be ready to spawn. The poor fit between simulated and observed data suggests that the seasonality in female vertical migration was not a good representation of the fraction of mature females in the population. In the Oyashio region, field observations of maturity stage composition reported the fraction of actively spawning females during the spring bloom as 0.25 (Shoden et al., 2005) or 0.64 (Yamaguchi et al., 2010b). Here we use the average of the two observed values, 0.45, which also corresponds to the average proportion of females in the upper 30 m when females were observed in this depth range in the 2010 vertical data. The same studies demonstrate that mature females appear in the population only after the onset of the bloom, defined by chlorophyll concentrations above the thermocline of at least 2 mg m\(^{-3}\) (Shoden et al., 2005, Yamaguchi et al., 2010b). Given the lack of experimental and field data, this food dependency on the number of mature females was very simplistically modeled as a step function. If chlorophyll were at or above optimal levels (i.e. during the bloom), 0.45 of \textit{E. bungii} females would be mature, if not, none would be. Different optimal values of chlorophyll were adopted until the best fit between
observed and simulated abundances for all years was obtained. The concentration that produced the best fit was $2.1 \text{ mg m}^{-3}$.

However, comparison of the newly parameterized 2009 model results with observations for 2009 clearly demonstrated that the week in mid-April 2009 with chlorophyll values above $2.1 \text{ mg m}^{-3}$ did not produce a cohort. Indeed, the model shows C1 copepodites appearing earlier than the observations (Fig. 5.4). It appears that female mature only if there are 8 consecutive days of chlorophyll concentrations higher than $2.1 \text{ mg m}^{-3}$. The parameterization of the fraction of mature females was thus adjusted to reflect this observation. Shoden et al. (2005), in their analysis of spawning conditions of *E. bungii* females over the spring bloom period in the Oyashio current, showed that mature females were a majority only for a period of 10 days after the onset of the bloom. The model was run with a variety of durations of optimal spawning conditions (5-20 days) to determine how long mature females would persist in our system. A 15-day duration produced the best fit across stages and years.

In both 2008 and 2010 chlorophyll concentrations were higher than $2.1 \text{ mg m}^{-3}$ since the model start date, on March 20. Daily chlorophyll data for the upper 30 m were available from March 8, and showed that in 2008 high chlorophyll concentrations were present since the start of daily sampling (Fig. 5.5). In 2010, consistent chlorophyll values above $2.1 \text{ mg m}^{-3}$ were observed only on March 11 (Fig. 5.5). Therefore, in 2008 the period of optimal spawning conditions was started on March 8, leaving 3 days of active spawning after the start of the model (blue box in Fig. 5.5). In 2010 the spawning period was set to start on March 11 and therefore lasted 6 days from the start of our model run on March 20 (black box in Fig. 5.5). The duration optimal spawning conditions for 2009 are shown in the red box of Fig. 5.5. The fit between simulated
and observed data was largely improved, with both the simulated abundance and timing of peak abundance being more similar to observations in every year (Fig. 5.6).

### 5.3.1.2 Comparison of simulated and observed abundances

The model with the new reproduction parameterization captured the major seasonal dynamics of each stage and the interannual differences in phenology and peak abundance well (Fig. 5.6). As observed from the field abundance estimates, the simulated timing of peak C5 copepodite abundance was more similar in 2008 and 2010 and occurred later in 2009 (Fig. 5.6 and Table 5.1). Peak C5 abundances were highest in 2008 and lowest in 2010 (Fig. 5.6 and Table 5.1).

Nevertheless, some inconsistencies between observed and simulated abundances remained. For instance, abundances of C1 were still overestimated (Fig. 5.6). In all years C1 copepodites peaked in abundance during the period of highest chlorophyll concentrations (Fig. 5.5 and Fig. 5.6). Vertical distribution data from 2010 demonstrates that C1 had the shallowest Weighted Mean Depth, 15 m during the day and 10 m at night, of any stage in April 2010 (Fig. 3.5). While the 150 um mesh would capture copepods of the size of *E. bungii* C1 (Nichols and Thompson, 1991), the fine mesh net is prone to clogging. Clogging is especially problematic during the bloom period and may lead to underestimates of the abundance of zooplankton with a shallow vertical distribution. In April 2008 the filtration efficiency of our bongo net dropped to 70%, indicating that significant clogging was occurring. This may have reduced the abundance of *E. bungii* C1 stages and resulted in the discrepancy between simulated and observed abundances.
The model also did not predict the increase in C3, C4, and C5 at the end of the model run in 2008 and 2010 (Fig. 5.6). *Eucalanus bungii* C3 to C5 copepodites undergo diapause. The decline in C3, C4 and C5 and the increase in C6 may due to the lack of diapause parameterization in the model. Finally the seasonal increase in C3 densities in 2010 occurred slightly earlier in the model than in the observations (Fig. 5.6).

### 5.3.1.3 Sensitivity analysis

To quantify the effects of different forcing variables (initial abundances, temperature, chlorophyll, mortality, or advection) on the peak C5 abundances and its timing, 30 sensitivity tests were run. We chose to focus on the C5 indices for the sensitivity analysis as C5 make up the bulk of the diapausing stage and as such are the ones recruited into the generation of adults of the following year. In each test one of the forcing variables was replaced with one from another year while other variables remained the same as in the base run. The runs and their effects on the quantity and timing of peak C5 abundances are shown in Table 5.2.

#### 5.3.1.3.1 Initial abundance

Generally, variations in the initial abundance of *E. bungii* did not substantially change the timing of appearance of the peak in C5 (Table 5.2). One exception was the run of 2009 with initial abundances of 2008 (Table 5.2). The numbers of females at the start of 2008 were 88% lower than in 2009 and by the time of the 2009 bloom females abundances were not high enough to produce a substantial cohort. The peak in C5 produced by the development of the overwintering C3 cohort was actually larger than the new annual cohort of C5. Increasing initial abundances resulted in a marked increase in maximum C5 abundance. The relationship between
the change in peak numbers of C5 and the initial numbers of overwintering C5 copepodites and adult females was particularly significant (Fig. 5.7).

5.3.1.3.2 Temperature

Temperature (in the range experienced by the three years of study, which included an El Niño year) was not a strong direct determinant of C5 abundance or of its temporal dynamics (Table 5.2).

5.3.1.3.3 Chlorophyll

The difference in the timing of optimal spawning conditions, defined as the first seasonal occurrence of at least 8 consecutive days with chlorophyll values in the upper 30 m higher than 2.1 mg m$^{-3}$, was a strong determinant of changes in the timing of peak C5 abundance (Table 5.2, Fig. 5.7). When 2008 or 2010 chlorophyll data were used in the 2009 base model, the maximum C5 abundance was early by 50 and 55 days respectively (Table 5.2). Clearly, the later E. bungii phenology in 2009 was a result of the later phytoplankton bloom timing, which dictated the timing of female spawning and gonad maturation.

Higher phytoplankton concentrations in the timing of optimal spawning (highest in 2010, lowest in 2009) produced a higher C5 cohort (Table 5.2). An exception was running the 2010 base year with 2009 chlorophyll data. Densities of the C5 cohort, albeit still 3 times lower than in 2008, increased compared to the 2010 base run when 2009 chlorophyll conditions were used in the base model (Table 5.2). This pattern was a reflection of the interaction between the phytoplankton and advection temporal dynamics. Advection rates of early copepodites were highest in 2010 as compared to other years and were also higher early in the season (Fig. 5.8).
The later cohort, produced under 2009-like bloom conditions, occurred when advection rates were low, and therefore a larger fraction of this cohort was able to remain in the inlet and develop into C5 copepodites.

5.3.1.3.4 Mortality

Mortality, averaged over the season and across years, was highest for the youngest stages (Fig. 5.9). In general copepodite stages C2-C4 experienced lower mortality during the period of highest chlorophyll concentration (Fig. 5.10). By contrast egg/nauplii mortality, and, in 2008, C1 copepodite mortality appeared to be lowest earlier, when chlorophyll concentrations first reached 2.0 mg m\(^{-3}\) (Fig. 5.10) and to then increase as the bloom progressed (Fig. 5.10). Early season mortality was highest in 2009 and lowest in 2008 for all stages (Fig. 5.10). Despite such interannual differences in the temporal dynamics of the mortality rate, variability in mortality did not have a large effect on the timing of peak C5 abundance (Table 5.2).

Higher mortality led to lower maximum C5 abundance (Table 5.2, Fig. 5.7). Mean mortality over time and across stages was lowest in 2008, while 2009 and 2010 showed comparable average mortalities. When mortalities of year 2009 or 2010 were inputted in the 2008 base model, C5 peak abundance was 20% of the base run estimate (Table 5.2). Similarly, when 2009 mortalities where inputted into the 2010 base run, the size of the C5 cohort was halved (Table 5.2) because of the higher copepodite mortality early in the season. Correspondingly, 2009 C5 peak densities became comparable to those in 2008 when 2008 mortality rates were used in the 2009 model run, and slightly increased when 2010 mortalities were used in the 2009 base run (Table 5.2). This pattern was a result of both lower adult mortality rates, which led to higher egg production, as well as of lower egg/nauplii and
copepodite mortalities (Fig. 5.10). The 2010 base run with 2008 mortality rates also led to an increase in C5 abundance, albeit not high enough to produce a C5 cohort similar in size to the one in 2008 (Table 5.2).

5.3.1.3.5 Advection

Changes in advection influenced both the abundance and temporal pattern of C5 copepodites. Advection rates were highest early in the season (Fig. 5.8). Therefore, advection only produced a change in the temporal dynamics of those years with an early spawning period, 2008 and 2010. When either the 2009 or 2010 advection rates were input into the 2008 base year, the eggs and nauplii experienced higher advection rates, particularly between day 15-40, leading to the nauplii and eggs present on day 0-15 to developing into the main C5 cohort instead, and resulting in an earlier appearance of maximum C5 abundance. Similarly, when the 2008 advection rates were used in the 2010 run the peak in C5 was later (Table 5.2) as more eggs/nauplii and early copepodites were retained after day 15 in comparison to the base run.

Variation in advection rates also resulted in changes to the size of the diapausing C5 cohort. In 2009 there was a higher advective input of eggs at the start of the model run (pre day 15) (Fig. 5.8). Thus, when 2009 advection rates were input into the 2008 base run, a larger C5 cohort was produced (Table 5.2), even if overall advection rates were higher in 2009. Likewise, when the 2008 advection rates were used in the 2010 run, the maximum abundance of C5’s were substantially higher and comparable to 2008 levels (Table 5.2) due to advection rates of eggs/nauplii and early copepodites stages, particularly C2 and C4, being lower in 2008 compared to 2010. This suggests that size of the C5 cohort in 2010 was less than 2008 due to higher early season advection rates in 2010. To test that it was the difference in early season advection and
not an artifact of the interpolated 2008 advection rates that led to the observed difference in C5 abundance between years, the advection rates of 2010 were input in 2008 only for the missing advection rate period, day 34 to 68. This resulted in an increase of maximum C5 abundance from 4185 individuals in the base run to 6627 individuals, an opposite pattern to the decrease in peak C5 numbers observed when the entire 2010 advection time series was used in the 2008 base run. Similarly, when only the 2008 advection rates during the period of missing wind data were inputted into the 2010 base model, the C5 cohort, rather than increase, remained comparable, at 764 individuals, to that of the base 2010 run. Thus, it can be concluded that it was indeed the difference in the early season advection between 2010 and 2008 that led to lower abundances in 2010.

In 2009, the bulk of recruitment to the new generation occurred in the second half of the season, when advection rates were low (Fig. 5.8). Maximum numbers of C5 copepodites actually increased when 2010 advection rates were used in the 2009 base run (Table 5.2), even if overall advection, averaged over the entire season, was higher in 2010 than in 2009. This is a result of an immigration event of females from day 40 to 60 in 2010 following an intermediate water renewal event (Chapter 3). The higher number of females led to a higher egg production and to a doubling of the C5 cohort (Table 5.2).

5.3.2 *Calanus marshallae*

5.3.2.1 **Refined parameterization of the fraction of mature, spawning females**

Initially, it was assumed that the fraction of mature females would be approximated by the number of females in the upper 30 m. Vertical distribution estimates were available only for the monthly 2010 cruises at DFO2, and showed that 0.60 of the females were in the upper 30 m
at the start of the sampling season, 0.30 at the end of April, 0.70 in May, and 0.20 in June. It was assumed that the seasonality in vertical distribution remained constant across years. This parameterization led to an overestimation of the abundance of every stage in 2008 and 2010, especially late in the season (Fig. 5.11). In 2009, numbers of C1 were overestimated late in the season, while abundances of C2 and C3 were comparable to observed abundances for the first half of the season, but overestimated for the remainder of the season (Fig. 5.11). All other stages were overestimated (Fig. 5.11). It appears that the fraction of females at the surface did not represent the fraction of mature, spawning females. Since this initial parameterization overestimated the abundance of copepodite stages late in the season in every year, a *C. glacialis* like reproductive strategy was employed instead to parameterize the fraction of mature, spawning females, as the spawning activity of *C. glacialis* peaks prior to the bloom (Niehoff and Hirche, 2005). More specifically, the fraction of *C. glacialis* mature, spawning females in a Norwegian fjord peaked at 0.8 two weeks prior to the bloom, when mean chlorophyll concentrations in the upper 45 m were 1 mg m$^{-3}$, and averaged 0.05 during the bloom, when chlorophyll concentrations were between 2 and 5 mg m$^{-3}$ (Niehoff and Hirche, 2005). The main parameter to be determined for a *C. glacialis*-like reproductive strategy formulation was the date of the switch from a fraction of 0.8 mature females to one of 0.05, set by the change from pre bloom to bloom like conditions. In 2008 and 2010 chlorophyll concentrations were lower than 2 mg m$^{-3}$ only sporadically (Fig. 5.5). Thus, the best formulation of a *C. glacialis*-like parameterization was set with data from 2009. Niehoff and Hirche (2005), with a weekly sampling frequency, never sampled chlorophyll values between 1 and 2 mg m$^{-3}$. However, in Rivers Inlet chlorophyll concentrations were higher than 1 mg m$^{-3}$ while remaining lower than 2 mg m$^{-3}$ for a large part of the 2009 sampling season (Fig. 5.5). Thus, different “spawning
termination” values between 1 and 2 mg m\(^{-3}\) had to be tested to determine which one would present the best fit between simulated and observed data in 2009. The start of “spawning termination” conditions was set on March 31\(^{st}\), when chlorophyll concentrations first consistently remained higher than 1.7 mg m\(^{-3}\) (Fig. 5.5). The \textit{C. glacialis} like parameterization estimated abundances of early copepodites quite well, but underestimated C5 abundances late in the season in every year (Fig. 5.12). Clearly, as for \textit{C. finmarchicus}, the number of mature females may increase during the bloom. Thus, a \textit{C. finmarchicus}-like parameterization was also tested to assess if the fit between simulated and observed C5 densities could be improved. Niehoff et al. (1999) studied the reproductive biology of \textit{C. finmarchicus} in the Norwegian Sea and observed that the fraction of mature, spawning females peaked at 0.46 during the spring bloom. Numbers of spawning, mature females was 0.18 prior to the bloom, and 0.01 post bloom. In their study they present integrated chlorophyll (mg m\(^{-2}\)) concentrations for the upper 100 m, a value difficult to convert into the upper 30 m mean chlorophyll (mg m\(^{-3}\)) that was measured in this study. Therefore, different chlorophyll values were tested to determine what would provide the best definition of bloom conditions in Rivers Inlet. Preliminary simulations showed that there was low reproductive output in early 2010, even if chlorophyll concentrations were at intermediate values of 3-5 mg m\(^{-3}\) (Fig. 5.5). The start of the bloom that produced the best fit between simulated and observed abundance estimates was the time when chlorophyll reached values greater than 6 mg m\(^{-3}\). Peterson (1988) showed that number of clutches produced by \textit{C. marshallae} females decreased below 6 mg m\(^{-3}\), supporting our choice of parameterization. The bloom was set to end when chlorophyll concentrations first decreased below 4 mg m\(^{-3}\) without increasing back to values higher than 6 mg m\(^{-3}\) (Fig. 5.5). Furthermore, to produce the best fit, the numbers of mature, spawning females had to be adjusted to be 0.05 pre-bloom, 0.2 during the
bloom, and 0.005 post bloom, instead of 0.18, 0.45, and 0.01 as reported by Niehoff et al. (1999). The *C. finmarchicus*-like parameterization captured the seasonal abundance pattern of *C. marshallae* in 2008 and 2010 well, but underestimated abundance of C1-C3 copepodites in early 2009 (Fig. 5.13). Thus, it was concluded that *C. marshallae* behaves like *C. glacialis* prior to the bloom, but that after the first spawning, which must be largely supported by stored lipids, females display a *C. finmarchicus* like dependence on high bloom concentrations for reproduction. In 2008, and 2010, as chlorophyll concentration were already higher than 1.7 mg m\(^{-3}\) at the start of the sampling season (Fig. 5.5), it was assumed that females had already undergone the first *C. glacialis*-like spawning event and behaved like *C. finmarchicus* for the entire model run period, with the highest fraction of mature, spawning females, 0.2, during the bloom. By contrast, in 2009, the first spawning event was *C. glacialis*-like, with 0.8 of the total females being mature and spawning until chlorophyll concentrations reached values higher than 1.7 mg m\(^{-3}\), and then following a *C. finmarchicus* like reproduction.

### 5.3.2.2 Comparison of simulated and observed abundances

The simulated abundances were able to characterize the general seasonal and interannual *C. marshallae* dynamics in 2008 and 2010 (Fig. 5.13). As in the observations, density of C5 copepodites was larger in 2008 and the timing of appearance of the C5 diapausing cohort was comparable (Fig. 5.13, Table 5.1). Since our model does not account for diapause, a C5 cohort could be defined as diapausing when inconsistencies between simulated and observed abundances of C5 and C6 copepodites followed its appearance. For example, the large increase in simulated C6 abundance at the end of the model run in 2010 that was absent in the observations was likely a result of most C5 from the first 2010 cohort entering diapause rather
than maturing into adults (Fig. 5.13). Similarly, the lack of diapause parameterization inflated final C6 densities and underestimated final C5 numbers in 2008 (Fig. 5.13). By contrast, simulated and observed C5 abundances were comparable after the first C5 abundance peak in 2009, implying that the majority of the first C5 cohort in 2009 did not descend into diapause (Fig. 5.14). However, abundance of females resulting from this C5 cohort was overestimated (Fig. 5.14), suggesting that female advection or mortality was higher than estimated, or that densities of preceding stages were overestimated. This slight increase in the simulated abundance of females in mid-season resulted in higher egg production and to an overestimation of the final cohort size, as is evident when comparing observed and simulated final C5 and C6 abundances (Fig. 5.14). The actual size of the final cohort in 2009 was likely more similar to what was estimated by the *C. finmarchicus* parameterization, when numbers of females during day 40-60, the time of the bloom, were comparable to observed abundances (Fig. 5.13).

To determine what may have led to discrepancy between observed and simulated number of females both mortalities and advection rates were examined. As the model captured well the dynamics of stages C1-C3, we focused only on the three oldest stages. Mortalities of C4 and C5 in 2009, averaging 0.13 and 0.15 day$^{-1}$, respectively, over the season, were the highest of any year (Fig. 5.10), and higher or comparable to *C. finmarchicus* mortalities for the same stages reported in the literature (Eiane et al., 2002, Eiane and Ohman, 2004). Mortalities of C6, at 0.031 day$^{-1}$, were lower than in 2008, but comparable to literature values (Eiane and Ohman, 2004). Therefore, it was concluded that the discrepancy between observed and simulated female abundances between days 40-60 was a result of underestimated advection rates rather than underestimated mortalities. Since advection rates are strongest for those stages that have a shallower distribution (Chapter 3), we focused on advection of stage C4 copepodites, as they
were distributed higher in the water column than C5 or adults (Fig. 3.4). Seasonally averaged advection rates of C4 were highest, -0.037 day\(^{-1}\), in 2010, but 2009 C4 advection rates were only slightly lower, at -0.031 day\(^{-1}\). However, since advection rates can change rapidly depending on wind and discharge conditions, a seasonal average may not provide a complete assessment of variability in advection losses (Chapter 3). Indeed, a large fraction of a zooplankton population can be washed out of the fjord in a day during a high outflow event (Chapter 3). The linear interpolation of missing advection rates would not have accounted for such outflow events.

Horizontal transport rates in a fjord are a function of both wind and river discharge (Chapter 3). Unlike in 2008, when discharge increased substantially only during the freshet in late May, a substantial, pre-freshet, high discharge event occurred on April 22 (day 34) in both 2009 and 2010 (Fig. 2.5). In 2010, the highest C4 advection rate, -0.33 day\(^{-1}\), occurred on the same day as this high discharge event. In 2009, peak discharge during the late April high flow event was actually 2.2 times higher than in 2010 (Fig. 2.5), and river flow was comparable to the values that initiated the 2010 advection event already 11 days prior to this peak (Fig. 2.5). Even if river flow was 2.2 times higher in 2009 than in 2010, the linearly interpolated advection rate on April 22 in 2009 was 0.036 day\(^{-1}\), nine times smaller than in 2010 (Fig. 2.5). Assuming a linear relationship between discharge and advection, the 2009 advection rate on day 34 should have actually been 2.2 times higher than the advection on day 34 in 2010. Advection rates 11 days before and after day 34 in 2009 were similarly adjusted by multiplying the ratio between their discharge and the discharge on day 34 in 2010 to the advection on day 34 in 2010. The adjustment of the advection rates improved the fit between the simulated and observed densities of adult females on day 40-60 as well as densities of the second cohort across all stages (Fig. 5.15). The newly parameterized model was able to portray the general seasonal dynamics of all
stages in 2009 and showed that the diapausing cohort appeared 20 days later in 2009 as compared to 2008 and 2010 and was intermediate in size (Fig. 5.15, Table 5.1).

While the model generally provided a good description of the seasonal and interannual variability in *C. marshallae*, simulations from all the three years overestimated C1 and C2 copepodites during the spring bloom (Fig. 5.13 and Fig. 5.15). A 150 μm mesh net would only capture approximately 75% of C1 copepodites because their size makes them vulnerable to extrusion through the net mesh (Nichols and Thompson, 1991). Furthermore, as for *E. bungii* C1 copepodites, *C. marshallae* C1 and C2 copepodites were shallow in the water column (Fig. 3.5) during the bloom and thus may have been under sampled because of clogging. Thus, the misfit between simulated and observed C1 and C2 abundances may be a result of sampling rather than model bias. Finally, the model underestimated C5 and C6 abundances on the third sampling cruise of 2008, in late April. The increase in abundance was highest at the outermost site. Temperature data showed that in late April a cooler water mass was inflowing from the shelf (Fig. 2.2). Since *C. marshallae* abundance is higher on the shelf, this inflow event may have transported copepodites C5 and C6 into the outermost station. It seems likely that the mismatch between simulated and observed abundances resulted from an underestimation of advective influx of these two stages when missing advection rates were linearly interpolated. Nevertheless, as the simulated C5 abundances still captured the main seasonal development and size of the C5 cohort, no attempt was made to adjust advection rates of C5 and C6 to improve the model fit.

5.3.2.3 Sensitivity analysis

As for *E. bungii*, the effects of different forcing variables (initial abundances, temperature, chlorophyll, mortality, or advection) on the size of the diapausing C5 cohort and its
timing, were quantified by running sensitivity tests. We chose to focus on the C5 indices for the sensitivity analysis as C5 constitute the bulk of the diapausing stage and as such are the ones recruited into the generation of adults of the following year. In each test one of the forcing variables was replaced with one from another year while other variables remained the same as in the base run. The runs and their effects on the quantity and timing of peak C5 abundances are shown in Table 5.3.

5.3.2.3.1 Initial abundance

As for *E. bungii*, an increase in the initial abundance of *C. marshallae* C5 copepodites and adult females resulted in a higher peak of newly recruited C5 copepodites (Table 5.3, Fig. 5.7). However, changes in the initial abundance condition did not result in a shift in the timing of appearance of the new C5 cohort (Table 5.3).

5.3.2.3.2 Temperature

Similar to what was observed for *E. bungii*, a shift in temperature (in the range experienced by the three years of study, which included an El Niño year) did not produce a significant change in *C. marshallae* peak C5 abundance or in its temporal dynamics (Table 5.3).

5.3.2.3.3 Chlorophyll

A delay in the timing of the spring bloom, defined as when upper 30 m chlorophyll concentration reached values of at least 6 mg m\(^{-3}\), resulted in a later appearance of maximum C5 abundance (Table 5.3, Fig. 5.7). When either the 2008 or 2010 chlorophyll data series were input into the 2009 base run, maximum numbers of C5 copepodites occurred 20 days earlier (Table
5.3. Changes in the size or duration of the chlorophyll bloom, however, did not result in parallel changes in the size of the diapausing C5 cohort (Table 5.3).

5.3.2.3.4 Mortality

Variability in *C. marshallae* mortality with stage was different from that of *E. bungii*. While mortality of *E. bungii* was highest for eggs/nauplii, mortality of *C. marshallae* increased with stage (Fig. 5.9). Mortality of females was particularly high in the second half of the sampling season, especially in 2008 (Fig. 5.10).

Mortality of stages C3-C5 was consistently higher than younger stages in all years (Fig. 5.10). All copepodite stages exhibited higher mortality early in the season, but the duration of this early season period of high mortality differed between years. In 2008 it lasted for approximately the first month of the sampling season, for 40 days in 2010, and for 60 days in 2009 with a decrease from day 20-40 in the latter (Fig. 5.10). Peak mortality of eggs/nauplii to C3 was comparable in 2008 and 2010, but the duration of the period of high mortality lasted longer in 2010 (Fig. 5.10). By contrast, mortalities of C4 and C5 were higher in 2010 than 2008. Mortalities of egg/nauplii and all copepodite stages were highest in 2009, while adult mortality was highest in 2008 (Fig. 5.10). This interannual difference in mortality contributed to the observed interannual difference in C5 peak abundance (Fig. 5.7). Size of the diapausing C5 cohort was reduced when either 2009 or 2010 mortalities were used into the 2008 base run (Table 5.3). Similarly, when mortalities of 2008 or 2010 were input into the 2009 model run, the size of the cohort increased and became comparable or higher than in 2008 (Table 5.3). Finally, when mortalities from 2008 were inputted into 2010, the size of the diapausing cohort was 3 times larger than the base run (Table 5.3). The increase in copepodite C4 and C5 led to the
presence of more females over the entire length of the bloom, increasing total egg production. Furthermore, the decrease in the length of the eggs/nauplii to C3 high mortality period allowed for high proportion of this egg production to develop into the diapausing C5 cohort. Changes in mortality did not result in large shifts in the timing of peak C5 abundance (Table 5.3).

5.3.2.3.5 Advection

Interannual differences in advection varied with stage. Advection of egg/nauplii and stages C1-C4 was absent in 2008 (Fig. 5.8) as no individuals were found at the inlet boundary. Advective losses of egg/nauplii, and stages C1-C2 were highest in 2010, while advection of stage C3 and C4 was highest in 2009 (Fig. 5.8). By contrast, advection losses of stage C5 were highest in 2008 and lowest in 2010 (Fig. 5.8). Advection of C6 was also highest in 2008 and comparable between 2010 and 2009 (Fig. 5.8). Stage C6 transport losses, highest early in the season (Fig. 5.8), had the largest influence on the abundance of the new cohort of C5 in 2008 and 2010. For instance, when 2008 advection rates were input into the 2010 base run the size of the diapausing C5 cohort was greatly reduced (Table 5.3). Correspondingly, maximum C5 abundance increased when 2009 or 2010 advection rates were used into the 2008 base model (Table 5.3). The lower advection rates increased numbers of females and consequently egg production early in the season, leading to a larger new generation of C5 copepodites. By contrast, mean advection across stage C1-C4, which was comparable between 2009 and 2010 and lowest in 2008, had the strongest influence on the size of the C5 cohort in 2009. The number of diapausing C5 increased when 2008 advection rates were inputted in the 2009 base run (Table 5.3). The lower copepodite advection rates led to an increase in the size of the first cohort of the year, which developed into females during the bloom and produced a larger second cohort of C5 copepodites. Changes in
advection rates did not result in large shifts in the timing of appearance of the diapausing C5 cohort (Table 5.3).

5.4 Discussion

5.4.1 Model caveats

As eggs and nauplii were not sampled, abundances used in the mortality estimation were derived from literature-based relationships of egg production rate. Inaccurate eggs/nauplii abundance estimates would have led to inaccurate estimates of eggs/nauplii mortalities. Correct parameterization of the number of mature, spawning females also depends on an accurate eggs/nauplii mortality estimate. If eggs/nauplii mortality is underestimated, the fraction of mature, spawning females may be artificially low to compensate for the underestimation of mortality rates.

The *E. bungii* eggs/nauplii mortalities presented here, averaging 0.08 day$^{-1}$ over the season, are only slightly lower than average egg to N6 mortalities of *C. finmarchicus* reported in the literature of 0.12 day$^{-1}$ (Eiane et al., 2002) and 0.15 day$^{-1}$ (Eiane and Ohman, 2004). Furthermore, our parameterization of the numbers of mature females is consistent with results from field observations. It is widely acknowledged that *E. bungii* females start reproducing only at the initiation of the spring bloom and the highest fraction of females that are mature in a population has been reported to range from 25%-64% (Shoden et al., 2005, Yamaguchi et al., 2010b) Thus, we believe that both the eggs/nauplii mortality estimates and the parameterization of the number of mature *E. bungii* females are realistic. By contrast, the estimated average seasonal eggs/nauplii mortality rate of *C. marshallae*, 0.03 day$^{-1}$, were lower than values reported in the literature for *C. finmarchicus* (Eiane et al., 2002, Eiane and Ohman, 2004), and
values reported by Peterson (1979), who estimated \( C. marshallae \) egg mortality to be 0.9 day\(^{-1} \) and nauplii mortality to be 0.01 day\(^{-1} \), giving an eggs/nauplii average mortality of 0.5 day\(^{-1} \). Moreover, refinement of the reproduction parameterization for \( C. marshallae \) required that the fraction of spawning, mature females be half of that observed for \( C. finmarchicus \). This suggests that \( C. marshallae \) eggs/nauplii mortality may have been underestimated in our model. Therefore, while we are confident on the model ability to resolve the interannual and seasonal variation in \( C. marshallae \) abundance with the current parameterization, analysis of the drivers of the observed changes has to take into account, including the potential confounding effect between estimates of eggs/nauplii mortality and the fraction of mature females.

Both \( E. bungii \) and \( C. marshallae \) are well known to enter diapause mainly as stage C5, but some \( E. bungii \) C3 and C4 also diapause (Smith and Vidal, 1986, Shoden et al., 2005). The lack of diapause parameterization overestimated mortality of adults after the appearance of the diapausing cohort and led to a general overestimation of adult densities and to an underestimation of C5 copepodites (as well as C3-C4 for \( E. bungii \)) late in the season. This explains the general deviation from simulated and observed abundances for diapausing and adult stages at the end of the model run. However, as the aim of the study was to determine which vital processes drive recruitment to the diapausing cohort, the lack of diapause parameterization in the model would not have affected our conclusions, as it would only have affected mortality estimation post appearance of the diapausing cohort.

Estimation of stage durations assumed that development was solely a function of temperature. This assumption is supported by Peterson (1979)’s observation that \( C. marshallae \) development in the field was generally not food limited. Furthermore, experimental studies on \( C. finmarchicus \) have shown that somatic growth rate is more sensitive to food concentrations than
development is (Campbell et al., 2001). Campbell et al. (2001) determined that the critical food concentration required to achieve 90% of the maximum development rate was a chlorophyll concentration of 1.75 mg m\(^{-3}\) (assuming a C:Chl = 40). In Rivers Inlet, chlorophyll concentration was below 1.75 mg m\(^{-3}\) only for the first 10 days of the 2009 model run (Fig. 5.5). Therefore, it can be assumed that food concentration did not influence development for most of the model runs.

5.4.2 Reproductive strategies of *Eucalanus bungii* and *Calanus marshallae*

Interannual variability in the phenology of both *E. bungii* and *C. marshallae* C5 copepodites was related to the timing of the spring bloom. According to our model, the later bloom in 2009 led to a delay in the maturation and peak egg production of *E. bungii* females, which resulted in a later appearance of the C5 cohort. Similarly, the second major *C. marshallae* spawning event was later in 2009 because of a delay in the appearance of the high fraction of spawning, mature females following the shift in bloom timing.

The two species displayed two differing reproductive strategies. *Eucalanus bungii* behaved as an income breeder. Females started the process of gonad maturation at the onset of the bloom, when chlorophyll concentrations first increased above 2.1 mg m\(^{-3}\). This is in accordance with observations from the Oyashio region, where the phytoplankton bloom was observed to induce *E. bungii* spawning and final gonad development (Shoden et al., 2005, Yamaguchi et al., 2010b), and females spawned over a short period, 15 days, even if conditions of high chlorophyll concentrations lasted longer. Shoden et al. (2005) and Yamaguchi et al. (2010b) also showed that the peak fraction of mature *E. bungii* females lasted only a short period. However, approximately 20% of the female population was shown to maintain mature
gonads in the month (Yamaguchi et al., 2010b) or 10 days (Shoden et al., 2005) following the period of maximum concentration of mature females. Thus, our simple parameterization of 0% mature females after 15 days of spawning may have been an underestimate. Nevertheless, as no new C5 cohort was detected in the field data, it is clear that in Rivers Inlet reproductive success of *E. bungii* was greatly reduced 15 days following spawning initiation, even if chlorophyll concentrations remained high. Since eggs/nauplii and female mortality increased as the bloom progressed, the short spawning period may be a reflection of an adaptive tradeoff between increased fitness through higher egg production rates at higher chlorophyll concentrations and reduced fitness through increased predation risk at higher chlorophyll concentrations. As the predation risk on copepods varies considerably between systems (Eiane et al., 2002) the duration of optimal spawning conditions may also vary between regions.

While *E. bungii* behaved like an income breeder, *C. marshallae* appeared capable of capital breeding, with peak fractions of mature females occurring prior to the bloom. High percentages of mature *C. marshallae* females prior to the bloom have also been observed in other systems (Smith and Vidal, 1986, Osgood and Frost, 1994, Baier and Napp, 2003). Initial gonad maturation and spawning in *C. marshallae* is believed to be enhanced by lipid stores (Osgood and Frost, 1994, Baier and Napp, 2003). *Calanus marshallae* has much lower fecundity, maximum egg production rate is 24 eggs female\(^{-1}\) day\(^{-1}\) (Peterson, 1988), than *E. bungii*, which can produce up to 150 eggs female\(^{-1}\) day\(^{-1}\) (Takahashi and Ide, 2011). Given the low egg production rate of *C. marshallae*, Peterson (1979) proposed that it has to rely on an extended spawning period to maintain a high yearly reproductive output. Indeed, the different reproduction parameterization of *E. bungii* and *C. marshallae* in our model highlights the longer reproductive period and the importance of pre-bloom egg production for the latter species.
Our results show that in 2009 the initial, pre-bloom maximum fraction of mature *C. marshallae* females lasted longer than 2008 and 2010. Since exit from diapause and molting to the adult stage occurred in February in both 2008 and 2009 (Chapter 4), females must have matured more slowly in 2009. Niehoff et al. (1999) demonstrated that higher proportion of immature *C. glacialis* developed into mature females if fed than if starved. The higher March chlorophyll concentrations in 2008 and 2010 likely led to a faster maturation rate, to an earlier peak in the fraction of mature females, and to a spawning event prior to the start of the sampling period. Indeed, the abundance of *C. marshallae* copepodites stages C1-C3 was higher in 2008 and 2010 than in 2009.

We hypothesize that as lipid stores were utilized during the first oogenesis, females would have had to rely on concurrent feeding for further spawning. Indeed, our model demonstrated that the second major spawning event was only possible when chlorophyll concentrations increased to 6 mg m\(^{-3}\). Evidence of a reduction in the clutch size of *C. marshallae* at low food concentrations (Peterson, 1988) and of a stop and reversal of the gonad maturation process of starved *C. finmarchicus* females (Niehoff et al., 1999) supports the hypothesis that the timing of the second major spawning event was associated with high chlorophyll biomass through food limitation of the numbers of spawning females.

The fraction of spawning, mature females present during the bloom appears to be region-specific. In the Bering Sea, the proportion of mature females was as high (0.9-1) in February as during the bloom (Baier and Napp, 2003). This is in contrast with the fraction of mature, spawning females simulated prior to the bloom (0.8) and during the bloom (0.2) in this study, and in Dabob Bay, where the proportion of mature females was 0.8 a month before the bloom, and decreased to 0.4-0.5 during the bloom (Osgood and Frost, 1994).
According to Eiane et al. (2002), the increase of *C. marshallae* mortality with stage indicated that this species was experiencing a high vertebrate predation pressure in Rivers Inlet. Peterson (1979) also showed that *C. marshallae* mortality increases from early to late copepodite stages, with females experiencing the highest mortality rates, 0.16 day$^{-1}$, because of high predation from planktivorous fish. High predation pressure may have restricted the time *C. marshallae* females spent at the surface in Rivers Inlet. Indeed, Bollens and Frost (1989b) observed striking interannual differences in the fraction of *C. pacificus* females undergoing diel vertical migration in late April/early May following between year differences in the abundance of sandlance (*Ammodytes hexapterus*) larvae. Since the second major spawning event depends on adult females’ access to food resources, we suggest that predation pressure would have resulted in a reduced fraction of mature females being present at any given time during the bloom. We suggest that predation pressure from juvenile fish on *C. marshallae* females may play an important role in restricting the fraction of spawning females by limiting the time that *C. marshallae* females spend at the surface. Variation in predation pressure between systems and over the season may therefore have contributed to the differences in the fraction of mature females between regions and over time highlighted above. Nevertheless, given the uncertainty in our *C. marshallae* eggs/nauplii mortality estimates, the low fraction of mature females during the bloom compared to other areas or to the pre-bloom period may simply be a result of an underestimation of eggs/nauplii mortality during the bloom. Future research should directly assess densities of *C. marshallae* eggs and nauplii and the fraction of mature females from field data to achieve a better understanding of the interplay between predation pressure, the fraction of spawning females, and egg and nauplii mortality.
5.4.3 Effect of differential survival on recruitment

A late phytoplankton bloom was associated with a reduction in the diapausing cohort of both species in 2009, as compared to 2008, the year with a relatively similar spring temperature. For *E. bungii*, this pattern was a result of lower mortality of both females and younger developmental stages. Since female mortality increased over time, when a bloom was early the reproductive output was larger. The effect of lower egg production on C5 copepodite recruitment was further magnified by increased mortality of younger developmental stages. *E. bungii* copepodite mortality was lowest during periods of high chlorophyll concentration and mortality in every year was higher pre-bloom, especially in 2009, when early spring phytoplankton biomass was lowest. This supports observations by Tsuda et al. (2005) showing that *E. bungii* nauplii mortality is lower during the bloom because diatoms become important prey of their omnivorous copepod predators.

However, *E. bungii* copepodite survival was lower in 2009 also post bloom, even if chlorophyll concentrations were comparable. Takahashi and Ide (2011) demonstrated that *E. bungii* copepodites became more vulnerable to starvation with increasing temperatures. The 2009 diapausing cohort had a later birth date and experienced higher temperatures during development. Thus, it may have experienced higher mortalities in the post bloom period because of higher susceptibility to starvation. Indeed, mortality across all stages of *E. bungii* in 2010, an El Niño year, was also higher than in 2008, even if chlorophyll concentrations were comparable.

An increase in predation rate with temperature (Davis, 1984b, Ji et al., 2009) may have further increased *E. bungii* eggs/nauplii and copepodite mortality in 2010 and in the 2009 post bloom period. Unlike the abundance of *E. bungii* and *C. marshallae*, the abundance of potential invertebrate predators, such as chaetognaths, was higher in 2010 as compared to 2008 (Appendix
G). This may have led to higher predation pressure and the observed higher mortality in 2010. Reasons for the increase in predation numbers are unknown and should be investigated in the future.

According to our model, *C. marshallae* eggs/nauplii and copepodite mortality also had a significant effect on the size of its diapausing stock. In a year of a delayed bloom, more of the yearly reproductive output was lost to mortality, as conditions of high eggs/nauplii and copepodite mortality lasted longer, leading to a smaller overwintering stock. This reinforces the differential survival hypothesis (Ohman and Hirche, 2001) what has been put forward as the driver of *C. marshallae* in the Bering Sea (Baier and Napp, 2003). Eggs/nauplii and copepodite mortality was highest when chlorophyll concentrations were smallest. Our results are supported by observations by Plourde et al. (2009) of increased *C. finmarchicus* egg and naupliar mortality at low phytoplankton concentrations. Furthermore, experimental studies of Campbell et al. (2001) show that growth of *C. finmarchicus* nauplii and copepodes is food limited at chlorophyll concentrations below 1.9 and 2.5 mg m\(^{-3}\), respectively (assuming C:Chl = 40). Thus, somatic growth of *C. marshallae* may have been reduced for most of March and April in 2009. Smaller size may have led to slower predator escape responses and to the observed higher mortality at lower chlorophyll concentrations.

As for *E. bungii*, copepodite mortality of *C. marshallae* also increased at higher temperatures. Eggs/nauplii and copepodite mortalities were higher during the El Niño year of 2010 than in 2008, even though chlorophyll concentrations were comparable. This pattern further highlighted the potential for an increase in predation pressure at higher temperatures and the possibility for the presence of a different predatory community during the El Niño year. Data on predator abundance from our zooplankton samples do indeed demonstrate that the abundance of
some predator species differed between 2008 and 2010 (Appendix G). As interannual changes in mortality were the major driver of reduced recruitment of both E. bungii and C. marshallae we stress the need for a future assessment of predatory consumption rates and of their temporal dynamics in relation to temperature and chlorophyll concentration.

5.4.4 Effect of advection on recruitment

As pre-bloom egg production was important for C. marshallae recruitment, any loss of copepodites prior to the bloom decreased the size of the diapausing cohort. High advection rates in the early spring of 2009 did indeed reduce the size of the C. marshallae diapausing cohort. In Rivers Inlet wind forcing drives both the timing of the bloom and early spring advective losses of surface dwelling eggs/nauplii and copepodite stages (Wolfe, 2010, Chapter 3). Higher speed and more frequent outflow wind events delay the bloom (Wolfe, 2010) and increase advection losses of eggs and early copepodite stages (Chapter 3). Therefore, a late bloom may always be associated with higher advection rates of the early stages of C. marshallae. In 2009, a discharge driven outflow event in late spring further reduced the size of the first developing cohort by increasing advection rates of C4 copepodites.

Once the bloom was underway C. marshallae recruitment appeared to be limited by the number of females instead. Indeed, when the high eggs/nauplii and copepodite advection rates from 2009 were input into the 2008 base model, the size of the diapausing cohort increased because of lower female advection rates, and when 2008 bloom conditions were used in the 2009 model, size of the diapausing cohort increased even under the high advection and mortality rates.

The different reproductive strategy of E. bungii buffered this species from the impact of high advection rates during a year of a delayed bloom. High copepodite advection rates in 2009
did not affect the size of the diapausing *E. bungii* as substantial densities of copepodites only appeared in late May. However, as *E. bungii* focuses reproduction at the onset of the chlorophyll bloom, its recruitment is quite vulnerable to high advection rates on its developmental copepodite stages during and post phytoplankton bloom conditions. In 2010, most of the *E. bungii* eggs that would develop into the diapausing cohort had already been produced, and the high copepodite advection rates of early 2010 had a large effect on the size of its diapausing stock. Because of advection, even with the mortalities of 2008, the size of the diapausing cohort of 2010 did not reach the same size as in 2008. Early season advection of copepodites is largely driven by changes in wind driven flow (Chapter 3). The El Niño year was associated with a different wind direction and higher wind speed at the start of the sampling season as well as with a different hydrography on the shelf (Tommasi et al., 2013b). This may have led to the observed higher advection rates in 2010 as compared to 2008.

### 5.4.5 Effect of initial conditions on recruitment

Our model also demonstrated that initial abundances of diapausing stages and females influenced the size of the diapausing cohort of both copepod species. The higher density of females at the onset of the 2009 sampling season reduced the decrease in recruitment brought about by the combined effect of increased mortality and advection. Our results highlight the potential for a severe decline in *C. marshallae* and *E. bungii* population size after two years of consecutive late bloom conditions or high spring temperatures. However, populations of both copepods appeared able to capitalize on years of favorable conditions and to re-build their population to high levels in just one season, as was the case in 2008.
5.5 Conclusions

Here we tested for the first time a mechanism explaining observations of low *C. marshallae* and *E. bungii* biomass in years of a delayed bloom (Baier and Napp, 2003, Kobari et al., 2007, Coyle et al., 2008). A later seasonal timing of phytoplankton biomass was associated with higher mortality of *C. marshallae* and *E. bungii* and with lower recruitment to the diapausing stages of both species. Since the time of the spring transition may occur increasingly later under projected climate change scenarios in this region (Foreman et al., 2011), bloom timing may become later (Wolfe, 2010) and early spring advection rates of eggs and copepodites may increase (Chapter 3). Our model shows that these conditions may result in a reduced population size of both species through increased losses via mortality and advection. High mortality of both species was also associated with high temperatures. Thus, the most drastic effect on the population size of these two copepod species would occur in years of warm early spring conditions with a late bloom. The likelihood of such spring conditions arising should be examined.

Traditionally, studies of copepod population dynamics have focused on the importance of bottom up processes. However, it is now recognized that variations in mortality rate are as important as changes in birth rate in driving fluctuations in zooplankton recruitment (Ohman and Hirche, 2001, Plourde et al., 2009, Ji et al., 2013). Our model results do indeed demonstrate that temporal variability in mortality was the most important driver of the observed interannual differences in the size of the diapausing cohort. Unfortunately, knowledge of the basic drivers of mortality is still limited for most copepod species and the choice of mortality rate to input in models of zooplankton population dynamics remains difficult (Eisenhauer et al., 2009). Actually, this study presents the first mortality estimates ever computed for a *Eucalanus* spp. copepod. The
model was able to successfully reproduce the main seasonal and interannual variation in the abundance of both *E. bungii* and *C. marshallae* over the spring period by using mortality rates computed from field observations of abundance. To use the model as a predictive tool of future copepod densities, research efforts should be focused on developing functional curves of mortality in relation to chlorophyll and temperature.

The model outcomes of this study provide a mechanistic link between observations of decline in recruitment of upper trophic levels and the timing of the spring bloom (Borstad et al., 2011). In the Bering Sea shelf declines in the biomass of *C. marshallae* have resulted in a restructuring of the food web by lowering trophic transfer efficiency to upper trophic levels, and resulting in lower biomass of a commercially important fish species (Coyle et al., 2011). It is hoped that the new understanding of *C. marshallae* and *E. bungii* dynamics here presented may aid in the formulation of better assessment tools of future fish biomass.
5.6 Figures

Figure 5.1 Conceptual diagram of the 0 dimension, stage structured, mean age population model.
Figure 5.2 Simulated (blue line) abundances of *Eucalanus bungii* with parameterization of the fraction of mature females equal to the fraction of females observed in the upper 30 m during the 2010 stratified vertical hauls. Actual observed abundances averaged across inlet stations are displayed as black dots ± SE.

Figure 5.3 Functional relationship between egg production rate (epr) and temperature and epr and chlorophyll concentration for each species. Temperature was constant at 5 °C for the chlorophyll-epr relationship displayed, while chlorophyll concentration was maintained at 5 mg m⁻³ for the temperature-epr relationship.
Figure 5.4 Simulated (blue line) abundances of *Eucalanus bungii* in 2009 with parameterization of the fraction of mature females equal to 0.45 if mean chlorophyll concentration in the upper 30 m > 2.1 mg m$^{-3}$ and equal to 0 when < 2.1 mg m$^{-3}$. Actual observed abundances averaged across inlet stations are displayed as black dots ± SE.
Figure 5.5 Daily variation in mean temperature and chlorophyll concentrations for the upper 30 m at the Daily Florence Station from March 8 to June 19. Optimal spawning conditions for *Eucalanus bungii* since the start of model simulation (March 20), when 0.45 of the females were mature, are highlighted as dotted boxes in the middle panel (blue border = 2008, red border = 2009, black border = 2010). The horizontal dotted line in the same panel represents chlorophyll concentrations of 2.1 mg m$^{-3}$. The period of optimal spawning conditions for *Calanus marshallae*, when the fraction of mature females equals 0.2, is highlighted in the bottom panel. The green rectangle represents the first spawning period in 2009 supported by lipid stores, when 0.8 of females were mature. The vertical dotted line represents the start of the simulation. The horizontal dotted line represents chlorophyll concentrations of 1.7 mg m$^{-3}$. 
Figure 5.6 Simulated (blue line) abundances of *Eucalanus bungii* with final parameterization of the fraction of mature females. 0.45 of total females where mature for 15 consecutive days starting when mean chlorophyll concentration in the upper 30 m were first > 2.1 mg m$^{-3}$ for at least 8 consecutive days and equal to 0 otherwise. Actual observed abundances averaged across inlet stations are displayed as black dots ± SE.
**Eucalanus bungii**

- Change in peak C5 abundance vs. Change in initial abundance of C5 and females:
  - $y = 0.59x + 0.42$
  - $R^2 = 0.90$
  - p-value = 0.002

- Difference in timing of peak C5 vs. Difference in timing of bloom:
  - $y = 0.52x + 3$
  - $R^2 = 0.92$
  - p-value = 0.002

- Change in peak C5 abundance vs. Change in mean mortality rate:
  - $y = 14e^{-0.52x}$
  - $R^2 = 0.91$
  - p-value = 0.002

**Calanus marshallae**

- Change in peak C5 abundance vs. Change in initial abundance of C5 and females:
  - $y = 0.97x - 0.06$
  - $R^2 = 0.94$
  - p-value < 0.001

- Difference in timing of peak C5 vs. Difference in timing of bloom:
  - $y = 0.86x - 0.33$
  - $R^2 = 0.98$
  - p-value < 0.001

- Change in peak C5 abundance vs. Change in mean mortality rate:
  - $y = 4.24e^{1.21x}$
  - $R^2 = 0.95$
  - p-value < 0.001
Figure 5.7 Relationships between the change in the size or timing of the C5 diapausing cohort and selected variables used in the sensitivity analysis.

**Eucalanus bungii**

**Calanus marshallae**

Figure 5.8 Stage-specific advection rates of *Eucalanus bungii* and *Calanus marshallae* for the model run period in 2008, 2009, and 2010.
Figure 5.9 Stage-specific mortality rates ± SE of *Eucalanus bungii* and *Calanus marshallae* averaged over years and for the entirety of the model run period.
Figure 5.10 Stage-specific mortality rates of *Eucalanus bungii* and *Calanus marshallae* for the model run period in 2008, 2009, and 2010. The green rectangles represent the period of high chlorophyll concentration from when chlorophyll concentrations were first > 4 mg m\(^{-3}\) to when they dropped below 4 mg m\(^{-3}\) for more than 10 consecutive 10 days.
Abundance C1
Abundance (10^3 Ind m^{-2})
Time (days)
2008

Abundance C2
Abundance (10^3 Ind m^{-2})
Time (days)

Abundance C3
Abundance (10^3 Ind m^{-2})
Time (days)

Abundance C4
Abundance (10^3 Ind m^{-2})
Time (days)

Abundance C5
Abundance (10^3 Ind m^{-2})
Time (days)

Abundance C6
Abundance (10^3 Ind m^{-2})
Time (days)

2009

Abundance C1
Abundance (10^3 Ind m^{-2})
Time (days)

Abundance C2
Abundance (10^3 Ind m^{-2})
Time (days)

Abundance C3
Abundance (10^3 Ind m^{-2})
Time (days)

Abundance C4
Abundance (10^3 Ind m^{-2})
Time (days)

Abundance C5
Abundance (10^3 Ind m^{-2})
Time (days)

Abundance C6
Abundance (10^3 Ind m^{-2})
Time (days)

2010

Abundance C1
Abundance (10^3 Ind m^{-2})
Time (days)

Abundance C2
Abundance (10^3 Ind m^{-2})
Time (days)

Abundance C3
Abundance (10^3 Ind m^{-2})
Time (days)

Abundance C4
Abundance (10^3 Ind m^{-2})
Time (days)

Abundance C5
Abundance (10^3 Ind m^{-2})
Time (days)

Abundance C6
Abundance (10^3 Ind m^{-2})
Time (days)
Figure 5.11 Simulated (blue line) abundances of *Calanus marshallae* with parameterization of the fraction of mature females equal to the fraction of females observed in the upper 30 m during the 2010 stratified vertical hauls. Actual observed abundances averaged across inlet stations are displayed as black dots ± SE.
Figure 5.12 Simulated (blue line) abundances of *Calanus marshallae* with a *Calanus glacialis*-like parameterization of the fraction of mature females. Actual observed abundances averaged across inlet stations are displayed as black dots ± SE.
Figure 5.13 Simulated (blue line) abundances of *Calanus marshallae* with a *Calanus finmarchicus*-like parameterization of the fraction of mature females. This was the final parameterization in 2008 and 2010. Actual observed abundances averaged across inlet stations are displayed as black dots ± SE.

Figure 5.14 Simulated (blue line) 2009 abundances of *Calanus marshallae* with both a *Calanus glacialis*-like and a *Calanus finmarchicus*-like parameterization of the fraction of mature females. Actual observed abundances averaged across inlet stations are displayed as black dots ± SE.
Figure 5.15 Simulated (blue line) 2009 abundances of *Calanus marshallae* with both a *Calanus glacialis*-like and a *Calanus finmarchicus*-like parameterization of the fraction of mature females and adjusted advection rates for C4 copepodites during the high river discharge event on April 22. This was the final parameterization in 2009. Actual observed abundances averaged across inlet stations are displayed as black dots ± SE.
### Tables

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Table 5.1 Timing and size of peak abundance of the C5 copepodite cohort as simulated by model runs for each species in each year.
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Table 5.2 List of sensitivity test runs for Eucalanus bungii. The resulting timing and size of peak abundance of the C5 copepodite cohort was compared to that in the base run.
Table 5.3 List of sensitivity test runs for *Calanus marshallae*. The resulting timing and size of peak abundance of the C5 copepodite cohort was compared to that in the base run.

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Chapter 6: Conclusion

In this thesis my overarching goal was to establish and assess the controlling effects of different environmental forcing factors on the recruitment success of various zooplankton functional traits. More specifically, my main objectives were to: 1) identify the zooplankton seasonal succession cycle in Rivers Inlet; 2) identify those functional traits and life history strategies that characterize a shared response of different zooplankton taxa to environmental change; 3) identify the main environmental drivers of *Calanus marshallae* and *Eucalanus bungii* temporal dynamics; 4) develop a model of zooplankton population dynamics of *C. marshallae* and *E. bungii* to test my conceptual understanding of their response to environmental forcing.

This is the first detailed evaluation of zooplankton life history patterns in the region and constitutes an important contribution towards gaining a mechanistic understanding of the link between environmental forcing and changes in zooplankton biomass and community composition. This knowledge is critical to explain changes in the carrying capacity of the system and to predict future ecosystem responses in this era of increased climatic variability. In this section, I provide a summary of the main findings from each of the research chapters, discuss implications for higher trophic levels, and consider directions for future work.

6.1 Summary

Chapter 2 presented the pattern of zooplankton seasonal succession in Rivers Inlet over the late winter-early summer period. Both the abundance and biomass data showed an annually recurring zooplankton successional pattern marked by two separate successional stages in zooplankton community composition. The timing of zooplankton succession was consistently associated with the timing of the spring bloom. Small, omnivorous copepods belonging to the
genera *Oithona*, *Oncaea*, *Microcalanus* and *Microsetalla* and bryozoans dominated zooplankton abundance in the winter-spring community, prior to the bloom. Adults of the herbivorous copepods, *Calanus marshallae*, *Eucalanus bungii*, and *Neocalanus plumchrus* dominated zooplankton biomass at this time. These copepods belong to a Type I (sensu Atkinson, 1998, see Chapter 4) life history strategy and molt from diapausing stage C5 copepodites using lipid stores, prior to the bloom (Smith and Vidal, 1986, Mackas et al., 1998, Shoden et al., 2005). The lipid-rich euphausiid *Thysanoessa spinifera* (Ju et al., 2009) was also an indicator species of this winter-spring succession group. By contrast, the spring-summer community was dominated by carnivores such as amphipods, hydromedusae, polychaetes, siphonophores, *Clione limacina*, as well as those taxa such as appendicularians, cladocerans, euphausiids, and *Limacina helicina* that remain active in winter, feeding omnivorously, and switch to herbivory in spring, and by adults of the Type II (sensu Atkinson, 1998, see Chapter 4) copepods *Acartia longiremis*, *Candacia* spp., *Metridia pacifica*, *Paraeuchaeta elongata*, *Pseudocalanus* spp..

The major finding of this chapter was that different taxa, best suited to specific trophic niches, dominated during different phases of the seasonal phytoplankton cycle. Thus, seasonal anomalies in the annual climate cycle may directly influence the development of the zooplankton community through changes in phytoplankton dynamics. I have shown that different zooplankton groups may vary in their annual mean abundance estimates simply because of an expansion in the length of their period of dominance. For example, a longer winter period led to a higher mean March-June abundance of small, omnivorous copepods, as they were dominant in the winter-spring succession cluster.

Since this analysis was carried out using the entire mesozooplankton community, rather than a single species or taxonomic groups, it allowed for a preliminary assessment of
commonalities in zooplankton succession and of those life history traits that define a winter-spring vs. spring-summer taxon. More specifically, this chapter highlighted the distinct reproductive strategy of different zooplankton feeding guilds. High biomass of the adult stage of herbivorous copepods appeared prior to the bloom, thus capital breeding may consist of a larger portion of their total reproductive effort as compared to Type II copepods. The importance of the early spring period for their reproductive success was explored in Chapter 4 and 5.

In Chapter 3, I presented the vertical distribution of key mesozooplankton species in the fjord over the spring period, and assessed the existence of diel and seasonal vertical migration for each stage and species. By incorporating the vertical distribution data with water velocity profiles, seasonal estimates of daily exchange rates for the species discussed were determined. In this chapter, I showed that while local growth processes dominated over advection during the study period, in critical times of the year, when production rates were low (or mortality and moulting rates high), advection was one of the main forces acting on population dynamics, particularly for those stages and species in the upper layer of the fjord. Therefore, advection is a seasonally important parameter to consider in the context of population dynamics processes and prediction of future population sizes. In years with similar rates of growth, advection may prove to be a significant driver of population dynamics.

Chapter 3 also highlighted different life history tradeoffs that are at play for each taxon. More specifically, *E. bungii* and *C. marshallae* were observed to be ontogenetic vertical migrators. High abundances of their copepodite and adult stages were found in the upper layer in early spring during the period of highest flow rates and thus were exposed to high advective losses. However, this shallow distribution granted them access to the high spring phytoplankton concentrations in the upper layers, possibly allowing for higher egg production and growth rates.
By contrast, early stage copepodites of the omnivorous *M. pacifica* and carnivorous *P. elongata* were distributed deeper in the water column and experienced lower advection losses, but also lower phytoplankton concentrations. Cladocerans, appendicularians, and *A. longiremis* were also found in the surface layers, but dominated later in the spring season, when surface advection rates were lower. These findings emphasize how interactions between a zooplankton functional trait (e.g. herbivory) and the seasonality in phytoplankton dynamics and in advection rates may impact zooplankton variability and species success in fjord-like systems.

In Chapter 4, I selected five copepod species (*A. longiremis, C. marshallae* and *E. bungii* *M. pacifica*, and *P. elongata*) belonging to different feeding guilds, and successional groups as established in Chapter 2, and assessed their life history strategies, the temporal variability of each of their copepodite stages, their recruitment, and egg production and development rates derived from literature based empirical relationships. For continuously reproducing copepods, recruitment can be quantified by the size of the first new adult cohort of the year. However, *C. marshallae* and *E. bungii* only develop up to stage C5 over the spring period, entering diapause as C5, and molting into adults the following year. Thus, for this functional group, recruitment is defined by the size of the new C5 cohort of the year. A major result of this chapter was the observation that a copepod species response to variability in spring forcing was mediated by the interaction between its life history and feeding guild. Recruitment of *P. elongata, M. pacifica*, and *A. longiremis* is not impacted by a shift in phytoplankton phenology or by variability in spring temperature. These species have a varied diet and a long reproductive season and thus are able to adapt to variable food resources. Furthermore, their small size (*A. longiremis*) or deep vertical distribution (*P. elongata, M. pacifica*) may make them less conspicuous to predators. By contrast, recruitment of *E. bungii* and *C. marshallae* is reduced when the spring bloom is delayed.
or when spring temperatures are high, possibly because of poorer survival of adults and/or copepodites. These two species are herbivorous and concentrate their reproductive effort in the spring, with most of the population diapausing over the summer. They are therefore strongly dependent on the spring phytoplankton bloom for successful recruitment. *Eucalanus bungii* and *C. marshallae* accumulate large reserves of lipid stores to undergo diapause and as such may be an energy rich prey for upper trophic levels (Mackas et al., 2007, Trudel et al., 2007). Variability in their population size may therefore be an important determinant of recruitment success of upper trophic levels.

Chapter 5 was aimed at testing my conceptual understanding of the drivers of *C. marshallae* and *E. bungii* seasonal and interannual variability achieved in the preceding chapters using a modeling approach. I was able to answer questions raised in previous chapters, such as from Chapter 2, “Is the spring bloom the main determinant of the observed phenological changes of these two species?”; from Chapter 3, “Can advection impact their population size at critical time of years, when egg production rates are low, i.e. when phytoplankton bloom concentrations are low?”, “Can differences in advection be important determinants of their recruitment in years of similar phytoplankton bloom dynamics?”; and from Chapter 4, “Is recruitment of these two species reduced in years of a delayed bloom or in years of high spring temperatures because of higher mortality rates?”. The model was able to successfully reproduce the main seasonal and interannual variation in the abundance of both *E. bungii* and *C. marshallae* over the spring period. I demonstrated that the observed change in phenology for both species was dependent on the timing of the spring bloom, through control of the fraction of spawning mature females and egg production rates. In addition, I showed that the response of the two species to advection was specific to their reproductive strategies. *Calanus marshallae* started spawning prior to the bloom
and therefore advection of early copepodite stages strongly influenced its recruitment when the bloom was late. When chlorophyll values were high earlier in the season, the advection of adults became the limiting factor of population size as it reduced the number of spawning females and thus restricted egg production. By contrast, *E. bungii*’s reproduction was focused at the onset of the bloom, and thus a later seasonal timing of phytoplankton biomass was not associated with higher advection losses as no copepodites were present prior to the bloom. However, advection was an important driver of *E. bungii* recruitment in years of similar spring bloom timing. Finally, I demonstrated that high mortalities of both species were associated with both low chlorophyll concentrations and high temperatures. Recruitment of these two species may therefore have depended on the length of that window of high chlorophyll concentrations and low predation in spring, when temperatures remain low, and, presumably, predation rates are lowest. A major result of this modeling exercise was evidence that population size of both species would be reduced by a later spring bloom or in years of anomalously high spring temperatures, such as El Niño years.

### 6.2 Implications and future work

Comparison of which species are more likely to thrive under specific environmental conditions allows for a formulation of mechanistic hypothesis of which functional traits may lead to better fitness under particular environmental conditions. Here, I have highlighted, for a specific subset of copepod species, what functional traits that may be at a disadvantage in a fjord like system in years of a late, short spring bloom or of high temperature, i.e., reproduction focused on the spring bloom, herbivory, and ontogenetic vertical migration. While data from other systems (e.g. Bering Sea) and the nearby shelf (Appendix H) provided compelling
evidence supporting this mechanistic understanding, more species-specific zooplankton time
series need to be investigated to assess if this is a common ecological principle that can be
applied to copepod species sharing the same life history traits in other marine systems.
Additionally, it remains to be determined if the same life history understanding can be applied to
groups other than copepods. For example, the euphausiid *Thysanoessa spinifera*, which shares
some life history traits with *E. bungii* and *C. marshallae*, such as large lipid stores and a spring
reproduction, displayed a similar interannual variability and response to environmental forcing as
these two species. Such a life history based approach may provide means to reduce some of the
complexity of zooplankton communities and allow for meaningful representation of zooplankton
in large ecosystem and climate models. Therefore, we may be better able to assess how future
climate change may impact zooplankton, not only at a species specific, but also at a community
level.

I have highlighted that bottom-up dynamics, through changes in phytoplankton spring
bloom timing, determined the timing of spring succession and phenology of the major
zooplankton taxa in the study system. However, top-down processes were also a significant
driver of interannual recruitment variability. For example, temperature was shown to indirectly
affect recruitment of some copepod species via its effect of mortality. Predator abundances did
indeed increase over the course of each season (Chapter 2), and in years of high temperature
(Appendix G). However, the environmental drivers of predator abundances remain to be assessed
and many unanswered questions remain to be determined. For example, what is the possibility of
shifts in predator community composition during El Niño years? Do predators’ seasonal timing
in response to temperature change shift more readily than their copepod prey? What are the
commonalities in the response of predators in different systems to shifts in temperature?
In addition, to achieve a better understanding of how top-down processes impact zooplankton recruitment success estimates of mortality are needed. However, for most zooplankton species, the environmental drivers of variability in mortality remain uncertain. These uncertainties also hinder the use of zooplankton population models, such as the one employed here, as predictive tools of future copepod densities. Thus, research efforts should be focused on developing functional curves of mortality (or of predator consumption rates) in relation to environmental variables, such as chlorophyll and temperature.

Nevertheless, if the mortality relationship with temperature and chlorophyll shown here were maintained in the future, this model would suggest that *E. bungii* and *C. marshallae* might decline in a warmer world. Higher temperature would not only increase their mortality rates, but also be associated with higher advection, which would further increase population losses. Moreover, in Rivers Inlet, river discharge has been show to limit primary productivity through its effect on phytoplankton advection rates, stratification, and light attenuation (Shiller, 2013, Hodal, 2011, Wolfe, 2010). The arrival of the spring freshet of the Wannock River has advanced by 10 days in the past 50 years, and thus, it has been hypothesized that the duration of the spring bloom may shorten in the future (Hodal, 2011). Finally, the timing of spring transition may be delayed under future climate change scenarios in this region (Foreman et al., 2011), leading to later spring bloom timing (Wolfe, 2010), and higher early spring advection rates. According to my results, the reduction in spring bloom productivity, the shift to later bloom timing, and higher spring advection rates, would hamper spring recruitment of *E. bungii* and *C. marshallae* and result in lower abundances of these copepod species in the future. Resilience of both species may depend on their reproductive success during their fall spawning. Thus, the magnitude and
phenology of fall reproductive events, and their relationship to environmental forcing should be investigated.

Since recruitment success of fish larvae relies on synchronization with peaks of their zooplankton prey (Hjort, 1914, Cushing, 1969, 1990a), the observed phenological variation in zooplankton dynamics may result in phenologically driven ecosystem shifts. In this section, I explore the effect of the observed changes in zooplankton composition on juvenile sockeye salmon migrating through the inlet and assess the potential for a mismatch between the sockeye juveniles and their zooplankton prey.

Overall zooplankton biomass during the May and June period of salmon juvenile migration was depressed in 2009 because of the shift in zooplankton succession and the reduction in the biomass of specific species, such as C. marshallae and L. helicina. This may have resulted in a mismatch between sockeye juveniles and their zooplankton prey (Fig. 5.1). Higher feeding intensity of sockeye juveniles in Rivers Inlet in 2008 compared to 2009 seems to confirm this (Ajmani, 2012). There was also a shift in stomach prey composition (Ajmani, 2012), likely reflecting the observed delayed zooplankton succession and associated shift in community composition. Thus, in 2008 fish and large crustaceans were the most common prey items, while in 2009 barnacle larvae, cladocerans, and bivalves were the most common (Ajmani, 2012).

By contrast, in 2010, the timing and magnitude of the zooplankton biomass peak was relatively comparable to 2008 (Fig. 5.1). However, the biomass of Type I copepods, such as E. bungii and C. marshallae, and fish larvae was reduced (Fig. 5.1). I decided to show interannual variation in fish larvae and C. marshallae, as they, together with barnacle larvae, constitute the largest contribution to juvenile stomach prey content (Ajmani, 2012), and have a gross energy density higher than barnacle larvae (Foy and Norcoss, 1999, Tanasichuck and Routledge, 2011).
Stomachs in 2010 had a lower gut fullness index than in 2008 (Ajmani, 2012). Furthermore, as in 2009, the most common prey items were barnacle larvae, cladocerans, and bivalves rather than fish larvae and large crustaceans as in 2008 (Ajmani, 2012).

Clearly, changes in zooplankton community composition and timing of zooplankton succession impacted the prey field of sockeye salmon juveniles, which was reflected in interannual differences in stomach content. This resulted in 2009 and 2010 juveniles foraging on numerous but less energy dense prey, possibly reducing their nutritional condition. Such differences in nutritional status during the initial marine stage may have contributed to a reduced the juveniles’ survival over the winter and to the overall year class strength of 2009 and 2010 sea entry years. Preliminary return data do suggest that the 2008 sea entry year had higher survival than 2009 (Appendix A.2). Sockeye salmon returns in 2013 will have to be tallied to assess survival for the 2010 year of sea entry. However, the prey field elsewhere on their early migration journey would also be a factor in the survival success of the sockeye juveniles. Thus, it should be established if the interannual difference in zooplankton species composition observed in Rivers Inlet is reflected in similar changes in the shelf zooplankton population. Therefore, zooplankton and juvenile salmon stomach prey composition data along the entire juvenile migration route as well as zooplankton, stomach content, and salmon survival data over a longer time series and different salmon stocks, are needed to strengthen the suggestion that mismatch with their zooplankton prey quantity and quality may hinder sockeye salmon recruitment.

The mechanistic understanding of how environmental forcing impacts zooplankton recruitment in Rivers Inlet developed in this thesis may be employed to assess the potential for changes in bottom-up processes having driven the historical decline in Rivers Inlet sockeye salmon returns and survival. I demonstrated that zooplankton biomass and high quality prey
types are most abundant in cold years with an early spring bloom. The timing of the spring bloom in Rivers Inlet is delayed by frequent and strong outflow events and by high discharge in late winter and early spring (Wolfe, 2010). Outflow events in the inlet correspond to a southeasterly wind direction on the shelf and to a late spring transition (Wolfe 2010). Therefore, by using a time series of wind, temperature, and discharge data I may infer historical bloom timing and zooplankton dynamics. I have reconstructed such a time series in Fig. 5.2. This is a very preliminary analysis and I have only focused on the month of April, as wind direction during this month appeared to be a critical determinant of spring bloom timing in Queen Charlotte Sound, the shelf region at the mouth of Rivers Inlet (Borstad et al., 2011).

The data show that winds from the south in April became more common after 1970, that April temperatures were warmer after the well known regime shift of 1976-77 (Hare et al., 1999), and that April river discharge has increased since 1985 (Fig. 5.2). Assuming that the relationships between environmental forcing and zooplankton highlighted in my thesis, and those between atmospheric forcing and phytoplankton dynamics highlighted by Wolfe (2010), are maintained throughout this historical period, these data would suggest that the timing of the zooplankton succession may now on average be happening later and that the biomass of Type I copepods may, on average, be lower. Conditions pre-1970 appeared to have been the most favorable to Type I copepods and those between the late 1970s and the late 1990s the most disadvantageous.

However, when I constructed a generalized additive model of the sockeye salmon survival index (Return/Spawner) with the April environmental variables as predictors no significantly variability was explained (Appendix A.3). A more in depth look at the variables showed that the increase in southeasterly wind in the early 1970s did not result in decreased
sockeye survival (Appendix A.3), contrary to expectation. Temperatures were cold in this period, and it is plausible that different drivers were forcing phytoplankton bloom timing pre and post the 1976-1977 regime shift. Indeed, when I ran the model separately for the two periods I obtained a significant relationship between sockeye salmon survival and the environmental variables (Appendix A.3). Interestingly, the relationship with temperature was of opposite sign in the two time periods, being positive pre-1976/77 regime shift and negative post-1976/77 regime shift (Appendix A.3).

The analysis demonstrated that in the post regime shift period, 50% of the variability in sockeye salmon survival may be explained by variation in April wind and temperature (Appendix A.3). Therefore, this exercise showed that changes in bottom-up processes may have contributed to the decline of this stock. Since I have shown that zooplankton recruitment in one year is dependent on the size of its parent cohort, consecutive years of poor environmental conditions have the potential of severely impacting zooplankton concentrations. Such a period of consistently high April temperatures and high southeasterly winds existed from the late 1970s to the late 1990s (Fig. 5.2) and may have contributed to the low survival rates of sockeye salmon observed in those sea entry years. Clearly, a mechanistic understanding of lower trophic level dynamics is essential if we are to assess future sockeye salmon variability. Such conceptual explanations of how environmental variables are linked to salmon survival have the potential to inform the selection of potential variables to be input into stock specific models of salmon recruitment to improve their forecasting capabilities.
Figure 6.1 Temporal variation of total mesozooplankton biomass, Type I copepods (*Calanus marshallae*, *Eucalanus bungii*, and *Neocalanus plumchrus*), and fish larvae. Superimposed in blue is an artificial juvenile salmon seasonal cycle. Their abundance peaks in late May and early June and their timing is comparable between years (Ajmani 2012). I maintained this seasonality but numbers were scaled down to the biomass of the zooplankton for ease of comparison.
Figure 6.2 Historical (1961-2008) time series of Rivers Inlet sockeye salmon survival (Return/Spawner) and anomalies in mean April alongshore wind speed, sea surface temperature, and Wannock River flow. Winds from the south have a positive sign.
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Appendices

Appendix A

A.1 Rivers Inlet sockeye salmon returns

Numbers of adult sockeye salmon returning to Oweekeno Lake to spawn. This is the main sockeye salmon spawning area in Rivers Inlet. Catches are the numbers caught by the fishery, escapements are those fish that “escape” the fishery and continue on to spawn.
A.2  Comparison of 2008 and 2009 sockeye salmon survival

Sockeye fry spend two years in the freshwater environment before starting their seaward migration. Therefore, eggs spawned in fall of 2006 (brood year = 2006) would produce fry that enter the estuarine environment in May-June 2008 (sea entry year = 2008). Sockeye salmon spend two to three years at sea, returning as four or five year olds to spawn. Survival is calculated as a ratio of the numbers of adult returning, which is the sum of the numbers of four and five year olds for that brood year, to the number of spawners of that same brood year. The table below shows the numbers of spawners and returns for sea entry years 2008 and 2009. Note, however, that the ratio of four to five year olds is still being computed for year 2009. More specifically, the ratio of five year olds from the 2009 sea entry year to four year olds from the 2010 sea entry year for the escapements of 2012 has yet to be determined. Thus, the Return/Spawner ratio for 2009 here presented is an overestimate as it assumes all 150,000 escapees in 2012 were five year old fish from the 2009 sea entry year. Uncertain estimates are highlighted in bold. These data were provided by the Department of Fisheries and Oceans Canada.

<table>
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<th>Sea Entry Year</th>
<th>Spawners</th>
<th>% of 4 year olds</th>
<th>% of 5 year olds</th>
<th>Return from brood</th>
<th>Return/Spawner ratio</th>
</tr>
</thead>
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<tr>
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<td>108,000</td>
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</tr>
<tr>
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<td>2009</td>
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<td>NA</td>
<td>23,354 (2011)+150,000 (2012) = 173,354</td>
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Even if an overestimate, the Return/Spawner ratio of the 2009 sea entry year is lower than that for 2008, indicating that survival was higher for 2008 salmon juveniles.
A.3 Generalized additive model of sockeye salmon survival

Data exploration showed a clear non-linear relationship between environmental factors and sockeye salmon survival. To account for the non-linearity in the data, a generalized additive modeling (GAM) method was employed. This method allows for the relationship between mortality and the explanatory variables to be modeled non-linearly using smoothing curves (Zuur et al. 2007, Wood 2006). All models were analyzed using the mgcv library (version 1.7-18) in R version 2.15.1. The dataset considered was Rivers Inlet sockeye salmon survival (Return/Spawner) for the period of 1961 to 2008. This was the time frame when all the explanatory variables were available. The explanatory variables considered were mean April sea surface temperature, mean April wind speed in the alongshore direction, and Wannock River discharge. Sea surface temperatures were obtained from the Department of Fisheries and Oceans Canada BC Lighthouse Database (http://www.pac.dfo-mpo.gc.ca/science/oceans/data-donnees/lighthouses-phares/index-eng.htm, Accessed May 18, 2013) for the McInnes Lighthouse (52.16° N, 128.43° W). Mean April alongshore wind speed averaged from 50 to 52.5° N and 127.5° W were acquired from NCEP Reanalysis Derived data provided by the NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, from their Web site at http://www.esrl.noaa.gov/psd/, accessed May 18, 2013. Wannock River discharge was obtained from Environment Canada as detailed in Chapter 2. All explanatory variables were standardized prior to input into the model.

A preliminary generalized additive model of the entire sockeye salmon survival (Return/Spawners) time series against the April environmental variables was not significant. A more in depth look at the variables shows that the increase in southeasterly winds in the early 1970s did not result in decreased sockeye survival (Fig. 5.2). Temperatures were colder in this
period, and it is plausible that a different environmental variables were forcing phytoplankton bloom timing pre and post 1976-1977 regime shift and that thus the relationship between sockeye salmon survival and environmental forcing differed, producing an non-significant result. Indeed, when I run the model separately for the pre and post regime period, I obtained two significant models. This was after the removal of the 2001 outlier, whose high survival may have been due to density-dependence effects, since its parents consisted of the lowest number of spawners ever reported for this stock, 4257, which is one order of magnitude lower than the next minimum number of spawners, 21000.

Pre regime shift, sockeye survival increased with warmer temperatures and the other environmental variables did not influence sockeye survival variability. The table below presents a summary of the pre 1977 regime shift generalized additive model results. The p-values are shown to demonstrate the significance (or not) of each environmental factor. P-values highlighted in bold are significant at an alpha level of 0.05.

<table>
<thead>
<tr>
<th>Parameters</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alongshore wind speed (positive winds are blowing from the south)</td>
<td>0.14</td>
</tr>
<tr>
<td>Sea surface temperature</td>
<td><strong>0.02</strong></td>
</tr>
<tr>
<td>Wannock River discharge</td>
<td>0.50</td>
</tr>
<tr>
<td>Intercept = 3.13</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>R² (adj.) = 0.26</td>
<td>N = 15</td>
</tr>
</tbody>
</table>

The figure below shows the estimated smoothing curves for the significant environmental parameter, in this case, standardized mean April sea surface temperature. The rug plot on the x-axis displays a tick mark for each of the sampled values of temperature. The dotted lines are 95% point-wise confidence bands. This plot shows that salmon survival remained stationary at temperatures below 7.3 ºC (corresponding to the standardized value of -1), but increased almost
linearly with higher temperatures. The highest temperature ever recorded in this time period was 8.4 °C.

The table below presents a summary of the post 1977 regime shift generalized additive model results. The p-values are shown to demonstrate the significance (or not) of each environmental factor. P-values highlighted in bold are significant at an alpha level of 0.05.

<table>
<thead>
<tr>
<th>Parameters</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alongshore wind speed (positive winds are blowing from the south)</td>
<td>0.001</td>
</tr>
<tr>
<td>Sea surface temperature</td>
<td>0.06</td>
</tr>
<tr>
<td>Wannock River discharge</td>
<td>0.38</td>
</tr>
<tr>
<td>Intercept = 1.57</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>$R^2$(adj.) = 0.50</td>
<td>N = 31</td>
</tr>
</tbody>
</table>
In this time period, sockeye salmon survival variability was largely explained by fluctuations in alongshore wind speed in April. Sea surface temperature had a significant effect only at an alpha level of 0.1.

The figure below shows the estimated smoothing curves for the standardized mean April sea surface temperature for the post 1977 model. This plot shows that, unlike in the previous regime, salmon survival decreased linearly with higher temperatures. The highest temperature ever recorded in this time period was 9.7°C.

![Temperature vs. Survival](image-url)

The figure below shows the estimated smoothing curves for the standardized mean April alongshore wind speed for the post 1977 model. This plot demonstrates that salmon survival
decreased linearly with increasing alongshore wind speeds until a value of 0.9 m/s (corresponding to the standardized value of -0.5), after which it remained constant. Since positive wind speeds represents winds from the south, these results demonstrate that sockeye salmon survival is lower in years of a later spring transition.
Appendix B

Fluorescence calibration curves were developed by regressing fluorometer readings from the Hydrolab DS5X sonde fluorescence (volts) and RBR XR-620 CTD and SBE 25 CTD’s fluorescence (mg m$^{-3}$) on chlorophyll $a$ concentrations from the filtered samples. The regression equations were:

- **2008, Hydrolab**: $\ln(\text{Chl } a, \text{ mg } m^{-3}) = 4.5 + 1.1 \ln(\text{Hydrolab, volts})$ with an $R^2$ of 0.87
- **2008, CTD**: $\ln(\text{Chl } a, \text{ mg } m^{-3}) = -0.15 + 0.8 \ln(\text{CTD, mg } m^{-3})$ with an $R^2$ of 0.71
- **2009, RBR**: $(\text{Chl } a, \text{ mg } m^{-3}) = 0.94 + 0.8 (\text{RBR, mg } m^{-3})$ with an $R^2$ of 0.83
- **2009, CTD**: $(\text{Chl } a, \text{ mg } m^{-3}) = -0.01 + 0.3 (\text{CTD, mg } m^{-3})$ with an $R^2$ of 0.72
- **2010, RBR**: $(\text{Chl } a, \text{ mg } m^{-3}) = 1.75 + 0.6 (\text{RBR, mg } m^{-3})$ with an $R^2$ of 0.62
- **2010, CTD**: $(\text{Chl } a, \text{ mg } m^{-3}) = 0.41 + 0.2 (\text{CTD, mg } m^{-3})$ with an $R^2$ of 0.72
Appendix C

List of the major zooplankton taxa in Rivers Inlet and dry weight coefficients used to estimate biomass by taxa.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Body Weight (mg DW)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Acartia longiremis</em></td>
<td>0.0070</td>
</tr>
<tr>
<td><em>Aetideidae</em></td>
<td>0.1422</td>
</tr>
<tr>
<td><em>Calanus marshallae</em></td>
<td>0.2680</td>
</tr>
<tr>
<td><em>Calanus pacificus</em></td>
<td>0.2200</td>
</tr>
<tr>
<td><em>Candacia</em> spp.</td>
<td>0.2839</td>
</tr>
<tr>
<td><em>Corycaeus anglicus</em></td>
<td>0.0025</td>
</tr>
<tr>
<td><em>Eucalanus bungii</em></td>
<td>0.6800</td>
</tr>
<tr>
<td><em>Heterorhabdus tanneri</em></td>
<td>0.1833</td>
</tr>
<tr>
<td><em>Metridia okhotensis</em></td>
<td>0.5920</td>
</tr>
<tr>
<td><em>Metridia pacifica</em></td>
<td>0.1360</td>
</tr>
<tr>
<td><em>Microcalanus pusillus</em></td>
<td>0.0035</td>
</tr>
<tr>
<td><em>Microsetella</em> spp.</td>
<td>0.0015</td>
</tr>
<tr>
<td><em>Neocalanus cristatus</em></td>
<td>2.7300</td>
</tr>
<tr>
<td><em>Neocalanus plumchrus</em></td>
<td>0.6380</td>
</tr>
<tr>
<td><em>Oithona</em> spp.</td>
<td>0.0016</td>
</tr>
<tr>
<td><em>Oncae</em> spp.</td>
<td>0.0012</td>
</tr>
<tr>
<td><em>Paracalanus</em> spp.</td>
<td>0.0042</td>
</tr>
<tr>
<td><em>Paraeuchaeta elongata</em></td>
<td>1.6700</td>
</tr>
<tr>
<td><em>Pseudocalanus</em> spp.</td>
<td>0.0210</td>
</tr>
<tr>
<td><em>Scolecithricella</em> minor</td>
<td>0.0066</td>
</tr>
<tr>
<td><em>Hydromedusae</em></td>
<td>1.8700</td>
</tr>
<tr>
<td><em>Beroe</em> spp.</td>
<td>2.6000</td>
</tr>
<tr>
<td><em>Bivalves</em></td>
<td>0.0006</td>
</tr>
<tr>
<td><em>Bryozoans</em></td>
<td>0.0013</td>
</tr>
<tr>
<td><em>Brachyuran zoea</em></td>
<td>0.2200</td>
</tr>
<tr>
<td><em>Cirripedia</em> cyprids</td>
<td>0.3500</td>
</tr>
<tr>
<td><em>Cirripedia</em> nauplii</td>
<td>0.0400</td>
</tr>
<tr>
<td><em>Ostracods</em></td>
<td>0.1000</td>
</tr>
<tr>
<td><em>Epicarid larvae</em></td>
<td>0.2500</td>
</tr>
<tr>
<td><em>Euphausia pacifica</em></td>
<td>8.5000</td>
</tr>
<tr>
<td><em>Fish larvae</em></td>
<td>1.8000</td>
</tr>
<tr>
<td><em>Anomuran zoea</em></td>
<td>0.0640</td>
</tr>
<tr>
<td><em>Caridean zoea</em></td>
<td>0.0550</td>
</tr>
<tr>
<td><em>Limacina helicina</em></td>
<td>0.3683</td>
</tr>
<tr>
<td><em>Clione limacina</em></td>
<td>3.5000</td>
</tr>
<tr>
<td>Taxon</td>
<td>Body Weight (mg DW)</td>
</tr>
<tr>
<td>-----------------------</td>
<td>---------------------</td>
</tr>
<tr>
<td>Neomysis raya</td>
<td>5.6000</td>
</tr>
<tr>
<td>Appendicularians</td>
<td>0.0987</td>
</tr>
<tr>
<td>Chaetognaths</td>
<td>0.9549</td>
</tr>
<tr>
<td>Pasiphaea pacifica</td>
<td>2.1300</td>
</tr>
<tr>
<td>Cladocerans</td>
<td>0.0050</td>
</tr>
<tr>
<td>Sergestes spp.</td>
<td>0.6500</td>
</tr>
<tr>
<td>Siphonophores</td>
<td>1.4382</td>
</tr>
<tr>
<td>Amphipods</td>
<td>2.3500</td>
</tr>
<tr>
<td>Thysanoessa longipes</td>
<td>10.0000</td>
</tr>
<tr>
<td>Thysanoessa raschii</td>
<td>12.5000</td>
</tr>
<tr>
<td>Thysanoessa spinifera</td>
<td>15.7510</td>
</tr>
<tr>
<td>Polychaetes</td>
<td>0.9793</td>
</tr>
</tbody>
</table>
Appendix D

Daily time series of 5 m salinity (top) and temperature (bottom) from the Florence daily station (white circles). Black circles represent average (± 1 SD) conditions across all sampling stations for each sampling cruise.
Appendix E

Logarithmic regression of the EPR and chlorophyll concentrations reported in Smith and Lane (1991) for *Eucalanus californicus* used to model the relationship between *Eucalanus bungii* EPR and chlorophyll. The equation is presented in Table 4.2.
Appendix F

Species-specific average egg production rate (eggs female\(^{-1}\) day\(^{-1}\)) across inlet stations in 2010 computed for each zooplankton depth sampling interval. Error bars represent standard errors.

AL = *Acartia longiremis*, CM = *Calanus marshallae*, EB = *Eucalanus bungii*, MP = *Metridia pacifica*. 
Appendix G

The figure below shows the interannual variability in the mean abundance of different predator taxa observed in the Rivers Inlet zooplankton samples. Sampling events are, in order, LM = late March, EA = early April, LA = late April, EM = early May, LM = late May, EJ = early June, and LJ = late June. Taxa shown are AM = amphipods, AN = anomurans, CH = cheatognaths, FL = fish larvae, MD = hydromedusae, PY = Polychaetes, SP = siphonophores.
Appendix H

The figure below shows the stage-specific variation in the abundance of *Calanus marshallae* and *Eucalanus bungii* at the UBC7 station (51.50 °N, 127.82 °W), located on the shelf region at the mouth of Rivers Inlet, over the spring period.