COPEPOD DYNAMICS OF THE FRASER RIVER ESTUARY

by

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Abstract

How the zooplankton in estuaries of nival basins will respond to a warming water column and earlier peak flows is unknown. The goal of this dissertation is to increase our knowledge of zooplankton dynamics in snowmelt-dominated estuarine systems by studying the Fraser River Estuary (FRE). To describe the copepod community of the FRE and identify drivers of species composition and abundance, an intensive zooplankton sampling program was carried out over a period of 33 months, from August 2013 – May 2016. I coupled the sampling program with investigations of the depth distribution and egg production of the most abundant pelagic copepod in the estuary, *Eurytemora affinis*. Using the information gained in these studies and data from the literature, I built a stage-structured, concentration-based population model to explore the response of *E. affinis* abundance to projected changes in temperature and Fraser River discharge.

The results outlined in this dissertation demonstrate that mesozooplankton abundance, biomass, and production in the FRE were low in comparison to other studied estuaries and limited by water residence times in the estuary. Targeted study of *E. affinis* provided evidence of tidal vertical migration behaviour and a first record of the production of resting eggs to bridge periods of rapid flushing and low salinity. The presence of these retention mechanisms highlights the role advection risk has played in shaping both the behaviour and life history of the *E. affinis* population in the FRE. Results of model simulations suggest that the response of *E. affinis* abundance to predicted changes in water temperature and river discharge is dependent on how those changes influence spring contributions to the egg bank. My simulations suggest that warming of 1.5 °C, in combination with predicted changes to the Fraser River's hydrograph, has the potential to lead to a near doubling (+ 92%) of abundance of *E. affinis* and significant

changes in their phenology (from 50 days earlier to 25 days later, depending on the timeframe of

the river discharge scenario). I suggest that zooplankton production in snowmelt-dominated

estuarine systems may be sensitive to changes in hydrology, particularly where channelization

has occurred.

Lay Summary

Zooplankton are important to estuarine food webs, linking phytoplankton and detritus to fish and larger invertebrates. The typically high zooplankton abundance recorded in estuaries relies on species that are adapted to life within estuaries. The Fraser River Estuary, however, flushes very rapidly, which presents a challenge for small organisms that cannot swim against a current. My research found that zooplankton abundance in the Fraser River Estuary was low in comparison to estuaries worldwide and was limited by how quickly water moves through the estuary. Study of one of the most abundant zooplankton species in the estuary revealed that it uses several strategies to avoid being swept out to sea, but nonetheless, its distribution was limited to sheltered sloughs. I suggest that physical modifications made to the Fraser River and estuary have reduced zooplankton production in the estuary and may make zooplankton production more sensitive to the effects of climate change.

Preface

The research presented in this dissertation was conceived of by myself and undertaken under the supervision of Dr. Evgeny Pakhomov, with additional guidance provided by supervisory committee members: Dr. Susan Allen, Dr. Chris Harley, and Dr. Mary O'Connor. I was responsible for the bulk of the field work and lab work that supported this research and for the entirety of the data analysis and writing.

Chapter 2 has been published as: Breckenridge, J.K., E.A. Pakhomov, S. Emry, N. Mahara (2020) Copepod assemblage dynamics in a snowmelt-dominated estuary. Estuaries and Coasts 43(6): 1502 – 1518. I collected and processed the bulk of the samples used in this manuscript, and conducted all data analysis and writing, under the supervision of Dr. E. Pakhomov. S. Emry and N. Mahara assisted on many of the research cruises and, in 2016, led cruises and completed chlorophyll processing. N. Mahara additionally processed some of the net tow samples.

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List of Abbreviations

AIC_c: Akaike information criterion

CI: Confidence interval

CS: Clutch size (eggs clutch^{-1})

CTD: Conductivity temperature depth

DVM: Diel vertical migration

DW: Dry weight

EDT: Egg development time (days)

EPR: Egg production rate (eggs female^{-1} day^{-1})

ETM: Estuarine turbidity maximum

FRB: Fraser River Basin

FRE: Fraser River Estuary

ICT: Inter-clutch time (days)

LOESS: Locally-weighted smoothing

mab: Meters above bottom

NMS: Nonmetric multidimensional scaling

PDF: Probability density function

PL: Prosome length

PSM: Population surface method

REML: Restricted maximum likelihood

RWMD: Relative weighted mean depth

TCS1: Tidal cycle sampling 1

TCS2: Tidal cycle sampling 2

TVM: Tidal vertical migration

VLT: Vertical life table

WMD: Weighted mean depth

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In loving memory of my parents,

    Leona and John Breckenridge

Chapter 1: Introduction

1.1 Motivation

Estuaries are considered to be among the Earth's most productive environments (Nixon 1988, Kennish 2002). These relatively rare coastal ecosystems support abundant, diverse, and economically important megafauna, making accurate prediction of estuarine community responses to changes in climate particularly important. The high level of secondary production in estuaries is generally coupled with low biodiversity making these ecosystems sensitive to climate change (Elliott & Whitfield 2011). Estuarine zooplankton are typically dominated by only a few copepod species (Miller 1983) which follow a predictable seasonal succession guided by changes in temperature and salinity (e.g. Miller, 1983, Bollens et al. 2011). Increasing temperatures (Gerten and Adrian 2002, Lee et al. 2003) and changing precipitation/discharge patterns may affect population dynamics and seasonality of zooplankton, shifting or abbreviating their temporal distribution relative to their prey and predators. Although estuarine species appear well-adapted to life in a highly variable environment, our current ability to predict their population and community-level responses to changing climate is inadequate.

The timing of peak flow may be of particular importance to estuarine species through its structuring effect on estuarine zooplankton and by driving community succession (de Madariaga et al. 1992). Many estuaries in temperate and polar systems are in snow-dominated river basins, and these are predicted to experience the greatest changes to their hydrologic cycle compared to other estuaries (Nijssen et al. 2001). With climate change, precipitation increasingly falls as rain rather than snow (Dore 2005) and snow-melt occurs earlier, resulting in increased river discharge during winter, decreased late summer discharge, and earlier maximum water discharges (Morrison et al. 2002, Yang et al. 2002, Stewart et al. 2005, Wu et al. 2012).

The zooplankton in estuaries of snowmelt-dominated basins have received relatively little study, and how they will respond to earlier peak flows is unknown. Located at high latitudes, or in mid-latitudes with mountainous basins, snowmelt-dominated river systems have flow regimes that are characterized by a single strong peak in discharge. Termed the freshet, it occurs in the late spring to summer and results from the spring thaw. During the freshet, river discharge increases rapidly, often by an order of magnitude, and may flush all salt from the estuary. Snowmelt-dominated systems include the great rivers of Siberia (the Yenisei, Ob, and Lena) and of western North America (the Mackenzie, Yukon, Columbia, Colorado, and Fraser, among others). In addition to changes due to climate, the flow regimes of these rivers may also be substantially altered by human use. In such rivers, water from the freshet is often impounded for power generation or diverted for irrigation before reaching the estuary. For example, the Columbia River Estuary no longer experiences a natural flow regime and the Colorado River has been drained to such an extent that its once extensive estuary has been all but eliminated (Luecke et al. 1999).

The Fraser River is the second longest river in North America with an undammed main stem (Dynesius & Nilssen 1994) and its estuary provides rearing grounds for juvenile Chinook, chum, coho, and sockeye salmon (Levy & Northcote 1982, Birtwell et al. 1987a, Macdonald et al. 1990, Levings et al. 1991, Chalifour et al. 2019). The Fraser River Estuary (FRE) and its residents remain subject to a largely natural snowmelt-dominated hydrographic regime with discharge varying by an order of magnitude during the spring freshet. The overarching objective of this dissertation is to increase our understanding of zooplankton dynamics in snowmelt-dominated systems and how they will be influenced by predicted changes in water temperature and river discharge through study of mesozooplankton in the FRE.

1.2   Thesis main objectives

1. Provide a first description of pelagic copepod dynamics in the FRE (Chapter 2).

2. Identify environmental drivers of copepod community dynamics in the FRE (Chapter 2).

3. Identify factors limiting copepod abundance, biomass, and production in the FRE (Chapters 2 & 5).

4. Identify population retention strategies used by the estuarine copepod *Eurytemora affinis* in the FRE (Chapters 3 & 4).

5. Develop a population model able to explore potential effects of projected changes in temperature and Fraser River discharge on *E. affinis* population dynamics (Chapter 5).

1.3   Thesis structure and background

Zooplankton in estuaries are often separated into three groups according to salinity preference (Bousfield et al. 1975, Miller 1983, Laprise & Dodson 1994, Wooldridge 1999, Mouny & Dauvin 2002). Marine coastal species are found at the seaward end of the estuary (termed the outer or lower estuary). A subset of these species (often members of the genera *Acartia*, *Eurytemora*, or *Oithona*) thrive despite the reduced salinity and can attain abundances exceeding those observed in the coastal ocean (Bousfield et al. 1975). Estuarine endemic copepods, such as *Eurytemora affinis*, and some members of the genera *Acartia*, *Sinocalanus*, and *Pseudodiaptomus*, dominate the zooplankton community in the brackish waters of the upper (or inner) and middle estuary (Kibirige & Perissinotto 2003, Kimmel 2011). The final group are freshwater species whose distributions extend into the upper estuary. The salinity ranges associated with these three groups are often classified according to the Venice System

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(Anonymous 1959), with marine coastal taxa occurring in polyhaline waters of salinities 18 – 30, estuarine endemic taxa being most abundant in mesohaline (salinities 5 – 18) and oligohaline waters (salinities 0.5 – 5), and freshwater taxa occurring in oligohaline waters. The physical location of these estuarine zones and their associated zooplankton communities shifts landward and seaward with tide and magnitude of river discharge. Because there has been little research on the mesozooplankton of the Fraser River or estuary, the first step of my dissertation research was to describe copepod community dynamics of the South (Main) Arm of the FRE and identify environmental parameters correlated to changes in abundance and community composition. This was achieved through twice-monthly to monthly monitoring over a period of 33 months. I chose to focus my research on copepods because copepods are the most abundant zooplankton in estuaries (Miller 1983, Wooldridge 1999). The specific objectives of Chapter 2 were to 1) provide first descriptions of copepod abundance, biomass, and production for the FRE, 2) relate copepod dynamics to water column properties and river discharge, and 3) test the hypothesis that temperature and water residence time limit FRE copepod abundance, biomass, and production.

Estuarine endemic (or 'true estuarine') copepods are responsible for the high zooplankton abundances considered typical of estuaries (e.g. Bousfield et al. 1975, Peitsch et al. 2000, Kibirige & Perissinotto 2003, Devreker et al. 2008, Bollens et al. 2011). These copepods share a number of characteristics. Estuarine copepods have been characterized as being generalist feeders, taking advantage of a wide diversity of food sources including protozoans, phytoplankton, and detritus (Heinle et al. 1977, Rollwagen Bollens & Penry 2003, Gifford et al. 2007, Diodato & Hoffmeyer 2008, Kimmel 2011). Most species are small (1 – 2 mm) with short generation times (Miller 1983, Kimoto et al. 1986, Jerling & Wooldridge 1991, Ban 1994). Reproduction is continuous and requires repeated matings (Katona 1975, Miller 1983). Many

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estuarine calanoid copepods are members of the superfamily Centropagoidea (= Diaptomoidea), which contains many species capable of producing resting eggs (Lindley 1992, Winding Hansen 2019). While estuarine copepods are able to tolerate a wide range of salinity conditions, many cannot thrive at the salinity of fully marine waters and therefore need to avoid advection from the estuary. Estuarine retention mechanisms are the subject of chapters 3 and 4.

River discharge, through its influence on salinity and water residence time within the estuary, is a major determinant of the occurrence and character of estuarine zooplankton communities (Ketchum 1954, Miller 1983, Pace et al. 1992). For estuarine zooplankton, the ability to withstand advective forcings is critical to population maintenance. Behavioural strategies of estuarine copepods that promote retention, e.g. aggregating at the sediment-water interface during floods (Ueda et al. 2004), and actively migrating vertically to exploit differential tidal flows (Morgan et al. 1997, Ueda et al. 2010) are reviewed in Chapter 4. In this chapter, I used vertically discrete sampling to describe the depth distributions of abundant copepods over two complete tidal cycles. The specific aim of Chapter 4 was to test the hypothesis that *E. affinis* would migrate vertically with the tides in a manner that would promote retention (i.e., that they would have a deeper distribution on ebbing tides).

Seasonal peaks in river discharge are a predictable component of the annual hydrograph that increase the risk of advection for estuarine copepods. Estuarine species have likely experienced strong selective pressure for mechanisms to avoid resulting periods of reduced salinity and residence time. Some species employ benthic resting stages to avoid adverse conditions (Caceres 1997, Baumgartner & Tarrant 2017) and the literature on resting egg production by *E. affinis* is reviewed in section 3.1. The production of resting eggs to bridge periods of high river discharge has never been documented; however, this would be an effective

tactic to withstand the strong currents and low salinities typical of the freshet (Uye 1980, Runge & Simard 1990, Newton & Mitchell 1999). In Chapter 3, I incubated female *E. affinis* to determine whether the production of resting eggs in anticipation of peak river flows might be occurring in the FRE. The aims of Chapter 3 were specifically to 1) provide estimates of egg production and release by *E. affinis* in the FRE, and 2) to interpret variation in egg release with respect to underlying patterns of abundance, population structure, and environmental conditions.

By conducting research in the largely unstudied FRE we gain an understanding of mesozooplankton dynamics in estuaries of snowmelt-dominated basins and of how these systems will respond to climate change. In Chapter 5, I developed a stage-structured, concentration-based population model forced by water temperature and Fraser River discharge that is able to replicate observed population dynamics of *E. affinis* in Deas Slough. I used this model to 1) develop a more mechanistic understanding of *E. affinis* population dynamics in Deas Slough, 2) investigate the importance of resting eggs to the persistence of the population, and 3) explore potential effects of projected changes in temperature and Fraser River discharge on *E. affinis* population dynamics. In order to parameterize this model, I estimated annual variation in *E. affinis* mortality rate and egg production rate (EPR). I used literature-derived development times to estimate the effect of temperature on *E. affinis* development. Additionally, to better understand limits on *E. affinis* reproduction and population growth, I estimated annual variation in clutch size (CS), body size (prosome length), sex ratio, and prevalence of epibionts.

Chapter 2: Copepod assemblage dynamics in a snowmelt-dominated estuary

What limits secondary production in the estuaries of snowmelt-dominated basins? Due to substantial differences in their annual hydrographs, zooplankton dynamics in these estuaries are expected to differ from better-studied pluvial systems. We hypothesized that water residence time limited zooplankton production in the undammed, snowmelt-dominated estuary of the Fraser River, Canada. We sampled zooplankton and associated environmental variables bi-weekly to monthly in slough and channel areas of the estuary over a 33-month period. Annual mean copepod abundance at channel stations was low ($2,005 \pm 238$ individuals m^{-3}) in comparison to other studied estuaries, with minima occurring during spring, concurrent with the freshet. Higher abundances ($11,905 \pm 3,606$ individuals m^{-3}) observed at slough stations were attributed to estuarine copepods. Differences in abundance and species composition between slough and channel areas, and the coincidence of seasonal minima with the freshet, suggest that the low water residence time of this system limits zooplankton density and production. Heavy channelization of the Fraser River Estuary has further reduced water residence time in the estuary, likely affecting prey availability to fish and invertebrate predators. Given that peak river discharge in snowmelt-dominated basins occurs during the relatively short spring-summer growing season, the impacts of channelization on zooplankton production in the estuaries of snowmelt-dominated basins may be greater than in river-dominated estuaries subjected to different flow regimes.

2.1 Introduction

Zooplankton are generally diverse, abundant, and central to pelagic coastal food webs. In estuaries, however, zooplankton density is typically dominated by only a few estuarine endemic copepod species, which follow a predictable spatial and seasonal progression that is guided by changes in temperature and salinity (Miller 1983, Kimmel 2011, Elliott & Whitfield 2011, David et al. 2016). This low species diversity makes overall zooplankton production in estuaries vulnerable to perturbations and suggests that the productivity of these systems will be highly variable (Odum 1953; Margalef 1969; Lehman and Tilman 2000). Snowmelt-dominated basins are expected to experience the greatest change in their hydrograph as a result of climate warming (Nijssen et al. 2001), yet zooplankton dynamics in their estuaries have received little attention to date. Uncovering mechanisms controlling zooplankton production is instrumental to understanding the ability of these systems to support fisheries and to predicting their resilience to climate change and other anthropogenic pressures.

Snowmelt-dominated watersheds have been defined as having a peak in river discharge (often termed the freshet) that begins in late spring or early summer and a low flow period that persists from late summer until spring (Miller et al. 2014). At mid to high latitudes, estuarine zooplankton abundance typically peaks in spring and summer and snowmelt freshets thus occur during the period of highest potential zooplankton production (e.g. Escaravage and Soetaert 1993; David et al. 2006; Islam et al. 2006; Leandro et al. 2007; Bollens et al. 2011). Discharge during the freshet can be an order of magnitude greater than during the low flow period. The associated increase in advection can have a significant structuring effect on zooplankton in these estuaries because most estuarine taxa cannot thrive in fully marine waters (Ketchum 1954). With increases in global temperature, snowmelt and corresponding freshets are occurring earlier in the

year (Morrison et al. 2002, Stewart et al. 2004). The corresponding increase in water temperature, change in residence time, salinity, and mixing, and altered delivery of nutrients, sediments, and organic matter, are factors known to affect estuarine zooplankton (Vidal 1980, Ikeda 1985, Huntley & Lopez 1992, Schlacher & Wooldridge 1996, Livingston et al. 1997, Gillanders & Kingsford 2002, Vincent et al. 2002, Kimmerer 2002, Chiba et al. 2015). To date, however, we do not have sufficient knowledge of zooplankton dynamics in the estuaries of snowmelt-dominated basins to predict the effect of changes in the timing of snowmelt on estuarine zooplankton production.

The Fraser River, an undammed, snowmelt-dominated river on the west coast of Canada, is a major producer of sockeye, Chinook, coho, chum, and pink salmon in addition to supporting numerous other fish species including eulachon, herring, and Dungeness crab (Northcote and Larkin 1989; Department of Fisheries and Oceans 1998). Despite the importance of estuarine habitat to many fish, including salmon (Healey 1982, Bottom et al. 2005), and the importance of zooplankton to the diets of fish and larger invertebrates (Runge 1988, Moyle 2008, Strydom et al. 2014), to date there has only been a single study of zooplankton distribution in the Fraser River Estuary (FRE) and zooplankton dynamics of the FRE have never been described (Northcote et al. 1976).

The Fraser River remains subject to a natural river flow regime, however, the physical character of the FRE has been greatly altered through extensive channelization, land reclamation, and diking to promote farming and shipping and to mitigate the risk of flooding. Prior to the 1860s, during peak flows freshwater entering the estuary spilled across a large delta, slowing its course prior to reaching the Strait of Georgia. Dredging of the estuarine channels and removal of an estimated 99.9% of the floodplain (Butler & Campbell 1988) has increased the velocity of

water as it passes through the estuary and directly coupled water residence time in the estuary to river discharge.

This study aims to increase our understanding of what limits zooplankton production in the estuaries of snowmelt-dominated basins through description of copepod dynamics in the FRE in relation to environmental drivers, particularly temperature and river discharge. We focus on the Copepoda group because they typically dominate the zooplankton community in marine and estuarine environments (Miller 1983; Duggan et al. 2008). Here we present the results of zooplankton collections from 56 cruises that occurred over a 33-month period along the South Arm of the FRE. Our specific objectives are to 1) provide first descriptions of copepod abundance, biomass, and production for the FRE, 2) relate copepod dynamics to water column properties and river discharge, and 3) through comparison of dynamics in areas of the estuary that differ with respect to water residence time, specifically slough and channel areas, test the hypothesis that temperature and water residence time limit FRE copepod abundance, biomass, and production.

2.2   Materials and Methods

2.2.1   Study area

The Fraser River Estuary (FRE) receives considerable freshwater input and can be described as a river-dominated, salt wedge estuary. Originating in the Rocky Mountains, the Fraser River drains an area of approximately 217,000 km^2 and discharges an average 116 km^3 y^{-1} of freshwater into the Pacific Ocean via the estuary and the Strait of Georgia (Milliman 1980, wateroffice.ec.gc.ca). The estuary experiences a nearly natural volume of and variation in freshwater input because only ~3% of flow is removed and there are no dams on the mainstem of

the Fraser River (Church & McLean 1994). Discharge peaks during the snowmelt-dominated

freshet, often exceeding 8,000 m^3s^{-1}, and gradually declines over the late summer and autumn.

During high-flow periods, the salt wedge does not progress far inland of the tidal flats and all salt

is removed from the system during the greater ebb (Geyer and Farmer 1989; Kostaschuk and

Atwood 1990; Jay et al. 2007). Discharge is lowest in late winter and early spring. During this

period the estuary is partially mixed and salinity can intrude 30 km upstream (Kostaschuk &

Atwood 1990). On one occasion during this monitoring program, when discharge was < 700

m^3s^{-1}, we observed the salt wedge beyond the head of the delta at 49°12.099 N, 122°54.360 W,

approximately 35 km upstream from the Strait of Georgia. Residence times in the main

navigational channel of the South Arm of the estuary are estimated between 6 and 30 hrs and are

river discharge dependent (Ages & Woollard 1988). Tides are mixed diurnal and semidiurnal

with an average range of 3.1 m near the mouth (Kostaschuk 2002, Jay et al. 2007). Tidal

influence extends 75 – 120 km upriver, depending on river discharge (Thomson 1981).

The FRE delta consists of 4 main channels: South, North, and Middle Arms, and Canoe

Passage (Figure 2.1). Our sampling points were located along the South (Main) Arm of the FRE,

which discharges ~75% of total river outflow and acts as the main navigational channel. The

South Arm of the estuary is dredged to maintain a minimum navigable depth of 11.5 m

(portvancouver.com). Side channels and sloughs are also dredged and depths vary from

approximately 5 m to 15 m. During the first year of our study, we sampled 3 locations in the

inner part of the estuary (Deas Slough (S1), the confluence of Sea Reach and Canoe Passage

(C2), and Cannery Channel (C3)), one location in the river, and one in the Strait of Georgia

(Figure 2.1). During our second year of sampling, we added 2 sampling locations in the inner

estuary (in the main navigational channel (C1) and in Ladner Slough (S2)) and another in the

outer estuary along the Steveston Cut (C4) and halted sampling at the freshwater and marine stations. Data from the freshwater and marine stations are not presented in this paper. Sampling dates were selected within 3 days of neap tides and sampling was timed to coincide with a flooding tide.

2.2.2 Collection and processing methods

Depth profiles of salinity, temperature, turbidity, and fluorescence were collected to 1 m above bottom at each station, using an RBR Ltd. XR-620 CTD. These variables were binned by depth and summarized for each sample as water column minimum, maximum, and mean. Salinity stratification was obtained by subtracting minimum from maximum salinity. A Secchi depth measurement was taken. Two replicate water samples for chlorophyll biomass estimates were collected at the surface and filtered through Whatman GF/F filters. Filters were kept in the dark on ice until returning to the lab, where they were stored in the freezer until processing. Within one week of collection, pigments were extracted for 24 hours in 90% acetone and measured on a Turner Designs TD-700 fluorometer. Replicate chlorophyll values were averaged for statistical analyses.

Hydrometric data measured at Hope, B.C., were downloaded from the Government of Canada's wateroffice.ec.gc.ca. Mean daily discharge data were used to create two variables. Using a lag suggested by Kostaschuk and Atwood (1990), mean daily discharge from 2 days prior to our sample collection was used to estimate flow conditions during our sampling. To capture flushing flows that may have occurred between our cruise dates, we also calculated maximum daily discharge to have occurred in the previous 2 weeks.

Zooplankton were sampled by duplicate tows of a 0.5-m diameter, 2.5-m long, 100-µm mesh conical net and preserved immediately in 5% buffered formalin. Sampled volumes were measured using a flowmeter (General Oceanics Inc) mounted within the mouth of the net. At most stations, the net was towed obliquely from 2 m above bottom. At S2, the net was towed vertically from bottom due to space constraints and boat traffic. To correct for any difference in abundance due to tow angle, depth, and volume, we calculated the mean difference in abundance between 23 paired oblique and vertical tows (average filtered volumes 3.3 and 1.4 m^3, respectively) collected at S1 between January 2015 and May 2016. The mean difference (25%) was applied to reduce abundances estimated by the vertical tows at S2. All samples were collected during daylight hours.

Zooplankton were identified to the lowest taxonomic level possible under a dissecting microscope at 80x magnification. Identifications were confirmed through observation of dissected individuals under a light microscope. Adult calanoid and cyclopoid copepods were typically identified to species or genus and copepodites to genus or family. Copepod nauplii were counted but not identified beyond class. The primary taxonomic resources used were Gardner and Szabo (1982), Williamson and Reid (2001), and the websites https://copepodes.obs-banyuls.fr/en/ and https://www.glsc.usgs.gov/greatlakescopepods/. Harpacticoid copepods were not routinely identified beyond order, with exception of the most common (*Pseudobradya* spp.*, Coullana canadensis*), and the most distinctive (*Huntemannia jadensis*, *Microsetella* spp.) taxa. Based on the identifications made (e.g. *Leimia vaga*, *Tachidius discipes*), harpacticoid taxa, with exception of *Microsetella* spp., were assumed to be of estuarine origin. Calanoid and cyclopoid taxa were categorized as either freshwater, estuarine, or marine (Appendix A) based on the literature and through comparison of abundances to our marine and freshwater samples. Where

habitat could not be identified, either through lack of taxonomic detail or ambiguity (e.g. *Acartia* spp.), the taxon was not categorized.

Most zooplankton samples contained too many organisms to be counted in entirety so samples were typically diluted to a known volume and subsampled in 3 steps that targeted taxa of different relative abundances. First, small subsamples (2% of sample) were taken using a Stempel pipette and counted until > 200 individuals, excluding nauplii, had been identified and the subsample had been counted completely. This count was used to calculate abundances of the taxa with the highest relative abundances. Second, a larger subsample (~5-10% of initial sample) was counted for taxa that had low (< 20) counts in the initial subsamples. Finally, the remainder of the sample was scanned for rare and novel taxa. This final scan was biased towards large or conspicuous individuals. Abundances were calculated as individuals m^{-3} using filtered volumes calculated from flowmeter data.

2.2.3 Estimation of copepod biomass and production

Locally-derived estimates of individual biomass were available for most marine copepods and two of the estuarine harpacticoids sampled during this study. Specifically, dry weights (DW) of the brackish harpacticoids, *Pseudobradya* spp. and *Coullana canadensis*, were estimated in the Fraser River Estuary by Johnston (1981) and stage-specific DW for most marine copepods have been estimated in coastal British Columbian waters by Fisheries and Oceans Canada (Galbraith, pers. comm). Where local estimates were not available, literature estimates (Dumont et al. 1975, Hawkins & Evans 1979, Culver et al. 1985, Kankaala & Johansson 1986, Maier 1994, Conway 2006) of individual biomass, prosome length, or total length were used, except in the case of *Eurytemora affinis*, for which prosome length was measured directly. Most biomass

estimates were dry weight and were converted to µg C using the relationship presented in Wiebe (1988). Empirical relationships used to estimate individual biomass from prosome or total length were found in Dumont et al. (1975), Kankaala and Johansson (1986), Uye (1991), and Uye and Sano (1998), depending on the taxon. Where adult male length was not reported, it was assumed to be the same as that of the adult female. Copepod life cycles typically include 6 naupliar and 6 copepodid stages. Copepodites are subadult copepodid stages. During counting, copepodite stages were regularly separated into CI-V or CI-III and CIV-V. These were assigned the body weight values of CIII, CII, or CIV stages, respectively. Where estimates for these stages were not available, estimates were taken from the nearest stage for which they were available. For harpacticoid taxa, we were unable to find estimates of copepodite total length. Where copepodite stage CI-CV was indicated or was not specified, total length was assumed to be ¾ that of the adult female. Based on observations during counting, we believe that this length estimate is more accurate than assuming all individuals to be the size of adults. For further details of how copepod biomass was estimated see appendix B. Biomass of copepod eggs was ignored.

Copepod growth rates (g, d^{-1}) were estimated according to Hirst et al. (2003) using mean water column temperature (T, °C) and individual body weight (BW, µg C individual $^{-1}$) ,

$$g = \frac{a}{BW^b} 10^{\propto T}$$

where a = 0.0296 d^{-1} (µg C individual^{-1})^b,

b = 0.128,

and $\propto$ = 0.0345 (°C)$^{-1}$.

Production was calculated as a product of growth rate and biomass. Production was not estimated for 12 station-date combinations due to a lack of temperature data.

2.2.4   Statistical analyses

We investigated how the relationships of abundance and biomass of both total copepods (marine, estuarine, and freshwater copepodids + nauplii) and estuarine copepodids to river discharge and mean water column temperature varied between slough (S1, S2) and channel (C1-C4) stations. We repeated these analyses and restricted the response variables to abundance and biomass of estuarine copepodids, because these taxa are produced within the estuary, unlike marine and freshwater copepods who are primarily advected into the estuary from the Strait of Georgia and Fraser River, respectively. River discharge values used were the maximum average daily discharge that occurred in the 2 weeks prior to sample collection. Model selection and validation proceeded according to Zuur et al. (2009) using the nlme package (Pinheiro et al. 2019) in RStudio version 1.1.447 (RStudio Team 2016). Comparison of model AIC_c was used to test the inclusion of a variance covariate and a random effect (station) using restricted maximum likelihood (REML) estimation and to determine optimal model fixed structure using maximum likelihood estimation. The inclusion of a variance covariate (varIdent) that allowed variance to differ by station was included for all models except that for total copepod biomass. Station was included as a random effect in all models. For all models, all fixed effects and their interactions were retained based on AIC_c values. Parameters for final models were estimated using REML. For all models, the response variable was $\log_{10}$ transformed and model residuals met assumptions of homoscedasticity, normality, and independence. Variance explained by the final models was estimated using conditional and marginal R^2 calculated with the MuMIn package (Barton 2019) that is based on Nakagawa & Schielzeth (2013).

Nonmetric multidimensional scaling (NMS) ordination was used to investigate how copepod composition and abundance varied between samples and how that variation related to

environmental variation. To aid interpretability, rare taxa were grouped according to phylogeny and salinity preference (e.g. 'Marine calanoids' and 'Freshwater cyclopoids'). We did not have associated environmental data for 12 samples. These were excluded from the ordination. A species matrix with data for 238 samples and 38 copepod groups was ordinated using a Bray-Curtis distance measure. Copepod nauplii were not included in the species matrix. A second matrix containing corresponding environmental data (minimum, maximum, and water column averages of salinity, temperature, turbidity, and fluorescence, salinity stratification, measured chlorophyll a, day of the year, and two river discharge variables) was correlated to ordination axes. Ordination analysis were done using PC-ORD version 7.07 (McCune & Mefford 2018). Mean values of abundance, biomass, production, and of water column properties presented in this study were weighted to ensure that each year had equal influence on mean values, despite differing sampling effort between years. Because weighted means were used, standard errors were estimated using bootstrapping (1000 iterations).

2.3   Results

2.3.1   Environmental conditions

As an unregulated river, the annual hydrograph of the Fraser River can vary considerably from year to year. Our study encompassed a period of extreme values in river discharge. February through April 2015 was notable for record-breaking high river discharge that preceded record-breaking low summer river discharge. When compared to long term (1912 - 2014) statistics, discharge over our study period was far above average, typically exceeding the upper quartile of values for the period of February through May (Figure 2.2a). From mid-June through

mid-September, river discharge was lower than average, typically hovering near or below lower quartile values.

At our stations over the study period, water column average practical salinity was at a maximum in January and at a minimum in June. The water column at the most downstream station, C4 (the outer estuary location), was more saline than other stations as it was strongly influenced by marine waters year-round. Near freshwater (salinity < 1) conditions occurred at other stations during high river discharge. The period of near freshwater conditions was longest at C1, one of our most upstream stations, occurring from April to August. Though located a similar distance upstream, Deas Slough (S1), retained saline waters into June due to the presence of a sill. Average salinity was < 1 during May – June at S2 and C2 and during June at C3. With exception of spring months, channel stations were generally more saline than slough stations (Figure 2.2c).

Water column mean temperature in the estuary ranged between a low of ~ 5 °C in January and a high of ~ 20 °C in August (Figure 2.2d). Influence of marine waters moderated temperature variation at downstream stations (e.g. C4) resulting in average temperatures at channel stations being ~ 1 °C warmer in the winter and ~ 1 °C cooler in the summer than temperatures at slough stations.

Water column average chlorophyll *a* peaked in May and was generally elevated above winter levels (~ 0.3 µg l^{-1}) in the estuary from March – July at channels stations and February – August at slough stations. Light penetration (not shown) did not vary between slough and channel stations. It was typically lowest during the spring and early summer (~0.5 m) and greatest in winter (~1 m). Turbidity (not shown) also peaked towards the beginning of the freshet and tapered into winter.

2.3.2 Copepod abundance, biomass, and production

Copepods were the most abundant component of the sampled zooplankton, accounting for, on average, 79% of total zooplankton abundance. We present separate estimates of copepod abundance, biomass, and production, for channel and slough stations. Because there are few sloughs, estimates for channel stations were considered as representative for the estuary. Average annual total zooplankton and Copepoda abundance (inclusive of nauplii) in estuarine channels were $2,506 \pm 240$ ($\pm$SE) individuals m^{-3} and $2,005 \pm 214$ individuals m^{-3}, respectively. For comparison, average zooplankton abundance was an order of magnitude lower than that estimated for our marine station (~27,000 individuals m^{-3}) and approximately twice that estimated for our riverine station (~1200 individuals m^{-3}) during our first sampling year. Minimum copepod abundances at channel stations occurred April through June (~ 1,150 individuals m^{-3}) and peak abundances (~ 2,970 individuals m^{-3}) were observed in August and September (Figure 2.2e). This seasonality was evident for both copepodid and naupliar stages. Seasonal variation in biomass and production closely tracked abundance. Mean estimates of copepod biomass and production at channel stations were 702 ± 138 µg C m^{-3} and 60 ± 14 µg C m^{-3} day^{-1}, respectively.

Mean annual copepod abundance was much higher at slough stations ($11,905 \pm 3,606$ individuals m^{-3}) and seasonality was markedly different. Minimum abundances occurred in December (~ 850 individuals m^{-3}); densities peaked in September (~ 22,000 individuals m^{-3}) with a lower peak observed during April - May. Mean estimated copepod biomass and production at slough stations were $3,876 \pm 1,085$ µg C m^{-3} and 401 ± 138 µg C m^{-3} day^{-1}, respectively. As with channel station data, the seasonality of copepod biomass and production closely followed that of copepod abundance.

Results of our linear mixed effect models were largely similar (Table 2.1). In each case, the 3-way interaction term, discharge*temperature*station type was retained, indicating that there was an interaction between the effects of river discharge and temperature at one or both station types and that the interaction differed between station types. Total copepod abundance and biomass increased with temperature at both station types but the slopes at channel stations were much less positive than at slough stations (temperature*station type) (Figure 2.3). At slough stations, slopes decreased with increasing river discharge (discharge*temperature, where station type is slough). When the models were restricted to the abundance and biomass of estuarine copepodids, the positive effect of temperature on the response variable was stronger (i.e. the slope was more positive), as was the dampening effect of increased river discharge (i.e. the slope was more negative), and this interaction was significant in both channels and sloughs (Figure 2.3). The fixed effects retained in our models explained 54 – 60% of variation, depending on the response variable, and the full model (with random effects) accounted for 61 – 70% of variation (Table 2.1).

2.3.3   Community structure

The high copepod abundance at slough stations was attributed to estuarine copepods (Figure 2.4). In contrast, the copepod assemblage at channel stations had a much greater contribution of marine and freshwater taxa. The most abundant copepods in the estuary were *Eurytemora affinis, Diacyclops thomasi*, and *Pseudobradya* spp., but this was skewed by the high abundances seen in sloughs. When looking only at channel stations, the most abundant copepods were *Oithona similis*, *Paracalanus* spp., and diaptomid copepodites (primarily *Leptodiaptomus ashlandi* and *Skistodiaptomus oregonensis*). The copepod assemblage varied

seasonally. During winter and spring, until the onset of the freshet, the harpacticoid, *Pseudobradya* spp., was the most abundant taxon in sloughs. At channel stations, species composition was more variable but *Pseudobradya* spp. was frequently among the most abundant taxa along with diaptomid copepods, freshwater cyclopoids, and, at the outer estuary station (C4), *Oithona similis* (Appendix A). During the freshet, the copepod assemblage in the sloughs was dominated by *Diacyclops thomasi*. Densities of *D. thomasi* were much greater in the sloughs than at nearby channel stations where freshwater diaptomids were typically the most abundant (Appendix A). The abundance of freshwater diaptomids, conversely, did not differ between slough and channel stations. As peak flow decreased, *Eurytemora affinis* abundance increased in sloughs and typically dominated the slough copepod assemblage into autumn. The average summer-autumn abundance of *Eurytemora* spp. in sloughs was 4,064 individuals m^{-3} while, at channel stations in the inner estuary, it was only 47 individuals m^{-3}. At the outer estuary station (C4), *Eurytemora* spp. were virtually absent. The copepod assemblages at inner estuary channel stations during this period were most frequently dominated by either freshwater diaptomids, or the estuarine harpacticoid, *Pseudobradya* spp.

The NMS ordination explained 88.8% of the variation in copepod abundance and composition with 3 axes and a final stress of 13.5. The primary axis represented 53.2% of between sample variation and was driven by variation in the abundance of marine copepods, *Oithona similis* ($r = 0.847$), *Pseudocalanus* spp. ($r = 0.806$), Corycaeidae spp. ($r = 0.758$), *Paracalanus* spp. ($r = 0.718$), Oncaeidae ($r = 0.660$), *Microsetella* spp. ($r = 0.615$), *Oithona* spp. ($r = 0.499$), and taxa contained in our marine calanoid group ($r = 0.729$). This axis correlated strongly to mean water column salinity ($r = 0.823$, Appendix A) and separated samples collected

at station C4, where marine taxa dominated, and samples from slough stations (Figure 2.5), where marine taxa were infrequent.

The secondary axis represented 25.9% of between sample variation and was driven by variation in the abundance of estuarine copepods, specifically adults of *Eurytemora affinis* (r = -0.696), *Eurytemora* spp. copepodites (r = -0.807), *Pseudobradya* spp. (r = -0.592), *Coullana canadensis* (r = -0.590), and other harpacticoids (r = -0.592), and of the freshwater cyclopoid, *Diacyclops thomasi* (r = -0.626). No measured environmental variables correlated to this axis (Appendix A). Slough stations (S1 and S2) separated from channel stations along this axis (Figure 2.5).

Winter and spring samples separated from autumn and summer samples along the tertiary axis (not shown), which represented 9.7% of between sample variation. This axis was moderately correlated to water column average temperature (r = -0.594) and day of year (r^2 = -0.561). There was a moderate correlation (r = -0.621) between diaptomid calanoids and this axis.

2.4   Discussion

2.4.1   Abundance, biomass, and production

The zooplankton of the FRE differ from that of most other studied estuaries with respect to both average zooplankton abundance and seasonal dynamics of copepod abundance, biomass, and production. Given a mesh size of 100 μm, average annual total zooplankton abundance (2,506 ± 240 individuals m^{-3}) in channels of the FRE is on the low end of published values (Figure 2.6), which suggests that conditions are less favourable to zooplankton population growth in this estuary. Low abundances (approximately 1 individual m^{-3}) have been noted

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previously in the FRE by Northcote et al. (1976) who sampled the surface water drift fauna using a 350 μm mesh net. As is common for marine and estuarine environments (Miller 1983; Duggan et al. 2008), copepods dominated the sampled FRE zooplankton, accounting for 79% of total abundance. Copepodid abundance (~ 2,000 individuals m^{-3}) in the FRE channels was low in comparison to reported copepodid abundances in other estuaries, which (though often of a single species) frequently exceed 10,000 individuals m^{-3} and can even exceed 100,000 individuals m^{-3} (Haertel & Osterberg 1967, Heinle 1972, Escaravage & Soetaert 1995, Peitsch et al. 2000, Bollens et al. 2011). Though fewer in number than for abundance, literature estimates of copepod biomass and production (range 5.2 – 22.4 mg C m^{-3} and 1.18 – 5.2 mg C $m^{-3}d^{-1}$, respectively) were likewise greater than our estimates for channel areas of the FRE (Fulton 1984, Ambler et al. 1985, Mallin 1991, Kiørboe & Nielsen 1994, Escaravage & Soetaert 1995, Ara 2004, Leandro et al. 2007). While the above establishes that zooplankton abundance and copepod abundance, biomass, and production in the FRE were low in comparison to other estuaries in general, the lack of published studies makes it impossible to establish whether this is a feature common to the estuaries of snowmelt-dominated basins. Haertel (1969) reported abundances exceeding 10,000 individuals m^{-3} throughout most of the year in the Columbia River Estuary, however rivers within the snowmelt-dominated Columbia River Basin have been highly regulated and summer discharges dampened (Sullivan et al. 2001). Many of the estuaries that remain subject to snowmelt freshets occur at high latitudes and are studied only during summer. An exception is a 12-year study of the mesozooplankton of a large arctic estuary formed by the snowmelt-dominated Lena River (Abramova and Tuschling 2005). Mean mesozooplankton abundance (Feb – Oct) in the southeastern Laptev Sea was approximately 1,300 individuals m^{-3}

(Abramova and Tuschling 2005), which is lower than our estimates for the channels of the FRE, though the mesh size used for zooplankton collection is unclear.

Knowledge of seasonal copepod dynamics offers insight into what limits production in the FRE. In the channels of the FRE, estimated copepod abundance, biomass, and production were at their lowest during the late spring and peaked during the late summer (Figure 2.2e-g). Seasonal patterns of abundance, biomass, and production where minima occur during the spring are not typical in temperate estuaries (Escaravage & Soetaert 1993, David et al. 2006, Islam et al. 2006, Leandro et al. 2007, Bollens et al. 2011). These minima generally occur during winter, when low light and temperatures cause poor food and growth conditions. The coincidence of minimum copepod abundance with the freshet suggests that copepod populations were strongly limited by advective losses. At slough stations, copepod abundances were much higher and seasonal dynamics differed. While copepod abundance, biomass, and production decreased during the freshet, estimates remained much higher than the winter minima. Unlike at channel stations, during spring, copepod abundance at slough stations increased prior to the freshet (Figure 2.2e). A similar bi-modal peak in abundance occurs in the southeastern Laptev Sea, where the late May-June decrease in abundance has been attributed to displacement caused by peak discharge of the Lena River (Abramova and Tuschling 2005). Comparing species abundance, biomass, and composition between channel (lower residence time) and slough stations (higher residence time) allowed us to test our hypothesis that low residence time in the FRE limits potential zooplankton production. The results of our linear mixed effects model indicated that the positive effect of temperature on copepod population growth is decreased or completely negated during periods of high river discharge, particularly for estuarine copepods (Figures 2.4 & 2.5).

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Estuarine copepods employ a variety of methods to retain themselves in estuaries, such as remaining near bottom, undertaking tidal vertical migrations, and having short generation times (Ketchum 1954; Kimmerer et al. 1998; Ueda et al. 2004). Frequent flushing, however, can prevent the establishment of estuarine zooplankton (de Madariaga et al. 1992), and this appears to be the case in the channels of the FRE. Our ordination separated slough stations from channel stations along an axis driven by variation in the abundance of estuarine copepods (Axis 2, Figure 2.5). Indeed, the high abundances of copepods at slough stations can be attributed to the presence of estuarine endemic copepods, which dominated the copepod assemblage (Figure 2.4). Estuarine copepods represented a much smaller proportion of total copepods at channel stations, despite the availability of the appropriate temperature-salinity space. Somewhat analogous dynamics have been observed in the Illinois River system, where large differences in community composition between main channel and backwater habitats were ascribed to variable advective rates favouring taxa based on reproductive strategies and ability to feed in turbid and turbulent waters (Wahl et al. 2008).

In addition to reduced advective losses, copepods likely derive other benefits from the slough environment and we must consider alternative explanations for the differences in seasonal dynamics and abundance between slough and channel areas. Predation pressure, for example, could differ between slough and channel areas of the FRE. During our study, however, the density of invertebrate predators, such as the mysid *Neomysis americana* and the cladoceran *Leptodora kindti*, both predators of Copepoda, were higher in sloughs. Likewise, Birtwell et al. (1987a) found that Deas Slough (Station S1) supported higher densities of juvenile Sockeye salmon than did nearby channel areas. Another explanation for higher copepod abundances in sloughs is the improved feeding conditions that may also be linked to a longer water residence

time. During spring, chlorophyll *a* increased at both slough and channel stations, but that

increase was only accompanied by an increase in zooplankton in the sloughs. However,

chlorophyll *a* biomass was slightly higher in sloughs (Figure 2.2b) and reduced turbulence could

improve feeding of copepods (Visser et al. 2001, Saiz et al. 2003). While this may have

increased copepod abundance, it would not explain the difference in species composition

between slough and channel areas. The large difference in seasonal dynamics and overall

abundance and biomass, in conjunction with the large differences in species composition,

between slough and channel stations in the FRE strongly supports our hypothesis that residence

time is limiting copepod production in the FRE. Alternate hypotheses of improved feeding

conditions or lower predation in the sloughs which may explain differences in abundance and

biomass would not be expected to cause this difference in composition.

2.4.2   Copepod assemblage of the FRE

In the channels of the FRE, the copepod assemblage was dominated by a mix of marine

and freshwater taxa advected into the estuary via the salt intrusion and river flow, respectively.

Variation in species composition primarily correlated to salinity (Axis 1, Figure 2.5), which is

characteristic of an estuary that is limited by water residence time (Ketchum 1954). In the

sloughs, the copepod assemblage was similar to indigenous assemblages found in the upper areas

of other western North American estuaries, with abundant copepods being *Diacyclops thomasi*,

Eurytemora affinis, Coullana canadensis, and *Pseudobradya* spp. (Bollens et al. 2014,

Breckenridge et al. 2015). *D. thomasi*, though considered a freshwater species, reached higher

abundances in the sloughs than in the channels, despite the presence of brackish water,

suggesting autochthonous growth. *D. thomasi* has previously been reported to reach high abundance in areas of low salinity (Bollens et al. 2012).

While reaching high densities at slough stations, *E. affinis* was rarely collected at channel stations. *E. affinis* is a species complex (Lee 2000) that dominates the brackish region of temperate estuaries across North America and Europe (Haertel & Osterberg 1967, Sautour & Castel 1995, Lawrence et al. 2004) and is considered central to estuarine food webs (Simenstad et al. 1990, Winkler et al. 2003, Dauvin & Desroy 2005). *E. affinis* are known to vertically migrate and to produce resting eggs (Ban 1992, Morgan et al. 1997). In the Columbia River Estuary, another high discharge system, *E. affinis* is abundant and populations are retained through tidal vertical migration (Morgan et al. 1997). However, if employed, this strategy does not appear sufficient for retention in the channel areas of the FRE, perhaps due to the simpler and modified topography combined with greater river forcing relative to tidal prism noted by Jay et al. (2007). Indeed, depletion of the *E. affinis* population in the Columbia River Estuary has been recorded following periods of particularly high river discharge (Haertel and Osterberg, 1967). It is also notable that in the FRE, *E. affinis* abundance is highest in late summer, while in other estuaries, members of the *E. affinis* species complex typically peak in the spring (e.g. Haertel & Osterberg 1967, Heinle & Flemer 1975, Sautour & Castel 1995, Peitsch et al. 2000, Kimmel & Roman 2004, Lawrence et al. 2004, Devreker et al. 2010). *E. affinis* and its congener *E. americana* are present in FRE sloughs during the spring prior to the freshet, though at low (<1,000 individuals m^{-3}) abundances, possibly limited by low temperatures (McLaren & Corkett 1981, Ban 1994). *E. affinis* largely disappears as the water column warms and river discharge increases, likely due to the lack of suitable downstream habitat (i.e. an area of sufficient

residence time and appropriate salinity), and reappears in late summer as river discharge decreases.

Estuarine copepods dominate the zooplankton in the estuaries of the Ob, Yenisei, Lena (Russia), Mackenzie (Canada), and Columbia (USA) rivers, which suggests that the limitation of estuarine copepods by low water residence time that occurs in the FRE is not typical of snowmelt-dominated estuaries (Haertel and Osterberg 1967, Evans and Grainger 1980, Vinogradov et al. 1994, Abramova and Tuschling 2005). The Gulf of Ob and the Gulf of Yenisei have much longer residence times than the FRE, ranging from 140 to ~ 1000 days and from 11 to 156 days, respectively (Erlenkeuser et al. 2003). The main channel of the Columbia River Estuary is more comparable to the FRE, with residence times as low as 20 hours (Kärnä & Baptista 2016). The ability of the Columbia River Estuary to support dense populations of *E. affinis*, *C. canadensis*, and other estuarine zooplankton (Haertel & Osterberg 1967, Breckenridge et al. 2015) may be due to the presence of estuarine turbidity maxima (ETM; Jay et al. 2007) and extensive areas with higher water residence time adjacent to the main channel (Kärnä and Baptista 2016). ETM are important to the retention of estuarine copepods in the Columbia and other estuaries (Morgan et al. 1997, Roman et al. 2001, Winkler et al. 2003, Suzuki et al. 2013). Unlike in the Columbia River Estuary, the ETM of the FRE do not effectively retain particles during high river discharge (Jay et al. 2007).

In the FRE, estuarine copepods collected outside of sloughs were largely harpacticoids, which are often benthic or epibenthic. In a frequently flushed estuary in the Bay of Biscay, estuarine harpacticoid copepods were able to maintain their populations, while estuarine calanoid copepods could not (de Madariaga et al. 1992). In the FRE, epibenthic sled sampling in the tidal flats of the outer estuary has shown that they support populations of estuarine harpacticoid taxa

(Bravender et al. 1993). It appears that, as semiplanktonic meiofauna, harpacticoids in the FRE can exploit slow current velocities near the channel's bed to successfully retain their populations, though densities at channel stations (~230 individuals m^{-3}) were lower than what was sampled in sloughs (~1,535 individuals m^{-3}). Estuarine copepods which distribute themselves higher in the water column, such as *E. affinis*, were not abundant at channel stations and their limited presence may be due to individuals lost from backwater or slough environments.

A notable difference in the FRE copepod assemblage from other major port estuaries along the west coast of North America is the dearth of non-indigenous copepods. Despite significant propagule pressure (DiBacco et al. 2012), we detected only a single non-indigenous copepod species over the course of this study, a member of the genus *Oithona* tentatively identified as *Oithona davisae* based on its morphology. After first being recorded in 1963 in the San Francisco Bay Estuary, it has become one of the most abundant copepods in that estuary (Ferrari & Orsi 1984, Bollens et al. 2011). *O. davisae* was abundant in ballast water transported to Cherry Point, Washington, USA (Cordell et al. 2015), which is located less than 50 km south of the FRE mouth, and has also been recorded in ballast water immediately to the north in Vancouver Harbour (Levings et al. 2004). Cordell et al. (2015) reported that after not being found in samples from 2004, *O. davisae* was the most abundant copepod in samples collected in nearby Samish Bay, Washington, USA, in 2012. In the FRE, *O. davisae* typically occurred at abundances < 100 individuals m^{-3} (maximum 370 individuals m^{-3} at station S2) and peaked during autumn. In other port estuaries on the west coast of North America, i.e. the San Francisco Bay Estuary and the Columbia River Estuary, non-indigenous taxa now dominate the zooplankton during the warmest part of the year (Bollens et al. 2011, Breckenridge et al. 2015). The Asian copepods, *Pseudodiaptomus forbesi*, *Sinocalanus doerrii*, *Limnoithona tetraspina*,

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Tortanus dextrilobatus, and *Acartiella sinensis* are established in the oligohaline regions of these estuaries during warm months but were not found in the FRE over the course of our study. Colonization by non-indigenous copepod species may have been impeded by the low water residence time of the FRE. Indeed, Cordell et al. (1992) suggested that reduction of maximum Columbia River flows may have allowed the establishment of non-indigenous copepods in that estuary.

2.4.3   Implication for estuary management

Our study suggests that estuarine and river channelization may reduce zooplankton production in the estuaries of snowmelt-dominated systems, where peak river discharge occurs during the relatively short growing season. The coincidence of the minimum in copepod abundance with peak river discharge, the reduced abundances when compared to sloughs, and the restriction of estuarine copepods to sloughs support our hypothesis that copepod abundance, biomass, and production in the channels of the estuary are limited by low water residence time. Limitation by water residence time is common in Canadian river systems (Basu and Pick 1992) and has been suggested for some other river-dominated estuaries such the sub-estuaries of Waquiot Bay, USA, and the Saco River Estuary, USA (Gupta et al. 1994; Lawrence et al. 2004). Of key consideration for the FRE, is that this limitation occurs during spring and early summer, which, due to increased temperatures and phytoplankton biomass, is typically the most productive time of year for copepods in temperate estuaries. Estuarine copepods dominated zooplankton assemblages in other studied snowmelt-dominated systems (Haertel & Osterberg 1967, Evans & Grainger 1980, Vinogradov et al. 1994, Abramova & Tuschling 2005), suggesting that their production is not limited by water residence time, at least not to the extent

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that occurs in the FRE. It is plausible that in the FRE, limitation of zooplankton production may have resulted from, or been exacerbated by, human modifications of the estuary. Any further deepening of the channels in the FRE would further shorten residence time, likely reducing estuarine zooplankton populations in the estuary. It can be postulated that prior to channelization of the FRE, when the channels were shallower (approx. 2.5 m total depth across the tidal flats (Clague et al. 1983)) and the floodplain intact, zooplankton production was much higher with resultant increased tertiary production of estuary-dependent fish, such as salmon, eulachon, and herring.

The results of our study raise the question of whether the current low-water residence times in the estuary have reduced salmon survival, above any losses caused by habitat reduction. Chinook, chum, coho, and sockeye salmon rear in the FRE (Levy & Northcote 1982, Birtwell et al. 1987a, Macdonald et al. 1990). Juvenile sockeye are planktivorous, juvenile coho prey upon zooplanktivores, and, the more commonly benthic diets of juvenile Chinook and juvenile chum can also be dominated by zooplankton or zooplanktivores (Dunford 1975, Healey 1982, Hillgruber & Zimmerman 2009, Osgood et al. 2016). Beamish et al. (1994) found that years with anomalously high indices of Chinook, coho, and, less strongly, chum production corresponded to years with anomalously low Fraser River discharges. High salmon production may have been the result of increased production within the estuary, rather than in the plume, as hypothesized by the authors, and could explain why this relationship was not seen for pink or sockeye salmon. Sockeye that rear in the estuary are in Deas Slough, where secondary production would be less influenced by year-to-year variation in river discharge, and pink salmon do not rear in the estuary (Healey 1982).

Slough environments, though rare in the FRE, appear particularly important as hot spots of zooplankton production. Backwaters have been previously noted as principal to the retention of estuarine zooplankton (Köpcke 2004). In addition to reduced advective losses and improved feeding conditions, reduced removal of the sediments would allow the development of an egg bank. Counter to this, zooplankton may face increased predation pressure in sloughs as invertebrate and fish predators may also benefit from the lower turbulence (Dower et al. 1997, MacKenzie & Kiørboe 2000, Saiz et al. 2003, Mahjoub et al. 2012). Previous studies have noted the importance of sloughs to juvenile salmon (Birtwell et al. 1987a, Miller & Simenstad 1997). In a study of Deas Slough (station S1) and surrounding areas in the FRE, Birtwell et al. (1987a) found that under-yearling sockeye salmon were in far greater abundance and in better condition in Deas Slough than in the nearby channel, Ladner Reach. *Diacyclops thomasi* (as *Cyclops bicuspidatus thomasi*) was one of the most important prey items by mass in their diet during residence in Deas Slough.

The strong effects of temperature and river discharge on zooplankton production in the FRE make this system sensitive to climate change. Currently, zooplankton abundance increases in channels only after the freshet. Peak river discharges are occurring increasingly early in the Fraser River and other snowmelt-dominated rivers due to early onset of snowmelt (Morrison et al. 2002; Stewart et al. 2004), which will result in the lengthening of the post-freshet growth season in their estuaries. Further study is needed to predict whether the resultant lengthening of the post-freshet growing season will result in greater summer pelagic production in estuarine channels and any broader effects on the estuarine ecosystem.

2.5 Tables

Table 2.1 Model coefficients by response variable. Significance levels denoted as *p < 0.05, **p≤ 0.001, ***p ≤ 0.0001. Model form – $Y_{ij} = \alpha + Discharge_{ij} + Temperature_{ij} + Station\ Type_j + Discharge_{ij}:Temperature_{ij} + Discharge_{ij}:Station\ Type_j + Temperature_{ij}:Station\ Type_j + Discharge_{ij}:Temperature_{ij}:Station\ Type_j + \varepsilon_{ij}$, where ':' represents an interaction between terms. Shared terms presented with 'channel' as base condition, which affects the sign of the slope. The marginal R^2 (R^2m) and conditional R^2 (R^2c) represent the variance explained by the model fixed effects and the full model (fixed + random effects), respectively. To save space, discharge is written as 'disch', temperature as 'temp', and station type as 'ST'.

	Log Copepod abundance	Log estuarine copepodid abundance	Log Copepod biomass	Log estuarine copepodid biomass
Channel				
Discharge (disch)	-6.4×10^{-5}	1.2×10^{-4}	-3.3×10^{-5}	1.4×10^{-4}
Temperature (temp)	3.0×10^{-1}*	8.8×10^{-2}***	4.6×10^{-2}***	9.2×10^{-2}***
Disch:Temp	-1.2×10^{-6}	-2.4×10^{-5}**	-5.2×10^{-6}	-2.5×10^{-5}**
Slough				
Disch	3.3×10^{-4}***	6.6×10^{-4}***	3.3×10^{-4}***	5.3×10^{-4}***
Temp	1.3×10^{-1}***	1.7×10^{-1}***	1.4×10^{-1}***	1.7×10^{-1}***
Disch:Temp	-2.7×10^{-5}***	-6.1×10^{-5}***	-2.8×10^{-5}***	-5.1×10^{-5}***
Shared terms				
Station type (ST)	-7.0×10^{-1}	8.8×10^{-2}	-5.1×10^{-1}	2.6×10^{-1}
Disch:ST	-3.9×10^{-4}***	-5.4×10^{-4}***	3.4×10^{-4}***	3.9×10^{-4}*
Temp:ST	-9.9×10^{-2}***	7.9×10^{-2}*	8.1×10^{-2}**	-7.4×10^{-2}*
Disch:Temp:ST	2.5×10^{-5}***	-3.7×10^{-5}**	-2.1×10^{-5}**	-2.6×10^{-5}*
R^2m	0.54	0.58	0.59	0.60
R^2c	0.61	0.68	0.68	0.70

2.6   Figures
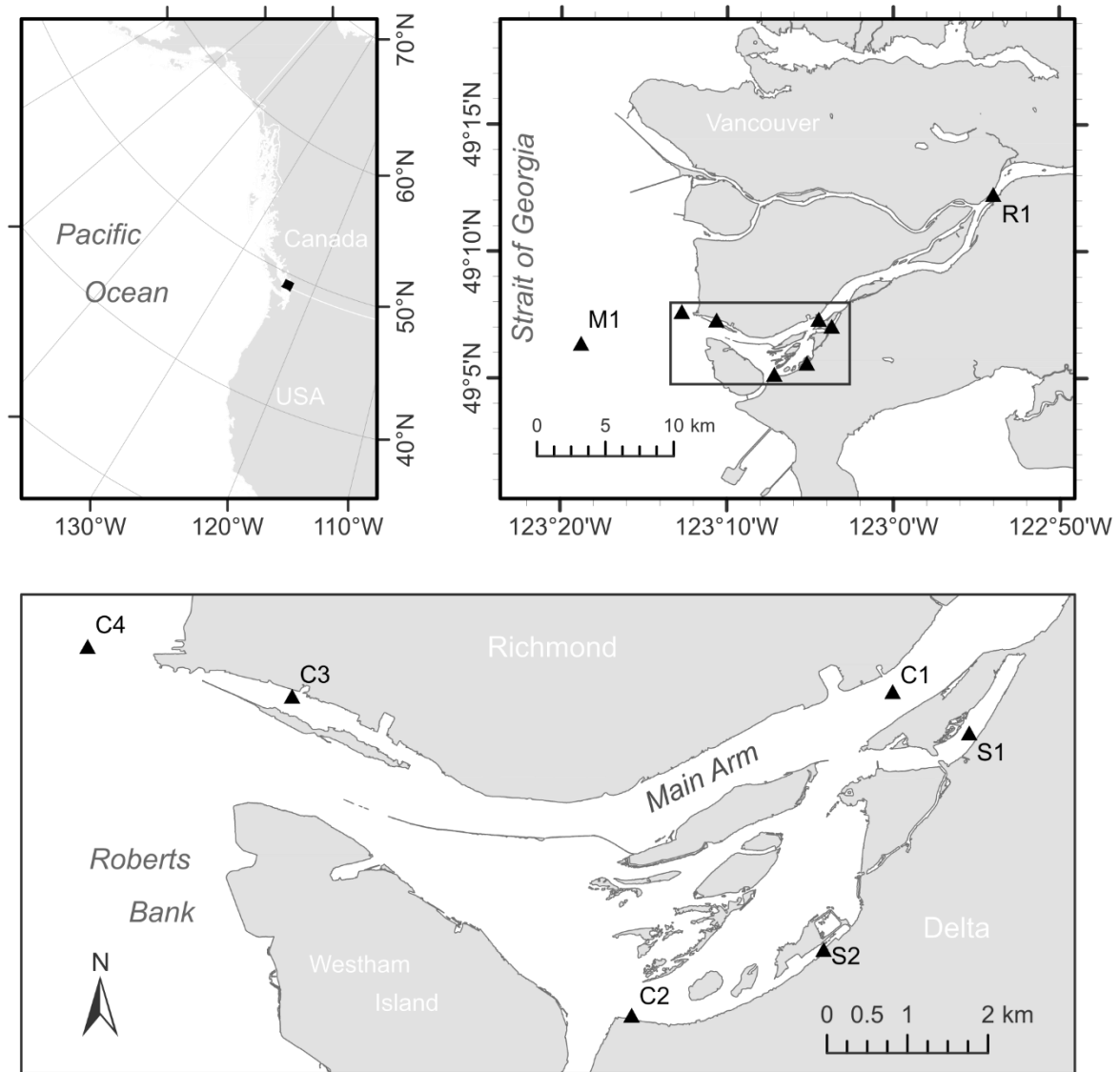
Figure 2.1 Map of study area (lower panel) within the Fraser River Estuary, Canada (upper right). Station locations are indicated with black triangles. Stations M1 and R1 were sampled only during the first year of the study (August 2013 – July 2014). Stations C1, C4, and S2 were added in the second year of sampling. Upper left panel indicates location of the Fraser River Estuary on the Pacific Coast of North America.
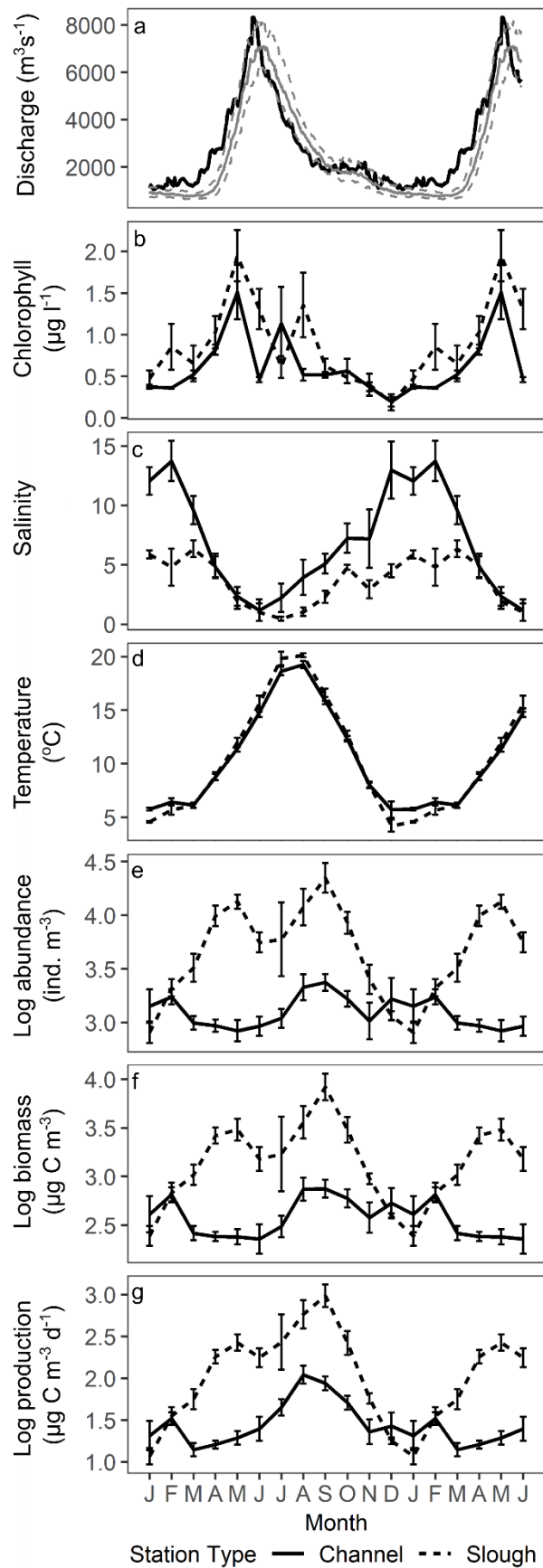
Figure 2.2 Mean annual variation for channel and slough stations from August 2013 – May 2016, in the Fraser River Estuary, B.C., Canada. Annual monthly averages have been extended over an 18-month period to improve interpretability. (a) River discharge (m^{-3}s^{-1}) measured at Hope, British Columbia, August 2013 – May 2017, plotted against long-term (1912 – 2014) discharge statistics (1st, 2nd, and 3rd quartiles) in gray. River discharge data from wateroffice.ec.gc.ca. (b) Water column average chlorophyll a (µg l^{-1}, from fluorescence), (c) Mean water column practical salinity, (d) mean water column temperature (°C), (e) estimated log copepod abundance (individuals m^{-3}), (f) log biomass (µg C m^{-3}), and (g) log production (µg C m^{-3} d^{-1}). Data for graphs B - G were weighted to ensure that each year had equal influence on mean values, despite differing sampling effort between years. Bootstrapping (1000 interactions) was used to estimate standard error because means were weighted
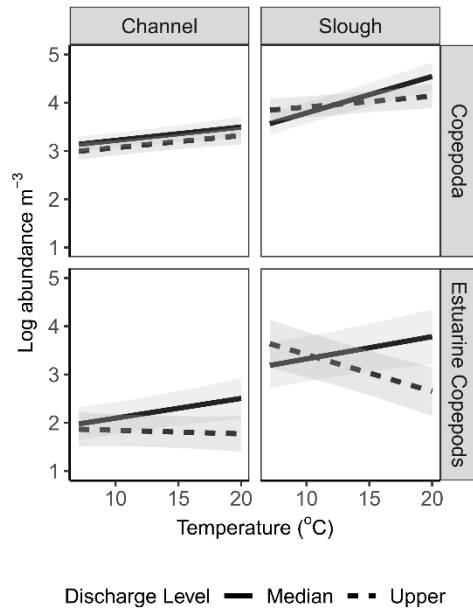
Figure 2.3 Predicted change in abundance (log individuals m^{-3}) of Copepoda (inclusive of nauplii) and estuarine copepodids with mean water column temperature (°C) by station type. Discharge levels approximate median and upper quartiles of long term (1912-2014) daily average discharge. Grey shaded areas represent 95% confidence intervals. Predictions have been generated for a restricted temperature range (7 – 21 °C) as high discharge conditions do not occur at cold temperature. The temperature range displayed reflects mean water temperatures that occur spring through autumn
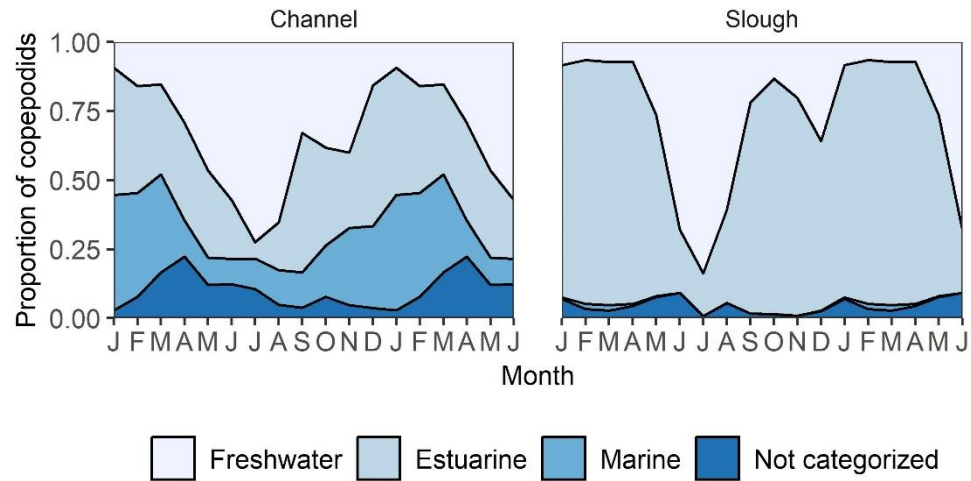
Figure 2.4 Mean proportional abundance of estuarine copepodids relative to that of freshwater, marine, and uncategorized copepodids at (a) channel and (b) slough sites. Proportions were weighted to account for unequal sampling effort in a month between years. Because the number of stations sampled increased over the course of the study, the first year of sampling has less influence on these means than subsequent years. Annual monthly averages have been extended over an 18-month period
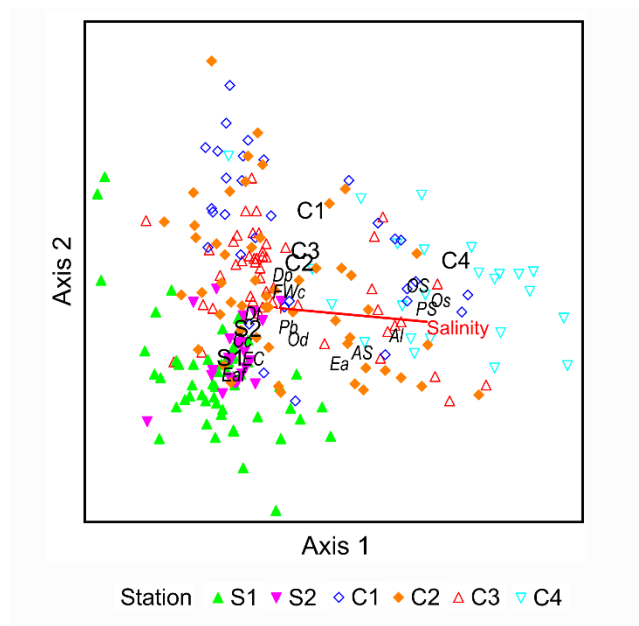
Figure 2.5 Ordination joint plot with environmental correlates, station and select species centroids overlaid on sample distribution across the two main axes. Centroid labels for stations C2 and C3 and for several taxa were partially overlapping and so have been shifted to improve legibility. Copepod groups included in overlay: Diaptomidae (Dp), freshwater cyclopoids (FWc), *Diacyclops thomasi* (Dt), *Pseudobradya* spp. (Pb), *Oithona davisae* (Od), *Coullana canadensis* (Cc), *Eurytemora affinis* adults (Eaf), *Eurytemora americana* adults (Ea), *Eurytemora* spp. copepodites (EC), *Acartia* spp. (AS), *Acartia longiremis* (Al), *Paracalanus* spp. (PS), *Oithona similis* (Os), Oncaeidae (OS)
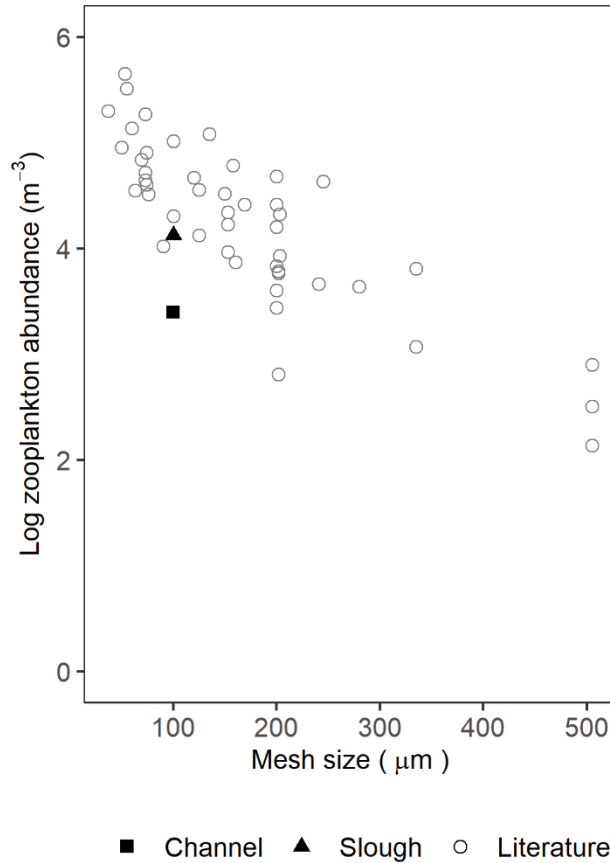
Figure 2.6 Mean log$_{10}$ zooplankton abundances for channel and slough area of the Fraser River Estuary, Canada, and from estuaries worldwide, by mesh size in μm, as reported in the literature. Where estimates are presented as monthly or seasonal averages, as ranges, or as surface and subsurface estimates, we present the average of those estimates. Where estimates are presented as night and day estimates, we used the daytime estimates. When presented graphically, abundance data were extracted using WebPlotDigitizer Version 4.2 (https://automeris.io/WebPlotDigitizer/). Mean annual total zooplankton abundance estimated for channel and slough areas of the Fraser River Estuary, Canada, are shown as solid symbols. Data sources: Haughton River Estuary, Australia (McKinnon and Klumpp 1998), Darwin Harbour[a], Australia (Duggan et al. 2008), the Schelde Estuary, Belgium and the Netherlands (Tackx 2004), Arcachon Estuary, France (Vincent et al. 2002), Ria de Aveiro, Portugal (Leandro et al. 2007), Mondego estuary, Portugal (Vieira et al. 2003), Mpenjati Estuary, South Africa (Kibirige & Perissinotto 2003), Rosetta (Nile River) Estuary, Egypt (Abo-Taleb 2014), Shatt Al-Basrah Canal, Iraq (Abbas 2015), Neuse River Estuary, USA (Mallin 1991; Mallin and Paerl 1994),

San Francisco Bay Estuary, USA (Bollens et al. 2011), Columbia River Estuary (Haertel et al. 1969), Peconic Bay, USA (Turner 1982), St. Andrews Bay, USA (Hopkins 1966), Tampa Bay, USA (Hopkins 1977), Pina estuary, Brazil (Eskinazi-Sant'Anna and Tundisi 1996), Taperaçu Estuary (Amazon), Brazil (Souza Júnior et al. 2013), Cananéia Lagoon Estuary[a], Brazil (Ara 2004), Phosphorescent Bay, Puerto Rico (Rios-Jara 1998), North Inlet, USA (Lonsdale and Coull 1977), Narragansett Bay, USA (Hulsizer 1976), Pensacola Bay, USA (Murrell and Lores, 2004), Long Island Sound, USA (Deevey 1956), Newport River Estuary, USA (Thayer et al. 1974), Pearl River Estuary, China (Tan et al. 2004; Li et al. 2006), Changjiang (Yangtze River) Estuary, China (Gao et al. 2008), Hangzhou Bay, China (Sun et al. 2016), Sergipe Estuary, Brazil (Araujo et al. 2008), Nueces Estuary, USA (Buskey 1993), Hii River Estuary, Japan (Uye et al. 2000), Jobos Bay, Puerto Rico (Youngbluth 1980), Navesink Estuary, USA (Knatz 1978), Sandy Hook Bay, USA (Sage & Herman 1972), Lower Delaware River Estuary, USA (Maurer et al. 1978), Senegal River Estuary, Senegal (Champalbert et al. 2007), Chikugo River Estuary and Ariake Bay[a], Japan (Islam et al. 2006), Cochin Backwater, India (Madhu et al. 2007), Punta Morales Estuary, Costa Rica (Brugnoli-Olivera et al. 2004), Chesapeake Bay, USA (Park & Marshall 2000), and the Bakkhali Estuary, Malaysia (Abu Hena et al. 2016)

[a]Copepoda abundance

Chapter 3: Spring resting egg production of the calanoid copepod *Eurytemora affinis* in the Fraser River Estuary

Seasonal peaks in river discharge, such as snowmelt-dominated freshets, are predictable events that can have a large effect on flushing rates and salinity in estuaries. Resting eggs, which many coastal and estuarine copepods are known to produce for overwintering or aestivation, could also serve to bridge predictable peaks in river discharge. To assess the timing of resting egg production of the egg-carrying estuarine copepod, *Eurytemora affinis* (Poppe), in relation to peak river discharge in the Fraser River Estuary, Canada, approximately 30 field-collected females were individually incubated on 12 occasions over the periods Feb – May 2015, Aug – Oct 2015, and Feb – May 2016. *E. affinis* abundance and population structure were investigated from vertical net tow samples collected twice monthly to monthly over the period Jan 2015 – May 2016. Eggs dropped from females primarily in May 2015 and May 2016 (6.5 and 9.2 eggs day^{-1}, respectively). *E. affinis* copepodids were present in the water column year-round and reached a minimum abundance in July 2015 of 8 individuals m^{-3}. At this time, the copepodid population was dominated by adults (86 %). Resting egg production in *E. affinis* is typically considered an overwintering mechanism but we suggest that the ultimate driver of resting egg production in this population is avoidance of flushing and/or low salinities.

3.1 Introduction

Estuarine endemic copepods face the persistent risk of advection from their required habitat (Ketchum 1954). These taxa typically cannot survive fully marine waters making the

consequences of advection from their estuary dire. These taxa live in an environment where net flow is out to sea, and yet, as plankton, they are unable to swim against a current. Nonetheless, estuarine endemic copepod species often reach high densities in this physically and chemically dynamic environment (Haertel & Osterberg 1967, Heinle 1972, Escaravage & Soetaert 1995, Peitsch et al. 2000, Bollens et al. 2011), exploiting abundant food resources and, in turn, being preyed upon by other invertebrates and planktivorous fish (Winkler et al. 2003, Strydom et al. 2014).

The influence of advection risk in the evolution of estuarine endemic copepod species is evidenced in the suite of traits they possess that increase the likelihood of retention. Most pointed are the many examples of these copepod species controlling their vertical position in the water column to avoid being flushed from the estuary, including engaging in active vertical migration with the tides (Hough & Naylor 1991, Kimmerer et al. 1998, Ueda et al. 2010, Chew et al. 2015), aggregation near bottom during floods (Ueda et al. 2004, Shang et al. 2008), and having an epibenthic distribution (Sibert 1981). Other traits that are common in estuarine endemic copepods that would promote retention include a short generation time (Miller 1983, Mauchline 1998) and possibly egg-carrying (Bayly 1964, Breckenridge et al. 2015). Some authors (Uye 1980, Runge & Simard 1990, Newton & Mitchell 1999) have suggested that benthic resting eggs could help estuarine-endemic copepod populations avoid flushing. This idea is very intuitive. Dormancy is the common evolutionary response to a variable environment for short-lived organisms (Caceres 1997) and dormant eggs in the sediment would allow pelagic species to bridge periods where losses due to flushing were greater than increases from reproduction. The production of benthic resting eggs appears common in estuarine copepods (Holm et al. 2018) and egg banks have been found in multiple estuaries (Marcus 1991, Marcus et al. 1994, Newton &

Mitchell 1999, Glippa et al. 2011). The stage is well set; however, we were unable to find any evidence in the literature in support of this hypothesis. When reported for estuaries, the production of resting eggs is instead most often considered a mechanism to avoid periods outside an organism's thermal tolerance (Holm et al. 2018).

Knowledge of the timing of resting egg production may provide some clue as to its adaptive significance. When dormancy occurs in avoidance of a predictable event, an optimal timing for the switch to resting egg production would be favoured over the continuous production of resting eggs (Hairston & Munns 1984, Hairston & Bohonak 1998), however, estuarine studies that investigate the timing of resting egg production under natural conditions are rare (but see Sullivan & McManus (1986)). Seasonal peaks in river discharge, such as those that occur in snowmelt-dominated systems, are predictable events that can have a large effect on flushing rates in estuaries. In the Hopkins River Estuary, Australia, river discharge peaks late winter-early spring and the salt wedge is flushed from the estuary for a period of 1-3 months (Newton & Mitchell 1999). Eggs from several abundant estuarine-endemic copepod species were hatched from estuarine sediments and the authors posited that these eggs likely served a role in retaining these populations (Newton & Mitchell 1999). Indeed, benthic resting stages could be expected to be of greatest benefit to populations in estuaries that experience periods of high flushing. In common with the Hopkins River Estuary, the Fraser River Estuary (FRE), Canada, experiences extended periods where salt wedge incursion is greatly reduced due to high river flow. The FRE is subject to scouring freshets that occur late spring-early summer with snowmelt. During this period the salt wedge incursion does not extend far beyond the tidal flats at the mouth of the estuary and all salt is removed from the system on the greater ebb (Kostaschuk & Atwood 1990, Jay et al. 2007). Low zooplankton densities and the restriction of estuarine species

to backwaters suggest that zooplankton production in the larger estuary is limited by low water residence time (Chapter 2; Breckenridge et al. 2020). That the FRE supports populations of estuarine endemic copepods, despite the freshwater conditions that prevail in the late spring and early summer (Chapter 2; Breckenridge et al.2020), suggests the availability of some refuge which allows for the retention of these populations. To my knowledge, production of resting eggs prior to a period of high river discharge and low water residence time has never been reported in the literature.

This study assesses the timing of resting egg production of the calanoid copepod *Eurytemora affinis* (Poppe) in relation to peak river discharge in the FRE. *E. affinis* is a species complex that occurs in estuaries throughout the Northern Hemisphere (Lee 2000) and often reaches very high densities (Heinle & Flemer 1975, Devreker et al. 2010). Resting egg production appears to be common in *E. affinis* (Johnson 1980, Ban 1992, Madhupratap et al. 1996, Marcus 1996, Glippa et al. 2011), though not necessarily ubiquitous (Choi & Kimmerer 2009), and is believed to occur in autumn as a mechanism to avoid winter conditions (Glippa et al. 2013, Holm et al. 2018). *E. affinis* are egg-carrying species and eggs are typically held until hatch (Mauchline 1998, Glippa et al. 2011). In the FRE, *E. affinis* abundance is at a minimum during the early summer, coincident with peak Fraser River discharge, and peaks in late summer and early autumn as discharge decreases (Chapter 2; Breckenridge et al. 2020). This annual pattern of abundance is in contrast to other estuarine systems where this species is at minimum abundance in the winter and peaks in the spring (Haertel & Osterberg 1967, Heinle & Flemer 1975, Sautour & Castel 1995, Peitsch et al. 2000, Kimmel & Roman 2004, Lawrence et al. 2004, Devreker et al. 2010). I hypothesized that *E. affinis* in the FRE produce resting eggs in the spring to avoid advection from the estuary. The aims of this paper are to 1) provide estimates of egg

production and release by *E. affinis* in the FRE, and 2) to interpret variation in egg release with respect to underlying patterns of abundance, population structure, and environmental conditions.

3.2   Materials and Methods

3.2.1   Study site

The FRE is classified as a moderately stratified or highly stratified salt wedge system, depending on river discharge and tidal range (Kostachuk and Atwood 1990). The Fraser River remains undammed leaving the estuary subject to an unmodified flow regime that is dominated by a snowmelt freshet that typically peaks mid-June (Morrison et al. 2002). During high river discharges typical of the freshet, all salt is flushed from the estuary on the greater ebb tide (Kostaschuk & Atwood 1990, Jay et al. 2007). Deas Slough was chosen as the collection site because *E. affinis* were found to be abundant at this location (Chapter 2, Breckenridge et al. 2020) and *Eurytemora* nauplii have been hatched from the sediments (Unpublished data). The slough is a former side channel that was dammed at the upstream end. The presence of a sill slows the loss of brackish water during the freshet. Oxygen levels in bottom waters decrease when the slough is cut off from the salt-wedge (Birtwell et al. 1987b).

3.2.2   Collection of individuals and water

Adult females of *E. affinis* were collected monthly during February 2015 – May 2015, August 2015 – October 2015, and February 2016 – May 2016 using gentle tows of a 1-m mouth, 100-µm conical net, and were diluted into a bucket with water from the collection site. Ambient water was obtained from the halocline depth (~5 m) and filtered through a 63-um mesh sieve

prior to use in incubations. Live specimens and water were kept in coolers and were returned to the lab within 2-3 hours.

3.2.3   Incubations

Zooplankton were sorted immediately upon return to the lab. Adult *E. affinis* females that were undamaged and displayed a level of activity were picked using a wide-mouth pipette under a stereomicroscope. I aimed for each set of incubations to include 30 females, though this number was reduced in some incubations due to insufficient collection of *E. affinis* and/or to mistaken incubation of the congener, *Eurytemora americana*. Females were rinsed and isolated using a welled Plexiglas® plate and the presence of eggs and spermatophores noted and their number estimated under a stereomicroscope.

Adult females of *E. affinis* were incubated individually in 250 ml Nalgene™ bottles filled with 63-µm pre-screened water collected from the sample site. Bottles were incubated in temperature-controlled rooms, where temperatures were set to approximate natural conditions (Table 3.1). Incubation durations ranged from 18 – 24 hours. At the end of the incubation, females were inspected to ensure that they were alive, filtered over a 20-µm sieve, along with the contents of the incubation bottle, and then preserved in 4% formalin. Upon processing, female prosome length and width were measured under a stereomicroscope, and clutches, if present, were removed and dissected to provide an accurate final clutch size (CS_f). On rare occasions, clutches contained 1-2 eggs that were degraded in appearance. These eggs were assumed to be nonviable and were not counted. Accompanying water was scanned and any *Eurytemora* nauplii, dropped eggs (DE), and egg casings enumerated.

I conducted additional incubations aimed at collecting live dropped eggs for further culturing on two dates. In May 2015, 6 ovigerous females were individually incubated and 5 CV females were incubated as a group with adult males to try to collect dropped eggs. In April 2016, 14 ovigerous females were incubated together in 500 ml of filtered estuarine water. Females were checked daily until they no longer held clutches (2-3 days) and then the incubation water was scanned via stereomicroscopy for dropped eggs and nauplii.

3.2.4   Estimation of daily EPR and resting egg production

A comparison of estimates of clutch size (CS) to counts of eggs in dissected clutches revealed that, for larger clutches, my estimation technique slightly underestimated the actual egg count. A corrective equation was calculated and applied, where CS_i = estimated CS/0.9676 - 0.3811. Estimates were perfect in clutches with fewer than 16 eggs. This correction adds less than 1 egg for clutch size estimates ≤ 40. Daily EPR was calculated as,

$$EPR = (CS_f + N_e + N_n - CS_i)\,/\Delta t$$

where N_e is the number of dropped eggs, N_n is the number of nauplii, and CS_f and CS_i are the final and initial clutch sizes, respectively. Negative EPRs were corrected to zero and, to be conservative in my estimates of dropped eggs, all missing progeny were assumed to be nauplii. Daily EPR was calculated as the average of individual EPR estimates, including those of females that did not produce eggs.

Dropped eggs could not be distinguished from subitaneous eggs via light microscopy, as was noted by Ban (1992) in his observations of subitaneous, diapause, and nonviable eggs of *E. affinis*.

3.2.5   Abundance and environmental data

Eurytemora spp. abundance and population structure at the study site were estimated as part of a larger zooplankton monitoring program through oblique (Aug 2013 – May 2016) tows from 2-m above bottom and replicate vertical tows (Jan 2015 – May 2016) using a 100 μm, 0.5-m diameter, conical net. The vertical tows, where the net mouth was lowered to the sediment, were added in the second year of sampling to avoid potential bias in the estimates of population structure and abundance due to vertical migration by *E. affinis*. Net tows were conducted during the day near high tide and were accompanied by casts of either an RBR XR-620 or a SeaBird SBE25 CTD and by collection of replicate surface water samples for chlorophyll analysis. Water samples were immediately filtered through Whatman GF/F filters, which were then kept on ice in the dark until returning to the lab, where they were stored in the freezer. Chlorophyll pigments were extracted for 24 hours in 90% acetone and measured on a Turner Designs TD-700 fluorometer. Chlorophyll processing occurred within one week of sample collection. Statistics for daily discharge for the Fraser River, as measured in Hope, B.C., Canada, were retrieved from Environment Canada at wateroffice.ec.gc.ca. *E. affinis* stages were identified according to Katona (1971) and Grice (1971). Samples with counts of fewer than 10 *Eurytemora* spp. were excluded from population structure statistics. Abundances of *E. affinis* may be overestimates due to the presence of *Eurytemora americana,* which is indistinguishable from *E. affinis* at younger

copepodid stages (CI-CIII). I expect that this bias is slight because when CIV-CVI *E. americana* are present (Nov - May), they are at much lower abundance than *E. affinis*.

The abundance of *E. affinis* nauplii was estimated for a subset of samples (May - Oct 2015) by examining nauplii at 1000x magnification. Forty to 60 individual nauplii were examined for most dates, though the number was far greater when *E. affinis* abundance was very low. Note that the mesh size was too large to provide accurate estimates of naupliar abundance. I therefore use these estimates only to get a rough idea of naupliar dynamics.

3.3   Results

3.3.1   Environmental conditions

The FRE experienced record-breaking high river discharge in spring 2015 (Fig 2B). Salinity at the collection site is typically stratified and the presence of a sill at the inlet retains salt in the slough even as river discharge increases. In 2015, salinity at depth began to decrease after mid-April, with most salt being flushed from the slough by mid-May (Fig 2G). The salt wedge again began to reach the slough in late July, as the freshet tapered. In 2016, the freshet began later and while average salinity again began to decrease in April, brackish bottom waters remained in the slough through the end of my monitoring in May 2016. Temperature at the collection site was relatively homogeneous, with typically less than a 1°C difference between surface and bottom waters. Average water temperatures at the collection site peaked in July and were at a minimum in winter and early spring (Fig 2F). Minimum *E. affinis* abundance coincided with the highest observed average water column temperature (20.8 °C) but increased rapidly while temperatures remained high. Temperatures were similar during both spring periods, and for the late April-May period where I observed dropping eggs, temperatures at the study site

ranged from 9.5 – 12.5 °C. Surface water chlorophyll was variable but generally elevated May through October (Fig 2H).

3.3.2   Resting egg production and daily EPR

I incubated a total of 335 *E. affinis* females on 12 dates. Dropped eggs were noted on multiple dates and their occurrence peaked in April 2016 and in May incubations of both years (Table 3.2). During this period, estimates of the rate of dropped eggs ranged between 1.7 – 9.2 female^{-1} day^{-1} (Fig 2A). In the May 2015 incubation, 87.5% of females with clutches at the onset of the incubation dropped eggs with one individual dropping 77 eggs. During the May 3, 2016, incubation, 72% of females with clutches dropped eggs with one individual dropping 63 eggs. Dropped eggs often remained loosely adhered to each other via secretions from within the clutch. Clutches often resulted in both nauplii and dropped eggs. Females that dropped eggs typically carried spermatophores and the proportion of incubated females with attached spermatophores was similar to or higher than those of incubations occurring at other times of the year (Table 3.2).

The production of eggs in the incubations was variable with the highest percentage of females (80%) extruding eggs during the March 2015 incubation and the lowest percentage (21%) during the 3 May 2016 incubation. My estimates of EPR ranged from a minimum of 1.5 eggs female^{-1} day^{-1} ($\pm$ 0.5 SE) in April of 2016 to a maximum of 24.4 eggs female^{-1} day^{-1} ($\pm$ 5.1 SE) in May 2015 (Fig 2A), both dates for which I recorded a relatively high number of dropped eggs (Fig 2E). EPR decreased in autumn and coincided with an observed decrease in average clutch size (Table 3.2).

The separate incubations to collect live resting eggs yielded only a single dropped egg and many nauplii. The egg was not monitored further. These incubations were flawed in that, while females were checked to determine whether they continued to carry eggs, no check was made for dropped eggs until the incubations were terminated a few days later. I therefore cannot exclude the possibility of dropped eggs that hatched before I terminated the incubation or the possibility that dropped eggs were cannibalized.

3.3.3 Abundance and population structure

E. affinis were present in the water column year-round in Deas Slough (Fig 2C). Comparison of paired vertical and oblique tows showed that while oblique tows estimated lower *Eurytemora* spp. abundance, patterns of abundance were comparable. Because depth distribution of *E. affinis* in Deas Slough may vary with developmental stage (Chapter 4), the results presented here are from the replicate vertical tows that sampled the full depth of the water column. In 2015, *E. affinis* copepodid abundance increased slowly to a low peak in mid-April (921 individuals $m^{-3} \pm 431$ SE), then decreased to a minimum on July 6 (8 individuals $m^{-3} \pm 3$ SE). Minimum abundances coincided with a copepodid population dominated by adults (Fig 2D). The highest abundance (35,155 individuals $m^{-3} \pm 9385$ SE) was recorded on August 20, 2015. Peak copepodid abundances, often exceeding 10,000 individuals m^{-3}, occurred August – November. In spring 2016, copepodid abundance was again low, with a peak abundance of ca. 1500 individuals m^{-3} recorded in mid-March.

Changes in naupliar abundance (underestimated and investigated only for the period of May – Oct 2015, as described above) tracked changes in copepodid abundance. For one of these

dates (6 July 2015), I examined 337 nauplii but did not observe any *E. affinis*, which suggests very low abundance for that date (< 8 individuals m^{-3}).

3.4   Discussion

The incubations revealed that *Eurytemora affinis* dropped eggs during the spring, as river discharge was increasing. *E. affinis* typically carry subitaneous eggs until hatch, which suggests that the eggs dopped during the incubations were resting eggs. If these eggs had been released in Deas Slough, they would have sunk to the oxygen-deplete environment that exists in its bottom waters after it is cut off from the salt wedge by the freshet (Birtwell et al. 1987b). Both burial in sediment and anoxic conditions have been shown to inhibit hatching (Uye 1980, Ban & Minoda 1992). The re-entry of the salt wedge as the freshet receded would have increased salinity and re-suspended the eggs, stimulating hatching. These nauplii may have contributed to the rapid increase in *E. affinis* that occurred in late summer.

Copepod resting eggs are typically categorized as being either quiescent or diapause (Uye 1985, Dahms 1995). Quiescent eggs are subitaneous eggs that become dormant in direct response to adverse conditions and will resume development immediately after the return of favourable conditions (Danks 1987). In contrast, diapause eggs are produced in anticipation of adverse conditions and undergo a refractory period before hatching. Because *E. affinis* were known to produce diapause eggs (Naess 1991, Ban 1992), I failed to consider the possibility of quiescent eggs or that dropped eggs would hatch during the incubations. The hatching of dropped eggs could explain the discrepancy when comparing the outcomes of the May 2015 and April 2016 EPR incubations, where nearly half of females dropped eggs (Table 3.2), and their concurrent, longer duration, incubations to collect live eggs, which yielded a single dropped egg

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and many nauplii. Glippa et al. (2014) have suggested that in the Seine estuary, France, *E. affinis* resting eggs may be either quiescent or diapausing. The disagreement between the two types of incubation in my study suggests that the dropped eggs may have been quiescent or delayed hatching eggs (diapause eggs with a short refractory period); however, a more rigorous investigation is warranted before categorizing these eggs as I cannot exclude the possibility of egg cannibalization.

The healthy appearance of dropped eggs, which were indistinguishable from subitaneous eggs, suggests that the dropped eggs were viable. Nonviable eggs have been noted to differ noticeably in appearance from viable eggs (Ban 1992). Further, while the extrusion of clutches of nonviable eggs has been observed under laboratory conditions in the absence of males (Katona 1975, Ban 1992, Glippa et al. 2013), the high percentage of females carrying spermatophores in the incubations suggests that females were not mate-limited (Table 3.2). Lasley-Rasher et al. (2014) suggested that carrying unfertilized eggs should be rare under natural conditions as egg-carrying increases the risk of predation for egg-brooding females (Hairston Jr. et al. 1983, Winfield & Townsend 1983, Svensson 1995).

An alternative purpose to the early release of clutches by egg-carrying copepods is provided by Koski et al. (2014), who suggest that this increases reproductive output by allowing females to produce the subsequent clutch more rapidly. They observed an abundance of loose clutches of the sac-spawner *Microsetella norvegica* in a Greenland fjord and inclusion of those loose clutches of eggs into EPR estimates was necessary to account for the high abundances of this species. During the present study, *E. affinis* eggs dropped during a period when overall EPR was relatively high and it is plausible that the time required for eggs to develop at observed temperatures (3-4 days) could limit their reproductive output. However, *E. affinis* population

structure shifted toward late stage copepodids following the period of dropping eggs, which is consistent with the eggs not hatching immediately following detachment. Given that the release of eggs occurred just prior to the seasonal collapse of the population, for these to remain subitaneous and hatch would suggest a large waste of reproductive effort.

E. affinis resting eggs are generally considered as an overwintering mechanism (Glippa et al. 2013, Holm et al. 2018); however, I was only able to find two studies which investigated the timing of resting egg production in the field. A freshwater population of *E. affinis* in Lake Ohnuma, Japan, produced diapause eggs in autumn (Ban & Minoda 1991 as cited in Ban 1992) in response to reduced photoperiod (Ban 1992). Based on the presence of eggs in the sediment and the seasonal pattern of abundance and population stage structure, *E. affinis* also produced diapause eggs for overwintering in the Baltic Sea (Katajisto et al. 1998). My results do not preclude the possibility of resting egg production in autumn or winter, however, the presence of a second, higher peak of *E. affinis* in the late summer and autumn suggests that springtime resting egg production by this population does not serve the purpose of overwintering. As *E. affinis* is a species complex (Lee 2000), within which optimal conditions and vital rates can vary significantly (Beyrend-Dur et al. 2009, Devreker et al. 2012), resting egg production could be expected to differ between clades or even between populations from differing estuaries (Glippa et al. 2013), as has been found for species of *Acartia* (Uye 1985, Avery 2005, Drillet et al. 2011). Springtime and summer resting egg production has been suggested previously for *E. affinis* in the Seine, based on the abundance of nauplii hatching from the sediment in the summer (Glippa et al. 2014). Springtime resting egg production in *E. affinis* has also been reported from a lab study where production of diapause eggs occurred in response to accumulation of their own metabolites, which may have served to avoid competition and resulting food shortage (Ban &

Minoda 1994). I consider crowding an unlikely cause of springtime resting egg production in the

FRE; however, as resting eggs were produced when copepodid densities were low, < 1200

individuals m^{-3}, in comparison to peak summer/autumn densities, which exceeded 30,000

individuals m^{-3}.

Springtime production of resting eggs is typically attributed to avoidance of high

temperatures and has been documented in many coastal calanoid copepods (Uye 1985, Sullivan

& McManus 1986, Chen & Marcus 1997, Castro-Longoria, E & Williams, J.A. 1999, Castellani

& Lucas 2003, Berasategui et al. 2012, Holm et al. 2018). During this study, the highest rate of

dropped eggs was observed when mean water temperatures were in the range of $11 - 12°C$. I do

not know the thermal tolerance of *E. affinis* in the FRE, but populations from other estuaries

have been raised at temperatures up to 25 °C (Heinle & Flemer 1975, Poli & Castel 1983).

Aestivation seems unlikely for *E. affinis* in the FRE given that the period of most rapid *E. affinis*

population growth coincided with the period of peak water temperatures (July/August). Predator

avoidance was the cited cause of springtime diapause egg production in the freshwater calanoid

copepod, *Diaptomus sanguineus* (Hairston Jr. et al. 1983). This study did not assess predator

abundance so I cannot exclude this possibility.

With respect to timing of resting egg production, the most proximate of 'catastrophes' is

the seasonal peak of river discharge, the freshet. The seasonal predictability of high river

discharge in snowmelt-dominated river basins would allow copepods to use correlated

environmental cues as a predictor of future adverse conditions (Dahms 1995). It has been

suggested that, in estuarine areas, benthic resting eggs could help endemic copepod populations

avoid flushing (Uye 1980, Runge & Simard 1990, Newton & Mitchell 1999). The estuary of the

Fraser River is fast-flowing, and residence times in the main channel have been estimated to be 6

– 30 hrs, depending on level of river discharge (Ages & Woollard 1988). During the freshet, the

salt-wedge is flushed from the estuary on a daily basis (Kostaschuk & Atwood 1990), which

means that, unlike in many other estuaries, there is no downstream refuge available to this

population during high river discharge. These conditions can be expected to pose great

challenges to an estuarine copepod, both with respect to position maintenance and

osmoregulation. Strong tidal vertical migration (TVM) behaviour in local *E. affinis* is evidence

that the threat of advection has shaped this population (Chapter 4). TVM is likely sufficient to

retain *E. affinis* in Deas Slough due to the sill; however, in the larger estuary this is likely not the

case given the increase in currents associated with the freshet. In areas where TVM is sufficient

for retention, *E. affinis* would still need to survive and develop in fully fresh waters. While *E.*

affinis has invaded freshwaters on multiple occasions (Lee 1999), *E. affinis* has not been found in

samples from freshwater stations in the FRE. The coincidence of resting egg production in this

population with the freshet, during a period when EPR was relatively high and conditions could

be considered as encouraging for growth (moderate temperatures, low population density,

relatively high chlorophyll; Figure 3.2), suggests that resting egg production may occur either in

anticipation of the low salinity and/or high current velocity conditions associated with the

freshet, or in direct response to conditions associated with the freshet.

  The present study did not attempt to identify cues for resting egg production; however,

two potential cues/triggers warrant mention. Hansen (2019) suggested low oxygen concentration

as a trigger for subitaneous eggs to enter quiescence. Low oxygen conditions exist in the bottom

waters of Deas Slough during the period of resting egg production (Birtwell et al. 1987b) and

female *E. affinis* have been shown to spend much of their time in bottom waters of the slough

(Chapter 4). Photoperiod, and photoperiod modified by temperature, are the most commonly

cited proximate cues of seasonal diapause egg production in calanoid copepods (Marcus 1980, Uye 1985, Hairston Jr & Kearns 1995, Baumgartner & Tarrant 2017, Takayama & Toda 2019, Hansen 2019) and reduced photoperiod has specifically been found to cue diapause egg production in *E. affinis* (Ban 1992, Glippa et al. 2013). While *E. affinis* in the FRE dropped resting eggs when photoperiod was increasing, perceived photoperiod may have decreased due to the rapid increase in suspended sediment that occurs at the beginning of the freshet (Kostaschuk et al. 1989). In this way, both reduction in photoperiod and decreasing oxygen in bottom waters could be reliable cues of increasing river discharge in Deas Slough. In the greater estuary, however, silled sloughs are rare and bottom waters would remain well-oxygenated throughout the freshet.

Understanding both the adaptive value of resting eggs and cues for their production is complicated by recent physical modifications made to the estuary. Our study was based in Deas Slough, a former side channel that was dammed in 1948, because *E. affinis* were largely restricted to slough environments (Breckenridge et al. 2020). It is therefore possible, given the flexibility of resting egg production (Glippa et al. 2013, Hansen 2019), that the occurrence and timing of resting egg production in Deas Slough differs from that in the larger estuary.

Given the extent to which modern river hydrographs have been altered through damming, water withdrawals, and changing climate (Haddeland et al. 2014), the possibility of estuarine copepods producing resting eggs for estuarine retention has important ramifications. Many estuaries no longer experience historical peak flows, and for others, such as the Fraser, the timing of peak flows is changing (Morrison et al. 2002). In this case, determining whether *E. affinis* resting eggs are quiescent or diapausing and understanding what cues their production is necessary to predict how the *E. affinis* population will respond to changes in the annual

hydrograph. If the eggs that are dropped are quiescent, this would suggest that the timing of production would shift with the hydrograph, whereas if they are diapausing, timing of production may be less flexible, which could result in reduced contributions to the egg bank with the early onset of the freshet.

3.5 Tables

Table 3.1 Summary of water column salinity and temperature (°C) during collection and incubation of

Eurytemora affinis **and incubation time (hours).**

| Date | Collection conditions | | Incubation conditions | | Incubation |
	Salinity range	Temperature range	Salinity	Temperature	Time (hrs)
2015-02-12	0.3 – 8.9	4.9 – 6.7	5.0	4	24
2015-03-17	0.6 – 9.5	6.7 – 7.5	8.8	4	24
2015-04-28	0.3 – 4.0	9.0 – 10.6	1.7	12.5	21
2015-05-12	0.1 – 0.4	11.8 – 13.2	0.3	12.5	23
2015-08-05	1.0 – 3.2	18.8 – 21.3	0.3	19	24
2015-09-03	0.1 – 7.8	16.8 – 18.2	5.2	19	21
2015-10-07	1.9 – 7.1	13.2 – 13.5	5	12.5	21
2016-02-17	0.3 – 14.7	5.8 – 6.5	5.5	12.5	22
2016-03-15	0.4 – 14.0	6.0 – 7.0	6.9	4	22
2016-04-20	0.2 – 13.4	7.5 – 11.8	9.5	12.5	22
2016-05-03	0.1 – 13.2	7.8 – 13.4	5.5	13	20
2016-05-17	0.1 – 13.0	8.4 – 14.0	5.2	13	18

Table 3.2 Summary of characteristics of incubated *Eurytemora affinis*. Number of females incubated (*N*), the percentage of incubated individuals that carried eggs (*F_{clutch}*) and had attached spermatophores (*F_{sperm}*) at the beginning of the incubation, mean clutch size (*CS* ± 1 SD), percentage of individuals that dropped eggs (*F_{drop}*), and the largest recorded egg drop (Max. drop).

Date	*N*	*F_{clutch}*	*CS_x* ± SD	*F_{sperm}*	*F_{drop}*	Max. drop
2015-02-12	40	67.5	29 ± 9	20.0	0.00	0
2015-03-17	10	80.0	36 ± 12	20.0	0.00	0
2015-04-28	29	72.4	44 ± 15	44.8	13.8	3
2015-05-12	30	53.3	47 ± 19	53.3	46.7	77
2015-08-05	30	85.7	39 ± 23	46.7	16.7	3
2015-09-03	29	79.3	11 ± 7	58.6	3.6	2
2015-10-07	29	65.5	6 ± 3	41.4	20.7	5
2016-02-17	29	63.0	45 ± 23	29.6	7.4	3
2016-03-15	20	70.0	40 ± 17	10.0	30.0	6
2016-04-20	27	74.1	27 ± 14	39.3	48.2	18
2016-05-03	30	63.3	61 ± 35	46.7	43.3	63
2016-05-17	30	50.0	39 ± 26	36.7	33.3	8

3.6   Figures
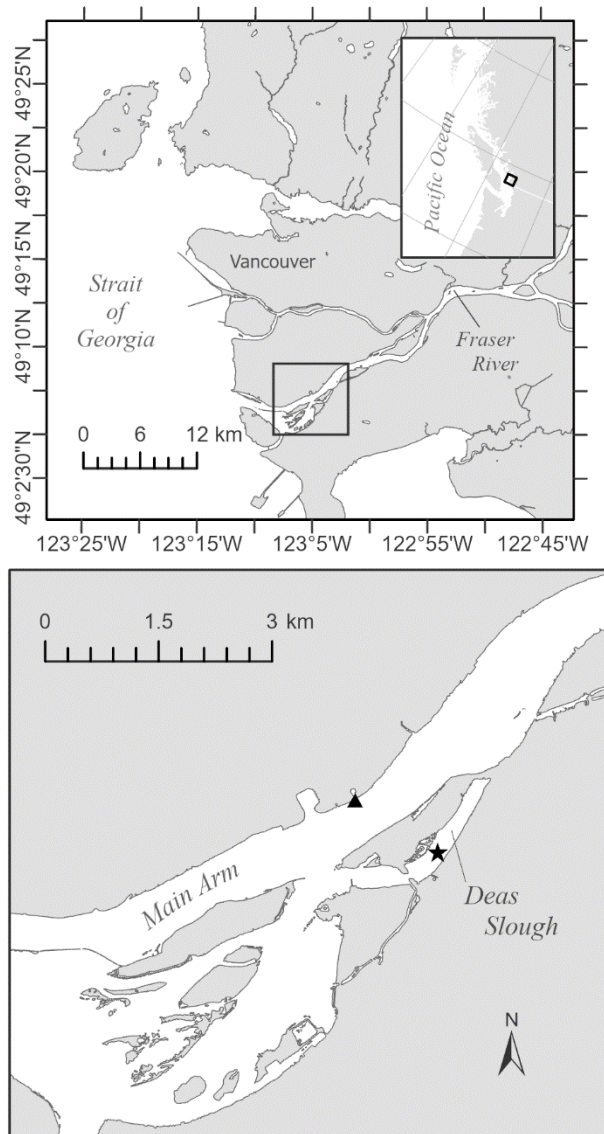
Figure 3.1 The Fraser River Estuary, Canada (upper panel). Station location is indicated by a black star and Environment Canada Station 08MH053 is indicated by the black triangle.
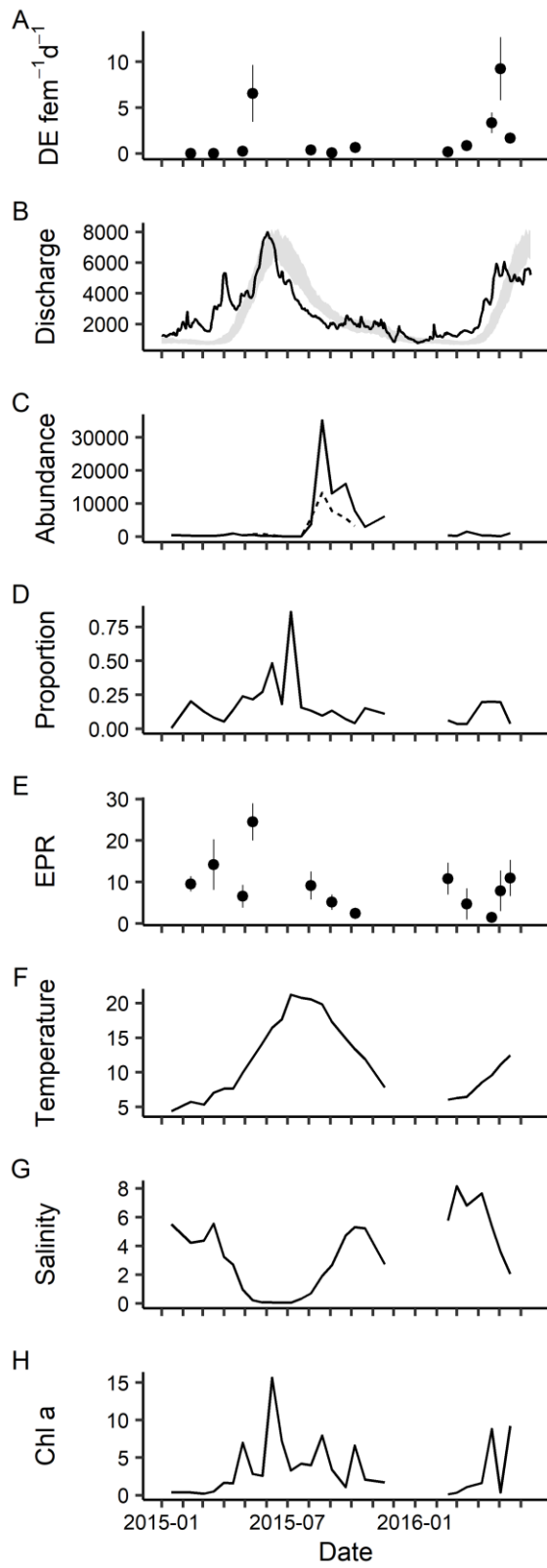
Figure 3.2 Average daily number of eggs dropped (± 1 SE) per *Eurytemora affinis* female (A) and environmental conditions over the study period (Feb 2015 – May 2016). (B) River discharge (m³ s⁻¹) for the Fraser River measured at Hope, B.C., presented with a band representing interquartile range of daily discharge values (1912 – 2014) using data retrieved from wateroffice.gc.ca. (C) Average abundance (individuals m⁻³) of *E. affinis* copepodids (solid line) and abundance of nauplii (dashed line) stages collected at Deas Slough in the Fraser River Estuary, B.C., Jan 2015 – May 2016 and May 2015 – Oct 2015, respectively, and (D) proportion of copepodids that were adult. Note that naupliar abundance is underestimated and is presented to give an indication of dynamics only. (E) Estimated daily egg production rate (EPR ± 1 SE) of *E. affinis*. (F) Water column average temperature (°C) and (G) salinity, and (H) surface water chlorophyll *a* concentration (mg m⁻³) at Deas Slough in the Fraser River Estuary, B.C. for 2015. There were no cruises in December 2015 or January 2016.

Chapter 4: Vertical distribution of Deas Slough copepods with emphasis on *Eurytemora affinis*

In Chapter 2, I attributed low pelagic secondary production in the Fraser River Estuary (FRE), Canada, to rapid flushing. Many estuarine taxa use tidal vertical migration (TVM) to avoid advection from estuaries. Here I report on the vertical distribution of the estuarine calanoid copepod, *Eurytemora affinis* (Poppe), in a sheltered slough of the FRE and contrast its distribution to that of non-resident copepods (*Diacyclops thomasi,* Diaptomidae, *Ditrichocorycaeus anglicus,* and *Paracalanus* spp.), and estuarine harpacticoids (*Coullana canadensis* and *Pseudobradya* spp.). Samples were collected at one meter intervals at a fixed station, from surface to bottom, over the course of two 24 hr stations. During both events, *E. affinis* were distributed deeper in the water column near mid-ebb and shallower near slack and on flood tides, particularly at night. The lack of relationship between either the abundance or vertical distribution of *E. affinis* and turbidity, together with the substantial difference in *E. affinis* distribution from that of most non-resident copepods, suggests that variation in their distribution was due to active TVM rather than hydrodynamic processes. A linear regression model including change in water depth and diel phase explained 63% of the variation in *E. affinis* weighted mean depth ($F_{(3,14)} = 10.71$, $p < 0.001$, adjusted $R^2 = 0.63$). That light suppressed tidal migration behaviours in *E. affinis* suggests that selective pressure from visual predators is strong in the FRE, despite high turbidity. While these results come from a sheltered slough location, they provide evidence that *E. affinis* in the FRE possess retentive TVM behaviour. Given the near absence of *E. affinis* in the more rapidly flushing channel areas of this estuary, I suggest that TVM is insufficient for retention in channels of the FRE.

4.1 Introduction

Modelling the dynamics of plankton populations that are influenced by advection requires knowledge of their vertical distribution (Aksnes et al. 1997). Pelagic environments vary with depth and thus vertical distribution of a population can influence advection rates, growth and reproduction conditions, and degree of interaction with predators and competitors (Hays 2003, Williamson et al. 2011). This is particularly true of stratified estuaries, where there can be large variation in the speed and direction of currents, as well as salinity and temperature, with depth. Zooplankton communities in estuaries are often composed of a mixture of freshwater, marine, and estuarine taxa, whose vertical distributions can be expected to differ based on salinity preference (Miller 1983).

True estuarine species require brackish waters for survival and so, unlike freshwater and marine taxa, are under substantial pressure to avoid advection from the estuary (Kimmerer & McKinnon 1987). Mechanisms for estuarine retention of plankton include a high enough reproductive rate to compensate for losses due to flushing (Ketchum 1954, Gupta et al. 1994), the production of resting eggs prior to periods of high flushing (Chapter 3), and passive residence in an area of particle accumulation, such as the estuarine turbidity maximum (ETM; Castel and Veiga, 1990). Because current speed and sometimes direction can vary with depth, retention can also be achieved through control of depth distribution, as evidenced by modelling studies (Simons et al. 2006, Kimmerer et al. 2014a). Examples of tidal vertical migration (TVM) come from estuaries and coastal areas worldwide (Kimmerer & McKinnon 1987, Laprise & Dodson 1989, Grioche et al. 2000, Ueda et al. 2010, Epifanio & Cohen 2016), and Kimmerer et al. (2014a) have suggested that tidal migration may be ubiquitous in estuarine zooplankton where net advection is seaward. In estuarine copepods, a range of vertical distributions and behaviours

adaptive to estuarine retention have been documented, including remaining near bottom where

current velocities are reduced (Sibert 1981, Ueda et al. 2004), attachment to the substrate (Shang

et al. 2008), remaining deeper in the water column during the ebbing tide and shallower on the

flooding tide (Xu et al. 2007, Ueda et al. 2010), and avoiding both ebb and flood currents by

migrating to surface waters only during periods of slack water (Wooldridge & Erasmus 1980,

Vineetha et al. 2015).

The Fraser River Estuary (FRE), on the Pacific coast of Canada, is a river-dominated

system where residence times have been estimated to be < 30 hrs (Ages & Woollard 1988).

Zooplankton abundances in the FRE are low in comparison to estuaries worldwide, though

substantial populations of estuarine copepods have been found in sheltered sloughs, where

residence time is presumably greater (Chapter 2; Breckenridge et al. 2020). The most abundant

estuarine copepod in the FRE is the brackish water calanoid, *Eurytemora affinis* (Poppe), a

species complex that is often judged as central to estuarine food webs of European and North

American estuaries (Simenstad et al. 1990, Sautour & Castel 1995, Lee 2000, Winkler et al.

2003, Dauvin & Desroy 2005). Reports of TVM behaviour in *E. affinis* have varied by estuary.

In the Columbia River (USA), northern San Francisco Bay (USA), and Conwy (UK) estuaries,

shallow flood tide distributions were attributed to active upward migration (Hough & Naylor

1991, Morgan et al. 1997, Kimmerer et al. 2002), whereas in the Gironde Estuary (France), and

the Chesapeake Bay (USA), hydrodynamic processes were sufficient to explain changes in the

vertical distribution of the species (Castel & Veiga 1990, Roman et al. 2001). In the estuary of

the Seine River, shallow distributions of *E. affinis* were attributed to passive resuspension with

subsequent descent hastened by active migration to the bottom waters (Devreker et al. 2008,

Schmitt et al. 2011). In the Nanaimo River Estuary (Canada), which neighbours the FRE, *E.*

affinis were found to maintain a close association to the bottom, regardless of tidal phase (Sibert 1981).

As part of a larger study to model potential changes in copepod abundance in the FRE, I described the vertical distributions of mesozooplankton over two mixed semidiurnal tidal cycles. Here I report on the vertical distribution of the estuarine-resident copepod, *E. affinis*, in the Fraser River Estuary and contrast its distribution to that of non-resident species. I hypothesized that *E. affinis* would migrate vertically with the tides in a manner that would promote retention (i.e., that they would have a deeper distribution on ebbing tides). Active migration can be difficult to distinguish from passive resuspension which may also result in shallower distributions on flooding tides (Castel & Veiga 1990, Morgan et al. 1997, Roman et al. 2001). To distinguish between these, I compare the vertical distributions of *E. affinis* to those of marine and freshwater copepods and to turbidity. Neritic species included in similar investigations have not been found to possess retentive tidal migration behaviour (Kimmerer & McKinnon 1987, Xu et al. 2007, Chew et al. 2015). As non-resident species in estuaries are unlikely to be subject to selective pressure promoting retention in estuaries (Kimmerer & McKinnon 1987), I assumed that they would not migrate actively with the tides. Any change, therefore, in the vertical distributions of non-resident species related to tides would alert us to the presence of other processes, such as resuspension, that might be affecting the distribution of *E. affinis*. Studies that collect samples from relatively few depths offer little information on migration amplitude and may document changes in abundances at the bottom without a corresponding change in the abundance near the surface, making it difficult to distinguish vertical migration from horizontal advection or predation losses. To address these limitations and allow more precise comparison of

vertical distributions of collected taxa, I focused on a high vertical resolution, taking samples from surface to bottom at one-meter intervals.

4.2 Materials and Methods

4.2.1 Study site description

The FRE is a deltaic, river-dominated, salt wedge system. River discharge peaks during the snowmelt-dominated freshet, which typically occurs in June and gradually declines over the late summer and autumn. Tides in the estuary are mixed semidiurnal and their influence extends 75 – 120 km upriver, depending on river discharge (Thomson 1981). Average tidal range near the mouth is 3.1 m (Kostaschuk 2002, Jay et al. 2007). Low zooplankton densities (~ 2,000 individuals m^{-3}) in estuarine channels have been linked to the low residence time (6 – 30 hrs) of the system (Ages & Woollard 1988, Breckenridge et al. 2020). Sampling occurred at a fixed station in Deas Slough (49°07.066 N, 123°03.735 W; Figure 4.1). The slough connects to the larger estuary via a shallow sill. Deas Slough has been found to support much greater densities of zooplankton than surrounding channel areas of the estuary (Breckenridge et al. 2020).

4.2.2 Collection and processing methods

Depth distributions of abundant Deas Slough zooplankton were studied during two cruises conducted 15 – 16 Sep 2014 (TCS1) and 29 – 30 Sep 2017 (TCS2). Both 24-hr stations were carried out over neap tides, with TCS1 coinciding with a three-quarter moon and TCS2 occurring 2 days after a quarter-moon. On both occasions, the *R/V Kraken* was anchored over the central, deeper, area of the slough. Fourteen vertical profiles of zooplankton samples were collected over TCS1 and 8 over TCS2, resulting in 133 and 71 samples, respectively. Vertical

profiles collected near high and low water were replicated during TCS1, by performing a second profile immediately following the first, resulting in a greater number of samples from this cruise. Vertical sample profiles consisted of depth-specific collections made every meter between the surface and bottom of the water column using a 0.5-m high, 31.25 litre, Schindler-Patalas trap with a 65 µm cod end. The design of the Schindler-Patalas trap allowed for sampling to occur directly on the bottom. Profiles took approximately 30 minutes to complete and included 7 – 11 samples, depending on the depth of the water column. Zooplankton samples were preserved immediately in 4% formalin.

CTD casts and total water depth measurements occurred every 1-2 hours over the sampling period. Different CTDs were used during the two cruises (RBR XR-620 for TCS1 and Sea-Bird SBE25 for TCS2). Salinity, temperature (°C), fluorescence (mg m^{-3}), and turbidity (in NTU during TCS1 and % beam transmission for TCS2) were measured. During TCS2, dissolved oxygen (ml l^{-1}) was also recorded. Because the CTDs were not intercalibrated, I made no comparison of fluorescence or turbidity between cruises. Change in water level over the course of the cruises was calculated by calibration of water depth measurements to river stage (wateroffice.ec.ga.ca), which was recorded at 5-minute intervals at the Deas Island Environment Canada station 08MH053 (49°07'27" N, 123°04'37" W; Figure 4.1). Tides were defined by change in water level with flood tides corresponding to periods of increasing water level and ebb tides to periods of decreasing water level.

Copepods were counted under a dissecting microscope at 80x magnification. To confirm identifications, individuals were dissected and observed under a light microscope. Copepodids of *E. affinis* were identified to developmental stage. Adults of other copepods were usually identified to genus or species and copepodites to family or genus. Among harpacticoid copepods,

only *Coullana canadensis* and *Pseudobradya* spp. were identified beyond order. Copepod

nauplii were not identified beyond class. Taxonomic resources included Gardner and Szabo

(1982), Williamson and Reid (2001), and the websites https://copepodes.obs-banyuls.fr/en/ and

https://www.glsc.usgs.gov/greatlakescopepods/. Most Schindler-Patalas trap zooplankton

samples were counted in entirety. Particularly dense samples were diluted to a known volume

and subsampled using a Stempel pipette. Subsamples were taken until > 200 individuals had

been identified and the final subsample had been counted completely. Depth-specific densities

were calculated as individuals m^{-3} using the volume of the Schindler-Patalas trap (31.25 l). Water

column abundances (individuals m^{-2}) were calculated by multiplying water column average

density by the height of the water column.

4.2.3   Statistical methods

Vertical distributions were compared using weighted mean depth (WMD; Bollens and

Frost, 1989),

$$WMD_t = \frac{\sum_{z=l}^{n} C_{zt} \times D_{zt}}{\sum_{z=l}^{n} C_{zt}},$$

$$RWMD_t = \frac{WMD}{Z_t},$$

where C_{zt} is the concentration (individuals m^{-3}) of the copepod taxon at depth, z, and time, t. D is

the depth of sampling, in meters above bottom, and Z is the total height of the water column. Use

of depth in meters above bottom causes WMD to describe distribution relative to the seafloor,

rather than to the surface and allows us to easily see how copepods are distributed in relation to

the slough's sill. Relative weighted mean depth (RWMD) was investigated in addition to WMD

because WMD is sensitive to changes in total water column depth and tides can cause water column depth to vary by > 30% in the system under investigation.

In addition to visual assessment of *E. affinis* vertical distribution, WMDs were analyzed in a linear mixed effects model including change in water level, as a proxy for tide, and diel phase as predictors and cruise as a random effect. During TCS1, sample profiles collected near the end of a tide were replicated 30-minutes later. Given that reported mean swimming speeds for *E. affinis* are ~1.6 – 4.5 mm s^{-1} (Mahjoub et al. 2011, Bradley et al. 2013, Michalec et al. 2013), I removed the replicate profile to ensure that the time between profiles was sufficient for *E. affinis* to traverse the water column. Thus, WMDs from 18 sample profiles were analyzed, 10 from TCS1 and 8 from TCS2. Change in water level was calculated over the 30-minute period prior to beginning the sample profile and sign of the change indicated whether water level was decreasing or increasing. Analyses were performed in RStudio version 1.1.447 (RStudio Team, 2016) using the nlme package (Pinheiro et al. 2019). Model selection and validation followed Zuur et al. (2009). Comparison of model corrected Akaike information criterion (AIC$_c$) values led us to exclude the random effect term and run a final linear regression model including only fixed effects. Variance explained by the model was estimated using the MuMIn package (Barton 2019), which calculates conditional and marginal R^2 based on Nakagawa & Schielzeth (2013).

Changes in vertical distribution can be caused by processes other than active vertical migration. Because resuspension can result in shallower distributions, for each cruise I correlated *E. affinis* WMD to both the WMD of turbidity and water column average turbidity using Spearman rank correlation. A sharp increase in turbidity typically occurs near the bottom so I excluded measurements deeper than the shallowest CTD cast (to 2.5 mab) to ensure that casts recorded to an equal height above bottom. If changes in *E. affinis* distribution were passive, I

also predicted that distributions of other small copepod species would vary in a similar manner. I assessed the similarity of distributions both visually and through Spearman rank correlation of WMD. Changes in vertical distribution may also occur as surface waters with differing zooplankton density are advected over more stationary bottom waters or because of differing predation rates with depth. To better determine whether changes in vertical distribution were the result of vertical migration, I monitored changes in *E. affinis* density in the bottom and uppermost 2 meters of the water column. In the case of vertical migration, any increase in zooplankton density in surface waters should correspond to decreased density in bottom waters.

Migration amplitude was calculated as the average change in WMD between the high tide and the long and short ebb tides. During TCS1, average WMD of the 2 vertical series taken near high tide was used. During both sampling events, I did not sample the long ebb that occurred prior to the diurnal high tide and so we used the WMD from the long ebb that would occur prior to the following day's high tide.

4.3   Results

4.3.1   Hydrography

Tidal magnitude was greater during TCS1 than during TCS2. Both series began on a diurnal flood tide that saw water height increase 2.5-m and 2.1-m, respectively. Total change in water height over the short ebb and short flood were 0.6-m and 0.2-m, respectively, during TCS2, compared to ~0.8-m for both tides during TCS1. The first samples collected in darkness occurred near high tide during TCS1 and near low tide during TCS2. Long ebbs during both series occurred at night, with water height dropping 2.4-m in TCS1 and 1.6-m during TCS2.

Water column conditions varied substantially between the two cruises. Reduced mean river discharge in the week prior to TCS2 (1320 m^3s^{-1} compared to 2035 m^3s^{-1} prior to TCS1) resulted in increased penetration of the salt wedge, a greater accumulation of saline waters, and increased stratification in Deas Slough, where a sill obstructs advection of bottom waters (Figures 4.2 & 4.3). During both cruises I recorded cooler, higher salinity water entering the slough on the lesser flood. This water remained at depth as warmer, fresher surface waters were advected over the greater ebb. Water temperatures were cooler during the second cruise, averaging 14.1 ± 0.5 °C, compared to 15.9 ± 0.3°C during TCS1. During TCS1, turbidity gradually decreased over the course of the cruise and its distribution appeared unrelated to salinity (Figure 4.2). The turbidity distribution during TCS2, conversely, largely followed that of salinity (Figure 4.3). Chlorophyll was concentrated near the surface over most of the cruise during both TCS1 and TCS2 (Figures 4.2 & 4.3). Dissolved oxygen concentrations were measured during the second cruise. Minimum readings (~2.5 ml l^{-1}) occurred near bottom during the lesser ebb (Figure 4.3). I have no measurements from the bottom meter of the water column during the long ebb and at lower low tide.

4.3.2   Community composition and abundance

The differing hydrography of the two cruises resulted in differences in the sampled copepod community. During TCS1, *E. affinis* and a freshwater cyclopoid copepod, *Diacyclops thomasi* (Forbes), were the most abundant copepods collected (Table 4.1, Figure 4.4). Freshwater diaptomid copepods (*Skistodiaptomus oregonensis* (Lilljebog) + *Leptodiaptomus ashlandi* (Marsh)) and two estuarine harpacticoid copepods (*Coullana canadensis* (Willey) and *Pseudobradya* spp.), which are considered primarily benthic, had much lower densities but were

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collected in sufficient numbers to allow estimation of their vertical distributions. These species were again present during TCS2, though abundances of the pelagic species were reduced (Figure 4.4). Increased marine influence during TCS2 resulted in the presence of marine copepods in the slough, particularly *Ditrichocorycaeus anglicus* (Lubbock) and *Paracalanus* spp. Water column total abundances (individuals m^{-2}) of *E. affinis* increased over the course of both the cruises, while abundances of Diaptomidae, *D. anglicus*, and *Paracalanus* spp. declined (Figure 4.4). Among benthic taxa, large differences in *Pseudobradya* spp. abundance m^{-2} were associated with diel phase (Figure 4.4).

4.3.3   Vertical distribution of pelagic copepods

During TCS1, pelagic copepods made full use of the water column. Highest densities of freshwater copepods (diaptomids and *D. thomasi*) occurred near bottom during the day. At night, coinciding with increased salinity in bottom waters, WMD of Diaptomidae was ~ 1.5-m shallower, with peak densities at approximately 5 meters above bottom (mab). *D. thomasi* remained concentrated near bottom except near the night high tide when their WMD was > 3-m shallower. *E. affinis* WMD varied considerably over the course of the cruise. Individuals were concentrated near bottom (~ 1.5 mab) during the mid-ebb profiles. From the diurnal ebb to the nocturnal high tide, the distribution of *E. affinis* shifted upwards, with the shallowest estimated distribution (~ 6.6 mab) occurring just prior to the night high tide. In the subsequent early-ebb profile, *E. affinis* were bimodally-distributed, with aggregations occurring near surface and near bottom. They were again concentrated near bottom during the mid-ebb profile (Figure 4.5).

During TCS2, salinity stratification was greater than during TCS1 and most non-estuarine copepod taxa segregated vertically in the water column according to salinity preference (Figure

4.5). Diaptomid copepods occurred in the upper half of the water column. Marine copepods remained in the more saline bottom waters but were slightly shallower during the night. Unlike diaptomids, *D. thomasi* was not restricted to surface waters and, as occurred during TCS1, densities were greatest near bottom during the day. At night, WMD was ~ 1-m shallower. *E. affinis* also occurred throughout the water column. A more even distribution than was seen during TCS1 resulted in reduced variation in WMD over the tidal cycle. *E. affinis* WMD was slightly shallower (~ 1.2-m) during the night low, night flood, and night high tide profiles than it was during diurnal profiles, and was deepest on the night ebb tide.

During neither cruise was variation in the vertical distribution of *E. affinis* strongly mirrored by other pelagic taxa (Figure 4.5). Spearman correlation of taxon WMD did reveal a weakly significant relationship between *E. affinis* WMD and WMD of *D. thomasi* during TCS1 (rho = 0.54, p = 0.04) that was driven by their common shallow distribution on the night high tide. More similarity in distribution was evident when comparing *E. affinis* distribution to that of estuarine harpacticoid taxa (Figure 4.5). *E. affinis* WMD was correlated to that of *C. canadensis* during both cruises (rho = 0.55, p = 0.04 for TCS1 and rho = 0.81, p = 0.01 for TCS2), though during TCS1 this relationship was driven by their shallow distribution on the night high tide.

4.3.4   Vertical distribution and abundance of benthic copepods

Pseudobradya spp. were collected throughout the water column during night profiles and the profiles which immediately preceded and followed night in TCS1 (Figure 4.5). During mid-day, they were largely absent from the samples and so I do not present WMD for these profiles. The shallowest distribution (WMD ~ 3.3 mab) and peak abundance m^{-2} occurred during the first profile after nightfall, which occurred near the high tide. Water column abundance was lower

during the following series, which occurred as the tide ebbed, and remained low for the remainder of TCS1. *C. canadensis* were collected throughout the water column in both day and night profiles (Figure 4.5). Like *Pseudobradya* spp., WMD was shallowest (~ 5 mab) near the nocturnal high tide but abundance m^{-2} peaked near both diurnal and nocturnal high tides. *C. canadensis* distribution was deepest during the day, with WMDs approximately 1.5 m deeper than those recorded during the night.

During TCS2, *Pseudobradya* spp. were concentrated immediately above bottom during the day, with abundance m^{-2} increasing in the profile immediately preceding sunset. WMD was again most shallow (4.7 mab) during the first series after nightfall, which on this cruise coincided with low tide (Figure 4.5). *Pseudobradya* spp. remained shallow over the flooding tide and were concentrated near bottom by the final night profile, which coincided with the ebbing tide. *C. canadensis* WMD was again at its shallowest (4.2 mab) during the night high tide profile (Figure 4.5). Its deepest distribution (1.3 mab) coincided with peak abundance m^{-2} and occurred on the diurnal ebb profile immediately preceding nightfall.

4.3.5   Vertical migration in *E. affinis*

The linear regression model was able to explain 63% of the variation in *E. affinis* WMD ($F_{(3,14)}$ = 10.71, p < 0.001, adjusted R^2 = 0.63). The effects of light (p = 0.001) and change in water depth (p > 0.05) interacted such that WMD became shallower with larger increases in water depth, but primarily at night (Day: 1.75 m ± 0.4 SE shallower, p = 0.001; Night: 8.90 m ± 3.2 SE shallower, p = 0.016; Figure 4.6). During model validation, one high leverage value (0.58) was identified where Cook's distance exceeded 3 times the mean Cook's distance. While excluding this value resulted in a better fit and reduced p-values for all terms, I ultimately

retained it in the model as it was a valid data point. Model residuals met assumptions of normality, homoscedasticity, independence, and linearity. While the multiple linear regression model provided an adequate fit to WMD data, I note that the response of WMD to change in water depth should be nonlinear as migration is bounded by the height of the water column (i.e. WMD would be expected to level off with larger increases or decreases in water height).

Vertical distributions of *E. affinis* varied in the manner I would predict in the presence of retentive TVM behaviour, with deepest distributions occurring near mid-ebb. During both cruises, WMD of *E. affinis* became shallower near the low tides, prior to the influx of higher density, saline water that occurred with the flood tides. This decrease in WMD of *E. affinis* was also not accompanied by an increase in mean water column turbidity or any change in the WMD of turbidity. For neither cruise did results of Spearman rank order correlations suggest a relationship between *E. affinis* WMD and turbidity ($p > 0.5$ for all tests). Shallow distributions that occurred near the nocturnal high tide were accompanied by increased *E. affinis* density in near surface waters and decreased density in bottom waters (Figure 4.7), further supporting that this change in WMD was the result of active vertical migration. The change in vertical distribution was greatest between ebb tides and the nocturnal lower high tide during both cruises, however amplitude of migration was greater during TCS1 (5.0-m versus 1.9-m). Separating the distributions by developmental stage revealed that migration amplitude over the nocturnal high tide generally increased with developmental stage during both cruises (Table 4.2, Figure 4.7). For all stages however, amplitude of migration during TCS1 was more than double that during TCS2.

4.3.6   Population structure of *E. affinis*

There was no evident effect of tidal or diel phase on population structure of *E. affinis*. There is some evidence that the distribution of early copepodites was shallower than that of later stages, but this difference was small in TCS1. Adult and CV stages made up a large percentage of total copepodid abundance during both cruises, averaging 63% and 49% of total abundance during TCS1 and TCS2, respectively. As noted above, preadult and adult *E. affinis* showed the strongest variation in WMD with the tidal cycle. WMD did not vary by sex and, among females, was not noticeably affected by ovigerity. No variation in the sex ratio (Female/Male) of either pre-adults (stage CV) or adults (CVI) or in ovigerity was detected with depth, tidal phase, or diel phase. Averaged over the cruises, the sex-ratio of CV *E. affinis* was near balanced (0.97 ± 0.05 SE during TCS1 and 0.94 ± 0.08 during TCS2). Adult sex-ratio was consistently male-biased (0.54 ± 0.05 SE during TCS1 and 0.48 ± 0.02 during TCS2).

4.4   Discussion

These results strongly suggest that *E. affinis* in the Fraser River Estuary migrated vertically with the tides and that this behaviour was modulated by light. During both cruises, *E. affinis* distribution was deepest during the vertical sample profiles that were collected near mid-ebb and, particularly at night, was shallower near slack and on flood tides. Eulerian studies of tidal migration require caution as apparent changes in vertical distribution may result from the horizontal advection of depth-varying zooplankton patches past the sampling point. However, advection is unlikely to explain increased flood tide densities in surface waters because the density of *E. affinis* outside of the slough is two orders of magnitude lower (Chapter 2; Breckenridge et al. 2020), and so incoming waters should have a dilutive effect on *E. affinis*.

That near surface increases in density corresponded to decreases in near bottom density provides further evidence that high near surface density was not the result of horizontal movement (Figure 4.7). It is also improbable that changes in *E. affinis* distribution were the result of resuspension, because distributions correlated to neither turbidity nor to distributions of other pelagic copepod taxa, with the exception of *D. thomasi* during the first cruise. These results suggest that changes in WMD were the result of active migration.

The high vertical resolution of samples, coupled with the relatively still waters of the sampling site, allowed us to record changes in *E. affinis* vertical distribution with greater precision than what has been reported previously (Castel & Veiga 1990, Hough & Naylor 1991, Morgan et al. 1997, Kimmerer et al. 2002, Schmitt et al. 2011). I observed an increase in migration amplitude with developmental stage and that the distribution of *E. affinis* was slightly shallower during diurnal flood tides than during diurnal ebb tides, which suggests that TVM continues to occur at reduced magnitude during daylight hours. Further, *E. affinis* became shallower between ebbing and low tides, which suggests that they began to ascend not with the flooding tide but with deceleration of ebbing tide, as suggested by Kimmerer et al. (2014a).

4.4.1   Variation in *E. affinis* vertical distribution with ontogeny

I observed a small increase in migration amplitude with development stage in *E. affinis* copepodids (Figure 4.7). Earlier developmental stages were generally shallower than later stages, except near the nocturnal high tide, when their WMDs were similar. During TCS2, TVM behaviour was only evident in CIII-CVI stages. To my knowledge, ontogenetic descent has been noted once before in tidally migrating copepods. In the Chikugo River Estuary, Japan, later stage *Pseudodiaptomus inopinus* and *Sinocalanus sinensis* typically had deeper distributions than early

stages during the day (Ueda et al. 2010). During my study, later stages had deeper distributions both day and night, but only during ebb tide profiles. Increasing amplitude of migration with ontogeny has been more frequently reported in dielly migrating species (Huntley & Brooks 1982, Lagergren et al. 2008, Holliland et al. 2012). Smaller copepods are generally considered to be at reduced risk to visual predators than larger/later stage copepods (De Robertis et al. 2000, Titelman & Fiksen 2004, Ueda et al. 2010). Maximizing growth may be prioritized in earlier copepodid stages, resulting in a shallower distribution (Clark 1994, Fiksen & Giske 1995). Indeed, improved feeding conditions near surface, where chlorophyll concentrations were greatest throughout both cruises (Figures 4.2 & 4.3) could promote more rapid growth and development and compensate for the greater risk of advection.

4.4.2 Variation in *E. affinis* vertical distribution between cruises

While I observed the same pattern of migration during both cruises, during TCS2 *E. affinis* distribution was more dispersed and migration amplitude was reduced. The weaker TVM observed in TCS2 is not fully explained by ontogenetic differences in TVM behaviour because reduced migration amplitude was observed in all developmental stages. Differences in swimming activity, either due to differing entrainment of endogenous circatidal swimming rhythms (Cronin 1982, Hough & Naylor 1992, Epifanio & Cohen 2016) or to salinity (Michalec et al. 2010), is a possible explanation. Tidal magnitude was lower in the days preceding and during TCS2, which could influence entrainment of endogenous circatidal swimming rhythms (Cronin 1982, Hough & Naylor 1992, Epifanio & Cohen 2016). Additionally, salinity was substantially higher during TCS2 and waters were cooler, both of which may have reduced copepod swimming activity (Larsen et al. 2008, Michalec et al. 2010).

4.4.3   Interaction of TVM and DVM

The present study adds to reports of TVM behaviour in *E. affinis* (Hough & Naylor 1991, Morgan et al. 1997, Kimmerer et al. 2002, Devreker et al. 2008, Schmitt et al. 2011) by showing that in the FRE the amplitude of migration is influenced by light. Interaction of TVM and DVM behaviour has been reported before in estuarine taxa (Kimmerer et al. 2002, Queiroga & Blanton 2004) and for copepods specifically (Ueda et al. 2010, Vineetha et al. 2015). During this study, *E. affinis* migrated upwards on the nocturnal flooding tide but the high vertical resolution of sampling also allowed us to record that *E. affinis* were shallower on the diurnal high tide than during the diurnal ebb. This result suggests that *E. affinis* in the FRE continue to migrate with the tide during the day, but at reduced amplitude. In the Chikugo River Estuary, Japan, the interaction was opposite, where *Sinocalanus sinensis* and *Pseudodiaptomus inopinus* remained shallow at night and underwent retentive TVM only during the day (Ueda et al. 2010). *E. affinis* has been reported to undergo DVM in the Baltic Sea, where residence time is on the order of decades (Vuorinen 1987, Döös et al. 2004, Holliland et al. 2012), but to my knowledge, this study is the first to report an interaction of TVM and DVM behaviours in this species complex. DVM in coastal environments is considered an adaptation to avoid visual predators (Bollens & Frost 1991, Hays 2003, Williamson et al. 2011). Lack of DVM in estuarine copepods has been attributed to reduced risk from visual predators due to high turbidity (Kimmerer et al. 2002, Schmitt et al. 2011) so its presence in *E. affinis* of the FRE suggests either higher pressure from visual predators or greater light penetration in this system (median 1.8-m estimated from our monitoring work in the South Arm of the estuary) than in systems where TVM has been reported in absence of DVM.

4.4.4   Comparison to distributions of non-resident copepods and benthic harpacticoids

E. affinis vertical distribution bore little resemblance to those of non-resident copepods, in agreement with previous comparisons of estuarine to neritic copepods (Kimmerer & McKinnon 1987, Xu et al. 2007, Chew et al. 2015). In comparing to non-resident copepods, I did not assume that they would act as passive particles, but rather that they would not possess behaviours adaptive to retention in estuaries. DVM is common in mesozooplankton and this behaviour has been reported in the non-resident copepods included in this study (Wells 1960, Ghan et al. 1998, Keister & Tuttle 2013, Scofield et al. 2020). Evidence of DVM was also observed in my study but, unlike *E. affinis*, distributions of non-resident copepods remained shallow over the nocturnal ebb, except for *D. thomasi* during the first cruise.

E. affinis distribution was more similar to that of collected harpacticoid taxa, whose habits were also suggestive of tidally-timed behaviour (Figure 4.5). While I did observe changes in their WMD that appeared related to tide, the relationships were weaker than what was seen in *E. affinis*. More evident were changes in their abundances that coincided with tide, and for *Pseudobradya* spp., their interaction with diel phase. My results suggest that *Pseudobradya* spp. emerged from the sediments near nightfall, migrated up through the water column, then returned to the sediments on the ebb tide. This pattern is evidenced in the brief peak in abundance that occurred during the first cruise, where ebb tide came early in the night, compared to the extended peak which occurred during the second cruise, where the ebb occurred later in the night (Figure 4.4). *Pseudobradya* spp. emergence from sediments has been reported previously (Sedlacek & Thistle 2006, Segelken-Voigt et al. 2018). In *C. canadensis* I see primarily the influence of tide on abundance, with peaks occurring near high tide (an exception during the second cruise being

due to a bottom sample of very high density). Light may have influenced vertical distribution during these peaks, with *C. canadensis* being closer to the surface on the nocturnal high tide than on the diurnal high tide, similar to what was observed for *E. affinis*. Morgan et al. (1997), who also employed meter-resolved sampling during some of their cruises in the Columbia River Estuary, concluded that *C. canadensis* was passively retained in that estuary's ETM. There, *C. canadensis* densities were consistently greatest in the bottom meter of the water column and their density was positively correlated to turbidity (Morgan et al. 1997). In the FRE, the average density of *C. canadensis* did not vary with turbidity and their distribution was not concentrated near bottom, particularly during the second cruise, where their abundance only peaked at the bottom during mid-ebb profiles. Like *E. affinis*, densities of *Pseudobradya* spp. and *C. canadensis* have been found to be much greater inside Deas Slough than in surrounding waters, so increases in abundance are unlikely the result of advection (Appendix A). Notably, these species made full use of the water column and their presence could not be explained by resuspension. Both *Pseudobradya* spp. and *C. canadensis* occur in intertidal sediments (Johnston 1981, Segelken-Voigt et al. 2018), where tidally-timed emergence would be particularly advantageous if these taxa have planktonic diets, as has been suggested for *C. canadensis* (Decho 1988, Pace & Carman 1996).

A large contrast in the distributions of estuarine and non-resident species occurred in their response to the strong halocline and wide range of salinities present during the second cruise. Diaptomids (which are freshwater copepods) and marine copepods segregated with respect to salinity preference. The halocline appeared to restrict DVM behaviour in these taxa. Distributions of *D. anglicus* and *Paracalanus* spp. became shallower at night (Figure 4.5) however these marine copepods remained below the halocline. Diaptomids remained in surface

waters, whereas during the first cruise, their vertical distribution showed evidence of DVM and individuals were distributed across the water column (Figure 4.5). These copepods may have been avoiding salinities outside their tolerated ranges or the density gradient may itself have been a barrier to vertical movement (Lougee et al. 2002, Woodson et al. 2005, 2007). In contrast, the estuarine copepods and *D. thomasi* were distributed across the water column. Woodson et al. (2005, 2007) investigated the response of 6 marine calanoid copepods and of *E. affinis* to gradients of velocity and density. *E. affinis* was the only species that routinely crossed the density gradient, which Woodson et al. (2007) attributed to adaptation to an estuarine environment.

The purpose of tidal vertical migration in estuarine holoplankton is retention. Given random vertical distributions, I would expect to see abundance (individuals m^{-2}) decrease as the volume of water in the slough decreased. It is notable that only where we observed vertical distribution to vary in the manner predicted for retentive TVM, did we see abundances hold steady or increase over the course of the cruises, both of which began near high water and ended near low water. *E. affinis* abundance did not decrease over either cruise and *D. thomasi* abundance did not decrease over the cruise where they appeared to migrate with the tide. Diaptomids, however, are likely the only copepods whose reductions in abundance were primarily due to advection. The presence of the sill would have blocked the advection of copepods in bottom waters and reductions in the abundances of marine copepods were likely primarily mortality due to salinity stress. The idea of estuaries as sinks for neritic zooplankton has been suggested previously (Soetaert & Herman 1994), and here regular inputs of dying marine copepods could represent an important contribution to the food web in the FRE.

Of the non-resident copepods sampled, only *D. thomasi* exhibited a change in distribution that appeared related to tide and the magnitude of that change (~ 3.5-m) was relatively large (Figure 4.5). The shallow WMD near the nocturnal high tide was accompanied by a decrease in *D. thomasi* density in bottom waters, which suggested that the increased density in surface waters was due to vertical migration. During the second cruise, I did not see evidence of TVM, but, like estuarine copepods, *D. thomasi* distribution was not restricted by the presence of a strong halocline. *D. thomasi* is one of the most abundant copepod taxa in the FRE, peaking during the early summer freshet when marine intrusion is minimal (Chapter 2; Breckenridge et al. 2020). Like the estuarine copepods, *D. thomasi* occurred in Deas Slough at much greater densities than in surrounding channel areas of the estuary (Appendix A) so I do not think that *D. thomasi* were imported with the flood tide. When considered in conjunction with these findings, these results suggest that *D. thomasi* in the FRE may be estuarine specialists. *D. thomasi* have been reported previously in saline lakes (Hammer 1993, Cooper & Wissel 2012) and their ability to diapause in sediments as late stage instars (McQueen 1969) may allow them to avoid high salinities.

4.4.5   Limitations of study

The lack of flow field data is a particular weakness for tidal vertical migration studies (Kimmerer et al. 2014a). I am, however, able to make some inferences on water movements from our CTD data during this study, along with knowledge gained from several years of environmental monitoring in Deas Slough. The presence of a sill, paired with the retention of saline bottom waters and reduction in dissolved oxygen that occurs when the slough is cut off from the salt wedge for extended periods (Birtwell et al. 1987b, Breckenridge et al. 2020),

allowed us to assume that near bottom vertical velocities on ebbing tides were negligible. On flooding tides during the study period, vertical velocities would be greater, as water of greater salinity crossed the sill and sank. I observed the resulting decrease in depth of the halocline during both cruises. This influx of higher density water could result in shallower distributions of copepods, however, during both of the cruises, *E. affinis* distributions became shallower prior to this influx, near the low tide.

Some studies have found that estuarine copepod species vary their vertical migration behaviour along the axis of the estuary (Hough & Naylor 1991, Xu et al. 2007, Ueda et al. 2010), while others have found that migration behaviour is rigid (Kimmerer et al. 2002). Because I sampled a single location on two cruises, I was not able to assess whether *E. affinis* vertical distribution varied with position in the estuary, but the cruises did sample markedly different salinity conditions (Figures 4.2 & 4.3). In the FRE, comparing the vertical distribution of *E. affinis* in sloughs to those in channel environments would also be of interest because of large differences in physical conditions between these two habitats (Breckenridge *et al.*, 2020; Chapter 2).

I cannot preclude the possibility of seasonal variation in vertical migration behaviour. *E. affinis* copepodids are present for most of the year, peaking twice – a low abundance spring peak prior to the freshet and a much larger late summer-autumn peak that occurs as river flow declines (Breckenridge *et al.*, 2020; Chapter 2). Of interest would be *E. affinis* vertical distribution during early summer, after the slough has been cut off from the salt wedge by high river discharge. During this period, surface waters in the slough are fully freshwater and anoxic conditions have developed below the level of the sill. Anoxic bottom waters have been shown to restrict vertical migration in some copepod species (Keister & Tuttle 2013). This period typically sees a near

disappearance of *E. affinis* from the water column (Breckenridge *et al.*, 2020; Chapter 2) and the dropping of resting eggs (Chapter 3).

4.4.6   Implications

My results suggest that *E. affinis* in the FRE possess TVM behaviour. Low densities of this species outside of slough environments (Breckenridge *et al.*, 2020; Chapter 2) suggest that this behaviour is insufficient for population retention in the larger estuary where residence times are substantially lower. Estuarine residence times continue to undergo change resulting from human interventions, such as channelization and water withdrawals, and from changes in climate, such as sea level rise and altered seasonality of freshwater inputs. Indeed, residence times in the FRE have been reduced through dredging and channelization. Further study and modelling of estuarine retention mechanisms and how their efficacy is influenced by physical oceanography will help us to more accurately predict how environmental changes might influence pelagic secondary production and food availability for fish and other consumers that depend on estuaries.

4.5 Tables

Table 4.1 Average densities (individuals m^{-3} ± 1 standard error) of select copepod taxa collected in vertical series of samples during two cruises, TCS1 (Sep 15-16, 2014) and TCS2 (Sep 29-30, 2017).

Taxon	TCS1	TCS2	Habitat
Calanoida			
Eurytemora affinis	10,466 ± 869	4,581 ± 270	Estuarine pelagic
Paracalanus spp.	Not present	3,466 ± 528	Marine pelagic
Diaptomidae	244 ± 39	68 ± 17	Freshwater pelagic
Cyclopoida			
Diacyclops thomasi	14,135 ± 1,509	1,442 ± 201	Freshwater pelagic
Ditrichocorycaeus anglicus	Not present	1,110 ± 83	Marine pelagic
Harpacticoida			
Coullana canadensis	436 ± 58	1,343 ± 259	Estuarine benthic
Pseudobradya spp.	373 ± 175	898 ± 267	Estuarine benthic

Table 4.2 Migration amplitude (m) of *E. affinis* developmental stages calculated as the average change in WMD between high tide and the long and short ebb tides. Note the diurnal high tide and the long ebb measurements were not consecutive.

Stage	Nocturnal high tide		Diurnal high tide	
	TCS1	TCS2	TCS1	TCS2
CI	3.1 m	0.7 m	0.5 m	2.0 m
CII	4.0 m	0.4 m	1.6 m	1.5 m
CIII	4.6 m	1.8 m	1.4 m	1.4 m
CIV	5.2 m	1.7 m	1.6 m	1.1 m
CV	5.4 m	1.8 m	1.6 m	0.5 m
CVI	5.2 m	2.7 m	0.8 m	0.7 m

4.6   Figures
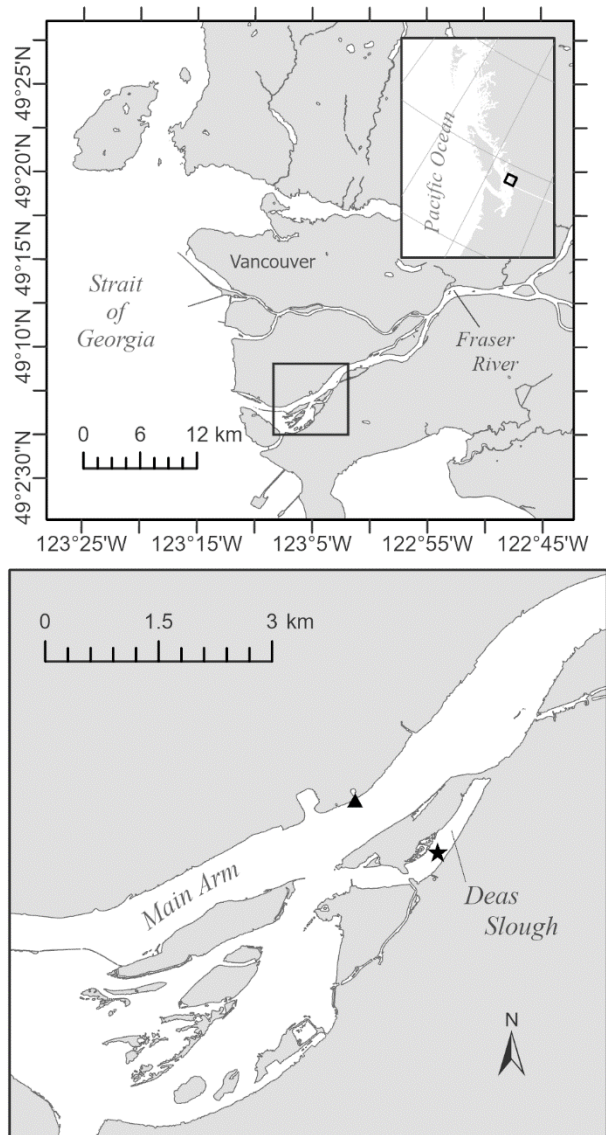
Figure 4.1 Study area (lower panel) within the Fraser River Estuary, Canada (upper panel). Station location

is indicated by a black star and Environment Canada Station 08MH053 is indicated by the black triangle.
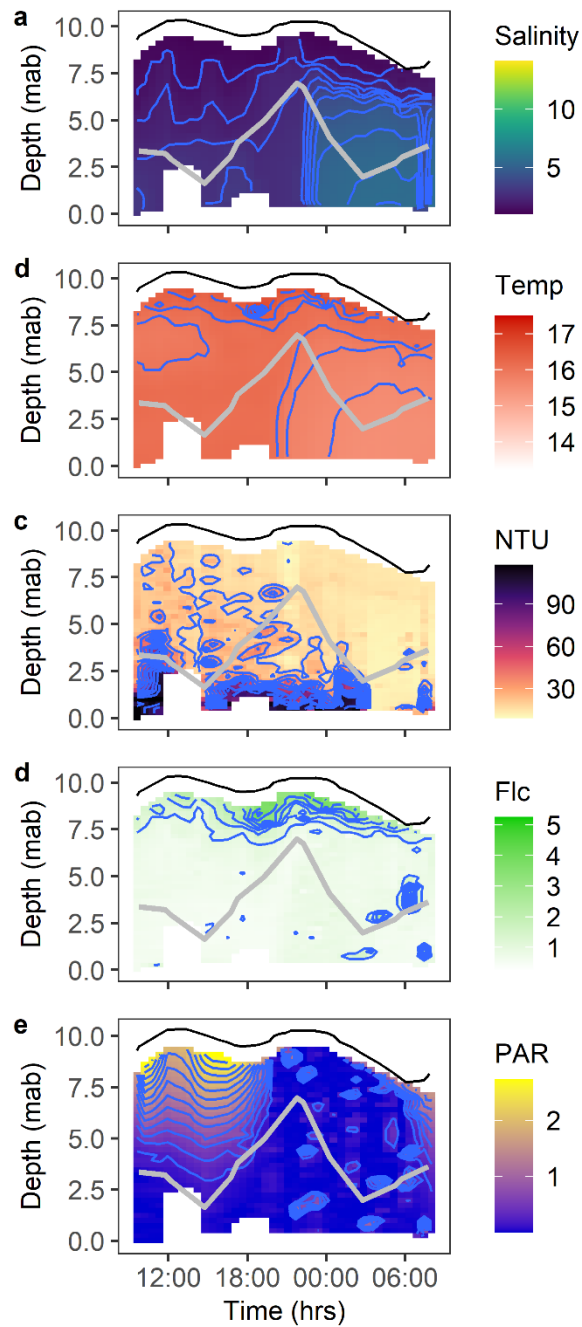
Figure 4.2 Hydrographic conditions during TCS1 (Sep 15-16, 2014). a) Salinity, b) temperature (°C), c) turbidity (NTU), d) fluorescence (mg m⁻³), and e) PAR (μMol m⁻² s⁻¹). Data are plotted in meters above bottom. Grey line represents WMD of *Eurytemora affinis* (CI-CVI).
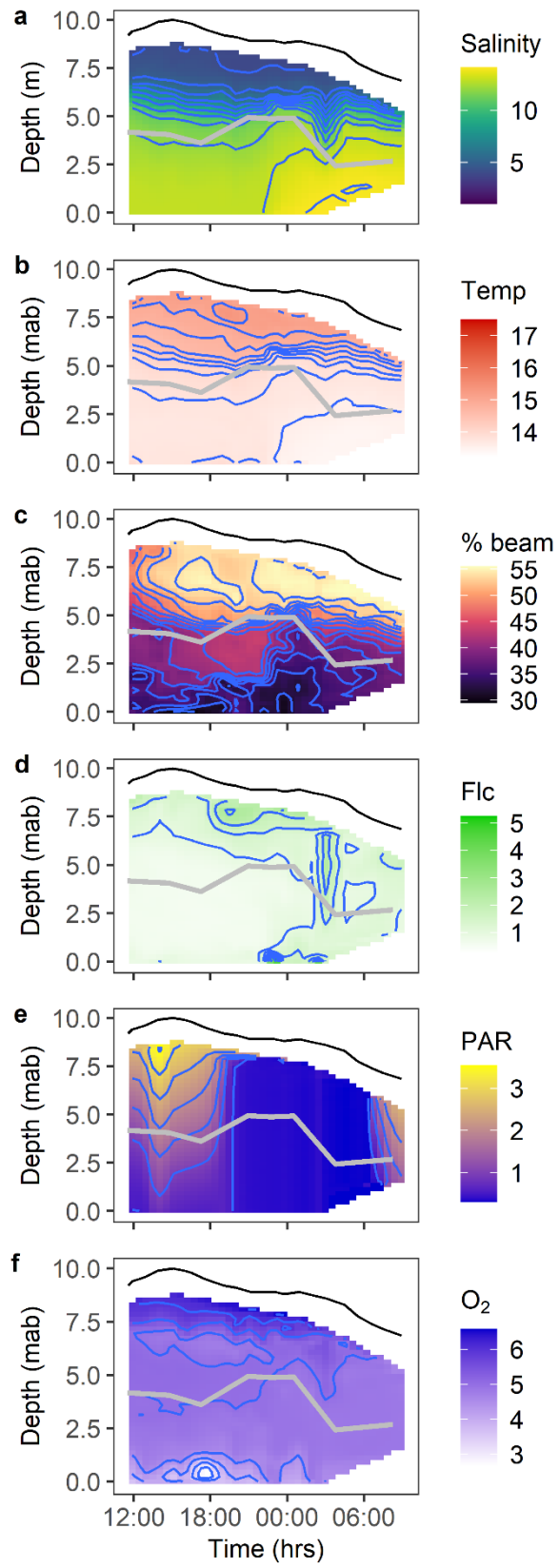
Figure 4.3 (Previous page) Hydrographic conditions during TCS2 (Sep 29-30, 2017). a) Salinity, b) temperature (°C), c) turbidity (% beam transmission), d) fluorescence (mg m^{-3}), e) PAR (μMol m^{-2} s^{-1}), f) oxygen (ml l^{-1}). Data are plotted in meters above bottom. Grey line represents WMD of *Eurytemora affinis* (CI-CVI).
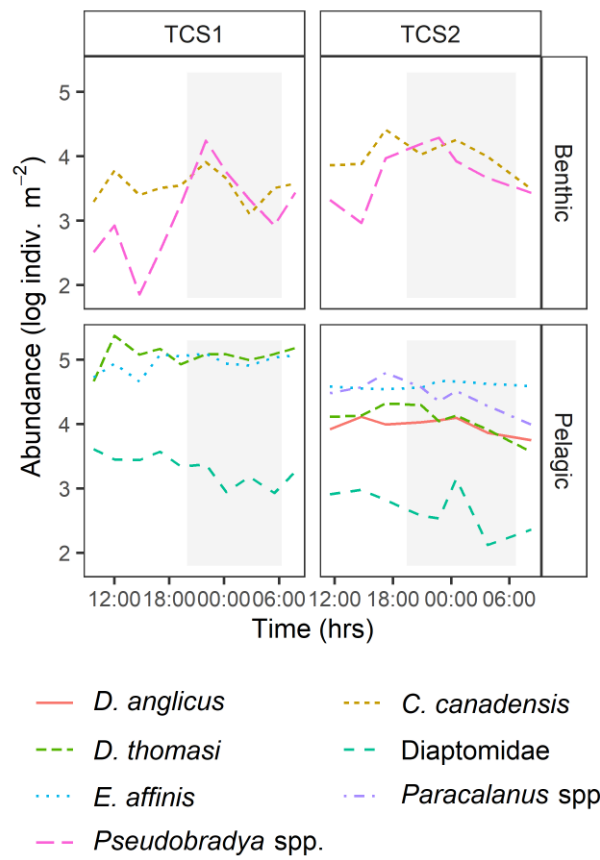
Figure 4.4 Variation in log$_{10}$-transformed water column total abundance (individuals m^{-2}) of pelagic and benthic copepod species over both cruises, TCS1 (Sep 15-16, 2014) and TCS2 (Sep 29-30, 2017). Shaded box indicates night.
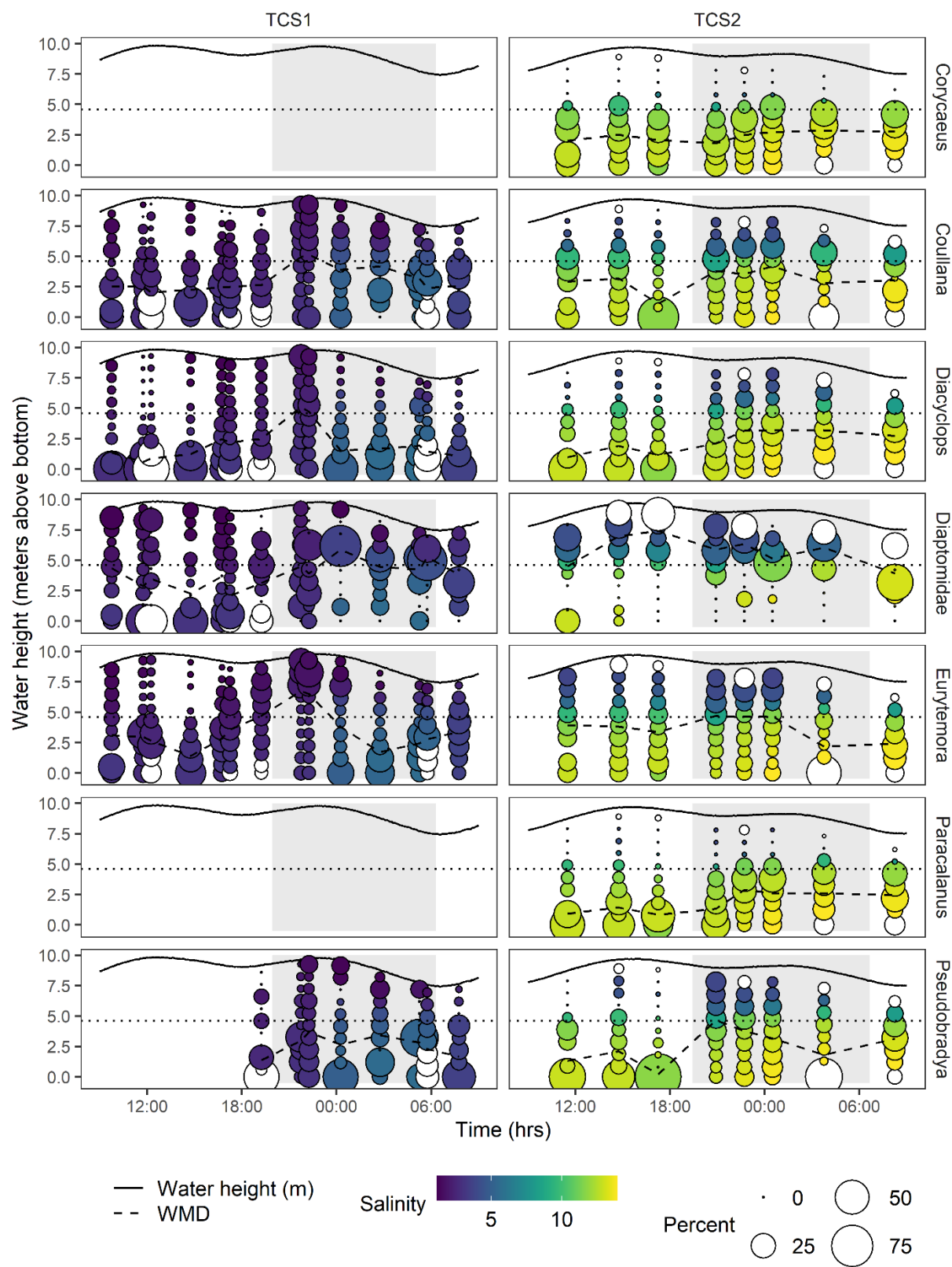
Figure 4.5 (Previous page) Vertical distribution of copepods collected in meterly sampling in Deas Slough of the Fraser River Estuary, BC, Canada, over 2 cruises: TCS1 (Sep 15-16, 2014) and TCS2 (Sep 29-30, 2017). Plotted taxa are *Ditrichocorycaeus anglicus* (as *Corycaeus*), *Coullana canadensis*, *Diacyclops thomasi*, Diaptomidae (*Leptodiaptomus ashlandi* + *Skistodiaptomus oregonensis*), *Eurytemora affinis*, *Paracalanus* spp., and *Pseudobradya* spp. *Pseudobradya* spp. data for the beginning of TCS1 are omitted due to low counts (< 10 individuals per profile). Bubble size indicates the percentage of the total individuals collected in profile that were collected at a given depth in meters above bottom (mab). Bubble colour represents depth-specific salinity as measured from the nearest CTD profile with white indicating no data. *Solid lines* indicates height of the water column in meters above bottom. *Dashed line* represents weighted mean depth (WMD). Shaded boxes represent night.
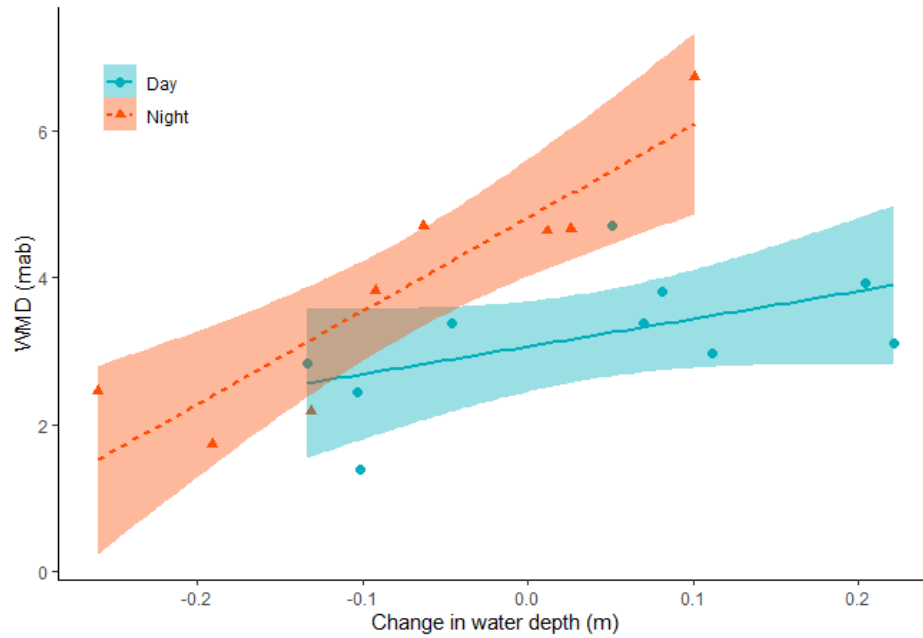
Figure 4.6 Change in weighted mean depth (WMD) of *E. affinis* (CI-CVI) in meters above bottom (mab) with change in water level (m per 30 min period) by diel phase. Water level data are from Environment Canada (Deas Island Station 08MH053). Change in water level was calculated over the 30-minute period prior to beginning the sample profile. Sign of the change indicates whether water level was decreasing or increasing. Shaded areas represent 95% confidence intervals.
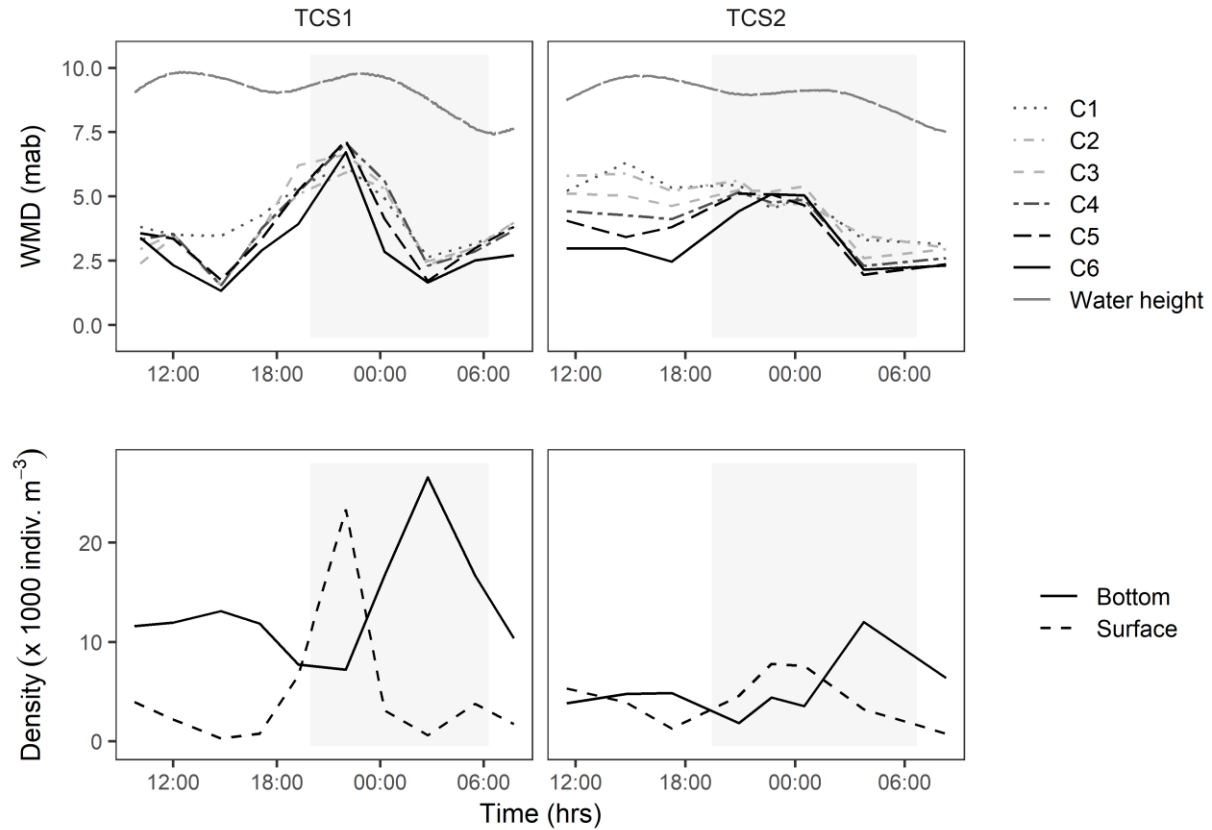
Figure 4.7 Top panels: *E. affinis* **weighted mean depth (WMD) in meters above bottom (mab) by developmental stage over the course of both cruises, TCS1 (Sep 15-16, 2014) and TCS2 (Sep 29-30, 2017). Bottom panels: Total** *E. affinis* **density (x 1000 individuals m^{-3}) in the top and bottom 2 meters of the water column. Shaded boxes represent night.**

Chapter 5: Modelling the response of *Eurytemora affinis* abundance to predicted changes in the Fraser River hydrograph and temperature

I developed a stage-structured, concentration-based population model to investigate the importance of resting eggs to the persistence of the *E. affinis* population in Deas Slough and to explore potential effects of projected changes in temperature and Fraser River discharge on population dynamics. Model results suggest that resting eggs are necessary to reproduce observed high post-freshet abundances of *E. affinis*. Predicted changes in water temperature and to the Fraser River's hydrograph have the potential to result in a 92% increase in mean annual *E. affinis* copepodid abundance and also in large changes in their phenology. Average Fraser River discharge predicted for 2010 – 2039 shifted the post-freshet occurrence of *E. affinis* to 25 days later, while discharge predictions for 2070– 2099 resulted in *E. affinis* occurring 50 days earlier.

5.1 Introduction

As global climate continues to warm, precipitation patterns are changing (Dore 2005). In the Pacific Northwest region of North America, precipitation is increasingly falling as rain rather than snow (Wu et al. 2012). For rivers whose discharge is dominated by snow-melt, this is predicted to result in peak discharges occurring earlier in the year (Wu et al. 2012). Earlier peak discharge has already been observed for the Fraser River (Foreman et al. 2001), and it has been predicted that by the end of the 21st century, Fraser River flow will have transitioned from a hydrologic regime dominated by snowmelt to a pluvial or nival-pluvial regime (Morrison et al. 2002, Shrestha et al. 2012, Islam et al. 2019a). The change in river discharge has been accompanied by ~1.5°C increase in lower Fraser River water temperatures between 1950 – 2015

(Islam et al. 2019b). This trend is projected to continue, with temperatures increasing by 0.14°C per decade over the 21st century (Ferrari et al. 2007). Given the control river discharge exerts on both zooplankton abundance and composition in the Fraser River Estuary (FRE; Chapter 2) and that zooplankton can develop more rapidly in warmer conditions (Huntley & Lopez 1992, Gillooly et al. 2002, Mackas et al. 2012), projected changes in the Fraser River hydrograph and in water temperature have the potential to profoundly affect zooplankton in the FRE.

In the FRE, the distribution and abundance of the calanoid copepod *Eurytemora affinis* is shaped by river discharge. *E. affinis*, a trophically important member of North American and European estuarine zooplankton communities (Winkler & Greve 2004, Shoji et al. 2005, Dauvin & Desroy 2005, David et al. 2006), was largely absent from the rapidly flushing channels of the FRE, while reaching densities > 30,000 individuals m^{-3} in sheltered sloughs (Chapters 2, 3). In Deas Slough, *E. affinis* copepodids have a bi-modal abundance distribution, consisting of a low abundance spring peak that appears to be terminated by the high Fraser River discharges associated with the spring freshet and a much larger late summer-autumn peak that occurs as river flow declines (Breckenridge et al. 2020, Chapters 2 and 3). Results from Chapter 3 suggest that *E. affinis* females begin to produce resting eggs near the beginning of the freshet, before the species largely disappears from the water column. The abundance of adult females in spring, during the period of resting egg production, will therefore determine that year's contribution to the egg bank. Early peak river discharge may reduce that contribution by truncating the warmest period of the spring growing season, when population growth potential would be the highest. In the context of rising water temperatures in the estuary, however, this effect may be mitigated by increased spring *E. affinis* abundance because generation time becomes shorter with increasing temperature (Pierson et al. 2016, refs in table 5.2)

In this chapter, I developed a stage-structured, concentration-based population model able to replicate observed population dynamics of *E. affinis* in Deas Slough. I used this model to 1) develop a more mechanistic understanding of *E. affinis* population dynamics in Deas Slough, 2) investigate the importance of resting eggs to the persistence of the population, and 3) explore potential effects of projected changes in temperature and Fraser River discharge on *E. affinis* population dynamics.

5.2   Materials and Methods

5.2.1   Study site description

Deas Slough, located ~18 km from the mouth of the Fraser River South (Main) Arm and ~16 km from the mouth of Canoe Passage (Fig 4.1), has a deep (10 m) basin protected by a 5 m sill. Saline waters are retained in Deas Slough for extended periods after high river discharge isolates the slough from the salt wedge (Birtwell et al. 1987a, Breckenridge et al. 2020). *E. affinis* abundances from Deas Slough were used because the location overcame two of the major impediments to the calculation of accurate vital rates: 1) the inability to sample the same population over time, and 2) advection being the predominant source of gains or losses (Ohman 2012). From Chapter 2, we know that the flushing time of Deas Slough is greater than the generation time of *E. affinis* and that any potential advective gains from surrounding channels of the FRE will be negligible. See sections 2.3.1, 3.3.1, and 4.3.1 for further description of the Fraser River Estuary and my study site within Deas Slough.

5.2.2   Data used for model fitting and loss estimates

E. affinis copepodid abundances (individuals m^{-3}) used to fit the model were from 66

vertical tows of a 100-μm 0.5-m ring net collected twice monthly (monthly in winter) from Deas

Slough between June 2014 and November 2015. Stage-specific *E. affinis* copepodid and egg

abundances from these samples were also used, with an additional 6 vertical tows collected from

February 2016 – May 2016, to estimate mortality rates. During vertical tows, the net mouth was

lowered onto the sediment to ensure that stage-based differences in depth distribution (Chapter

4) did not bias population stage structure. *E. affinis* copepodids were identified to developmental

stage and stages CV and CVI were further identified to sex. For a subset of samples, egg

abundances, clutch sizes (CS), and prosome lengths (PL) of CVI females were recorded. The

number of eggs per clutch was counted for 814 clutches that were collected over 42 sampling

dates. Dropped clutches identifiable as belonging to *Eurytemora* were included in egg counts.

However, single eggs were excluded as other copepod species were present that produce eggs of

similar size and appearance. Egg abundances were estimated as the product of female abundance

and average number of eggs female^{-1}. The PL of 823 adult females, collected over 37 sampling

dates, were measured to a 12-μm resolution using an ocular micrometer of a Leica

stereomicroscope at 80x magnification. Vertical tow samples were collected as part of a broader

sampling program, described in greater detail in Chapters 2 and 3, that ran from August 2013 –

May 2016. Copepodid abundances from 60 oblique tows collected as part of this program were

used in model fitting to provide additional information on dynamics of abundance, but not its

magnitude. CS and PL measurements, and estimates of the prevalence of epibiont infestation

(Appendix E), were also drawn from both vertical and oblique tow estimates. The model is of

female abundance, therefore all abundances of CI-IV copepodites and of eggs were halved,

which assumed an even sex ratio in these stages (Hirst et al. 2010). Female-specific abundances were used for CV and adult females.

Profiles of temperature and salinity and surface water chlorophyll samples were taken at the time of sample collection. Further details of the hydrographic sampling can be found in section 2.3.2 and section 3.3.5. Long term river discharge and water temperature data were available for the Fraser River at Hope (Station 08MF005), B.C., from Environment Canada at wateroffice.ec.gc.ca and aquatic.pyr.ec.gc.ca/webdataonlinenational, respectively. Tidal heights for Point Atkinson (Station 7795), B.C., were available from tides.gc.ca.

5.2.3 Model structure

I simulated population dynamics of female *E. affinis* using a concentration-based, 4 stage (ENCA) model based on difference equations that calculate the changes in abundance of a life stage (N_i) from stage-specific rates of reproduction (R), moulting or hatching (m), and losses (d), using a 1-day time step.

For subitaneous eggs:

$$N_{s,t} = N_{s,t-1} + f_s R_{t-1} N_{a,t-1} - m_{s,t-1} N_{s,t-1} - d_{s,t-1} N_{s,t-1}$$

For resting eggs:

$$N_{r,t} = N_{r,t-1} + f_r R_{t-1} N_{a,t-1} - m_{r,t-1} N_{r,t-1} - d_{r,t-1} N_{r,t-1}$$

For nauplii:

$$N_{n,t} = N_{n,t-1} + m_{s,t-1} N_{s,t-1} + m_{r,t-1} N_{r,t-1} - m_{n,t-1} N_{n,t-1} - d_{n,t-1} N_{n,t-1}$$

For copepodites:

$$N_{c,t} = N_{c,t-1} + m_{n,t-1} N_{n,t-1} - m_{c,t-1} N_{c,t-1} - d_{c,t-1} N_{c,t-1}$$

For adults:

$$N_{a,t} = N_{a,t-1} + m_{c,t-1}N_{c,t-1} - d_{a,t-1}N_{a,t-1}$$

The model distinguished resting and subitaneous eggs, with f_r and f_s, respectively, denoting the fraction of eggs allotted to each type. Terms for subitaneous eggs, resting eggs, nauplii, copepodites, and adults are denoted by the subscripts s, r, n, c, and a, respectively.

Model forcings were water temperature and Fraser River discharge measured at Hope, B.C. Temperature controlled variation of development rates and river discharge, through its control of salinity intrusion, influenced egg production rate (EPR), hatching of resting eggs, and naupliar and copepodite mortality. Salinity intrusion at high tide, S' (m), was calculated using equation 2 of Kostaschuk and Atwood (1990),

$$S' = 82419 - 9835 \ln Q + 22458 \, log_{10} H$$

where Q is daily river discharge ($m^{-3}s^{-1}$) measured at Hope, B.C. and H is the maximum daily tidal height (m) recorded at Point Atkinson, B.C. (tides.gc.ca).

E. affinis abundance was simulated for 365 model days with a start date of January 1. Identical starting values were used during fitting and for all scenarios. Starting abundances were taken from January 2015 samples. For scenarios that included resting eggs, their initial abundance was set to zero. The model was built in R version 4.1.2 (R Core Team 2021)

5.2.4   Egg production rate

EPR (eggs female^{-1}d^{-1}) was estimated using two methods, via incubation for the periods February – May 2015, August – September 2015, and February – May 2016, and via a modified egg ratio method (Edmondson et al. 1962, Lloyd et al. 2013) for various dates from

September 2013 – Nov 2015. Incubation methods and results are described in Chapter 3. For the modified egg ratio method, EPR is calculated as,

$$EPR = \frac{eggs\ female^{-1}}{ICT}$$

after Lloyd et al. (2013), where the mean number of eggs per female is divided by inter-clutch time (ICT), rather than egg development time (EDT). ICT includes both EDT and latency time, which is the period between the completed hatching of one clutch and the extrusion of the following clutch. I used the estimate of ICT (in days) derived for *E. affinis* by Devreker et al. (2012) using data on EDT and latency time from Vijverberg (1980), which is calculated using temperature (*T, ℃*) at time of collection:

$$ICT = 30.31\ \text{days}\ T^{-0.378} - 7.637\ \text{days}$$

In order to generalize EPR for use in the population model, I correlated it with river discharge, days since deepwater renewal (estimated as the days since the salinity intrusion at high tide fell below 18-km), temperature, surface water chlorophyll biomass, water column mean and maximum chlorophyll fluorescence, and copepodid abundance (individuals m^{-3}). Based on the results of these correlations (described in the results section), EPR was included in the model as a series of temporal averages with drops in EPR being triggered at a threshold of 90 days since deepwater renewal and after female copepodid abundance surpassed 10,000 individuals m^{-3}.

5.2.5 Development time and stage duration

Moulting rate was governed by the stage-structured, concentration-based, mean-age model developed by (Hu et al. 2008):

For eggs,

$$k_{s,t} = \frac{N_{s,t-1}[1 - m_s(k_{s,t-1})](1 - d_{s,t-1})(k_{s,t-1} + 1)}{N_{a,t-1}R_{t-1} + N_{s,t-1}(1 - d_{s,t-1})[1 - m_s(k_{s,t-1})]}$$

For nauplii and copepodites,

$$k_{i,t} = \frac{N_{i,t-1}[1 - m_i(k_{i,t-1})](1 - d_{i,t-1})(k_{i,t-1} + 1)}{N_{i-1,t-1}m_{i-1}(k_{i-1,t-1}) + N_{i,t-1}[1 - m_i(k_{i,t-1})](1 - d_{i,t-1})}$$

This method tracks mean age within a stage (k_i) and can be used to avoid the problem of numerical diffusion that results in underestimated generation times (Hu et al. 2008). Mean age at stage i was used to index Hu et al.'s (2007) model of the probability of individuals remaining at stage i moulting to stage $i+1$ (PMR) for molting rate, $m_i(k)$:

$$m_i(k) = \frac{p_i(k)\mathrm{d}t}{[1 - P_i(k)]}$$

Here, $p_i(k)$, a probability density function,

$$p_i(k) = \frac{1}{\sigma\sqrt{2\pi}} e^{-\frac{1}{2}\left(\frac{k-\mu}{\sigma}\right)^2}$$

and its cumulative density function, $P_i(k)$, are based on a normal distribution and generated using stage duration in days as the location parameter, μ, and a scale parameter, σ, for nauplii and copepodites of $0.4*\mu$, after Stegert et al. (2012), and of $0.1*\mu$ for eggs.

Development time (D) on a given model day was calculated from a time-specific temperature value (T, °C) and a Bělehrádek function (1935),

$$D = a(T + \alpha)^b$$

with *a* and α being fitted constants and using a *b* value of -2.05 (McLaren et al. 1969).

The function was fitted to *E. affinis* development times from both lab and field-based studies

(Table 5.1), similar to that of Pierson et al. (2016) for North Atlantic populations. In some cases,

only generation time (egg-to-egg) estimates were available and were included in the data, which

would have the effect of increasing my development time estimates. Where both egg-to-egg and

egg-to-adult female estimates were reported (or could be calculated), egg-to-adult estimates were

used. Where female-specific development times were available, these were used. By grouping

developmental stages within a single Bĕlehrádek function, rather than stage-specific ones, I was

able to include a greater number of populations and, importantly for our application, studies that

measured development time at temperatures below 5 °C. I calculated the duration of individual

developmental stages by multiplying *D* by the average proportion of time spent in that stage

(Table 5.2), which I estimated from studies that provided stage-specific development times

(Heinle 1970, Heinle & Flemer 1975, Escaravage & Soetaert 1993, Ban 1994, Devreker et al.

2007, 2009, Beyrend-Dur et al. 2009). This method assumes equiproportional development, i.e.

that the effect of temperature on developmental rate will not vary with stage, which has been

demonstrated for *E. affinis* (Devreker et al. 2012). Curve fitting was done using nlsLM in the

minpack.lm R package (Elzhov et al. 2016), which uses the Levenberg-Marquardt algorithm to

fit non-linear least squares models.

5.2.6   Mortality rate

Stage-specific weekly mortality estimates for eggs, nauplii, and copepodites were

generated using the population surface method (PSM; Wood 1994). The PSM is an inverse

method based on the McKendrick-von Foerster equation and can be used for continuously

reproducing species where discrete cohorts cannot be identified. As a horizontal method, PSM assumes that advection does not influence abundance or stage structure (Wood 1994, Aksnes et al. 1997). The tidal vertical migration behaviour of *E. affinis* (Chapter 4), in combination with the presence of a sill in Deas Slough and the very low abundances of *Eurytemora* spp. in the larger estuary, made this a realistic assumption for my study population.

The PSM requires stage duration and abundance estimates. My sampling method undersampled nauplii, so naupliar abundances were set to 0 and assigned weights 0.2% of that of other developmental stages, following Ohman and Wood (1996). To incorporate a resting stage, EDT was increased by 1 day/day beginning in mid-April and then decreased by 1 day/day until hatch, similar to what was done by Ohman and Wood (1996). The PSM was used to generate weekly mortality estimates over 3 separate periods: Jun 2014 – Dec 2014, Jan 2015 – Dec 2015, and Feb 2016 – May 2016. No December sample was taken in 2015 so abundances from December 2014 were used. The PSM was implemented using the R package posum (Wood 2002) in R version 1.6.2**.**

Mortality of adult females was estimated using the vertical life table (VLT) approach because the PSM was unable to resolve realistic estimates of adult female mortality, possibly as a result of low abundances (Wood 1994, Ohman & Wood 1996). The VLT approach calculates a shared mortality rate from the ratio of the abundances of two consecutive stages and stage duration. After Aksnes and Ohman (1996), the shared mortality (*d*) of CV and CVI stages is calculated as,

$$d_{CV-VI} = \frac{\ln\left(\frac{N_{CV}}{N_{CVI} + 1}\right)}{SD_{CV}}$$

where *N* is the stage-specific abundance and SD is the stage duration of CV females. VLT

mortality estimates are considered unreliable without high replication and I have only 1-2

vertical tow samples per date (Aksnes & Ohman 1996). To mitigate this source of error, I did not

vary adult mortality between scenarios.

Mortality rates of naupliar, copepodite, and adult female stages varied within and

between years and so were further generalized for use in the population model. I correlated

mortality estimates with river discharge, days since deepwater renewal, temperature, and

copepodid abundance (individuals m^{-3}). Based on the results of these correlations, naupliar

mortality was modelled using temporal averages with the exception of late spring and early

summer, where, when the slough had been cut off from the freshet for 25 days, I increased

mortality as a function of days since deepwater renewal. Late spring and early summer

copepodite mortality was similarly modelled as a function of deepwater renewal. After

deepwater renewal occurred, copepodite mortality was modelled as a function of copepodid

abundance. Winter, early spring, and late autumn copepodid mortalities were temporal averages.

Subitaneous egg mortality was modelled at a constant rate of 0.0591 d^{-1}. Resting egg mortality

was modelled at the same rate but was only applied during production and during the period that

resting eggs were hatching. For other periods, I assumed zero mortality for resting eggs.

Variation in adult mortality was modelled from a LOESS (locally-weighted smoothing) curve

(span = 0.2) fitted to the VLT estimates over day of the year. Thus, in the population model, only

naupliar and copepodite mortality varied between scenarios.

5.2.7 Model fitting and sensitivity analyses

During fitting, year-specific daily river discharge, maximum daily tidal heights, and temperatures were used. Model parameters that were not based on data, or that required narrowing down, were chosen by iterating values and comparing the resulting simulated copepodid abundances to observed abundances from 2014 and 2015. Specifically, I used this method to set the scale parameter used in the moulting functions for nauplii and copepodites, the hatching rate of resting eggs, and the copepodid abundance at which density dependence for EPR and copepodite mortality was initiated. The performance of the fitted model was evaluated against post-freshet abundances estimated in 2013 through oblique tows in Deas Slough.

I used a scale parameter of 10% of stage duration in the PDFs that governed egg hatching rate, and of 40% in the PDFs for naupliar and copepodite moulting rates, following Stegert et al. (2012). Increasing the scale parameter used for naupliar and copepodite moulting rate PDFs from 10% of the mean to 50% of the mean, in increments of 10%, resulted in smoother abundance distributions by spreading out the moulting period (Appendix F, Figure F.1).

In the model, resting egg production began April 15th at a rate of 50% of eggs produced and was increased to 90% for the period May 1 – July 1. The date to begin resting egg production was based on the results of Chapter 3 and the end date was set to ensure that resting eggs were not produced after deepwater renewal of the slough. The dates of resting egg production did not vary between model scenarios. Hatching of resting eggs typically occurs when resting eggs are resuspended from the sediment under favourable conditions (Ban & Minoda 1992, Marcus 1996). In our context, the resuspension of resting eggs in Deas Slough was likely initiated by the first post-freshet entry of high salinity water from the salt wedge. A salinity intrusion threshold of 18-km was set for deepwater renewal of the slough, based on

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salinity data for the freshet periods of 2013-2015 and the distance of Deas Slough from the Strait

of Georgia. After the high tide salinity intrusion exceeded 18-km, resting eggs hatched at a rate

that increased by 5% per day (Appendix F, Figure F.2). The model ignored potential

contributions to and from an egg bank. I explored the effect of this assumption during fitting by

adding and subtracting 5000 and 10,000 resting eggs at t=200 (Appendix F, Figure F.3). Post-

freshet, a copepodid abundance of 10,000 individuals m^{-3} was used to trigger density-dependent

copepodite mortality and the decrease in EPR that occurred following observed peaks in

abundance. This threshold was chosen by incrementing by 2000 individuals m^{-3} between 4000 –

12,000 (Appendix F, Figure F.4).

Model sensitivity to proportional changes in mortality rate and EPR, ranging from – 40 %

to + 40%, was estimated by calculating the proportional change in key abundance metrics,

specifically resting egg abundance, mean annual and mean seasonal copepodid abundance, and

the date of peak abundance.

5.2.8   Model scenarios

5.2.8.1   Subitaneous egg scenarios

To investigate whether observed *E. affinis* population dynamics could be replicated

without resting eggs, I compared the output of the fitted model for 2015 to two scenarios from a

model modified to include only subitaneous egg production. The first scenario used loess-

smoothed (span = 0.2) weekly mortality rates for eggs, nauplii, and copepodites, that were

estimated via the PSM using egg abundances from 2015 and subitaneous egg development times.

Because mortality rates generated in this scenario were generally higher than those generated for

the resting egg scenario, I termed this scenario the high mortality scenario (hmS) and ran a

second subitaneous scenario (lmS) using the lower mortality rates from the resting egg scenario.

5.2.8.2   Temperature and river discharge scenarios

I investigated the impacts of 3 discharge and 3 temperature conditions on *E. affinis*

dynamics in Deas Slough. For river discharge, the base condition was median daily Fraser River

discharge recorded between 1912 and 2013 at Hope, B.C (wateroffice.ec.gc.ca). For the other

two river conditions, I reconstructed the 2010 – 2039 mean Fraser River hydrograph predicted by

Morrison et al. (2002) and the 2070 – 2099 mean hydrograph predicted by Islam et al. (2019a;

Figure 5.1). Because no long-term temperature data were available for the estuary, I constructed

the baseline temperature by applying a LOESS smooth (span = 0.15) to water column average

temperatures from Deas Slough collected between August 2013 and November 2015. For the

'cool year' run I subtracted 1.5 °C from this curve and for the 'warm year', I added 1.5 °C

(Figure 5.1). I combined temperature and river conditions into 9 scenarios: Base river discharge

at temperature changes of -1.5 °C, 0°C, and +1.5 °C (RMed-1.5, RMed-0, RMed+1.5,

respectively), and both predicted 2010 – 2039 and predicted 2070 – 2099 hydrographs at

temperature changes of -1.5 °C, +0°C, and +1.5 °C (R2020-1.5, R2020-0, R2020+1.5, R2080-

1.5, R2080-0, R2080+1.5, respectively). Tidal height was kept constant across scenarios and was

calculated as the median maximum daily tidal height recorded at Point Atkinson, B.C. for the

period 2010 – 2019 (tides.gc.ca).

I compared all scenarios with respect to the number of days where copepodid abundance

exceeds 5,000 individuals m^{-3}, peak abundance, day of peak abundance, mean annual and mean

seasonal copepodid abundance (spring (Mar-May), summer (Jun-Aug), and autumn (Sep-Nov))
and resting egg abundance.

5.3   Results

5.3.1   Temperature and river discharge during study period

Water temperatures measured at Hope in 2015 were higher than average in May – July
but were otherwise mostly within one standard deviation of the mean (Figure 5.2). In 2014, water
temperatures were cooler than average during the spring and warmer than average during the
autumn. With respect to river discharge, 2015 was an atypical year that offered a glimpse of what
can be expected in the future, with record-breaking flows recorded for the Fraser River in the
spring and very low flows in July-August (Figure 5.3). Cumulative river discharge in 2015
reached ⅓ and ½ of the total for that year by May 14 and June 9, respectively, similar to the
predictions of Morrison et al. (2002) for 2070 – 2099 (May 14 and June 15). In contrast, 2014
was much more typical with respect to discharge timing and reached these milestones on the 16th
and 25th of June, respectively.

The temporal dynamics of *E. affinis* copepodid abundance in 2015 were shifted earlier
compared to 2014 with both the spring decline and the post-freshet increase in copepod
abundance occurring ~ 1 month earlier (Figure 5.4). Mean CS was largest in spring (35.5 eggs
clutch^{-1} ± 1.5 SE). In 2015, CS dropped after early May and did not increase until August, after
the salt wedge had re-entered the slough. These changes in CS coincided with a drop and slight
recovery of adult female PL. Both CS and PL of adult females decreased again in late August,
coinciding with peak *E. affinis* abundance (Figure 5.4). In 2014, mean CS during the freshet was
higher but varied more than in 2015. I again observed two periods of decrease in the PL of adult

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females, the first that occurred after early June and a second decrease that occurred after peak abundance and coincided with a decrease in CS (Figure 5.4).

5.3.2 Vital rate estimates

EPR estimates varied widely, but results suggest that the copepod productive season in Deas Slough extended from February to October (Figure 5.4). EPR estimates from incubations were generally higher than those calculated using the egg-ratio method during the spring, which is expected given that the incubation method would retain dropped eggs and allowed certainty in egg identification. I observed EPR < 1 from Nov – Jan and also during the freshet when the salinity of bottom waters of the slough was near zero (salinity < 0.4). Peaks in EPR occurred in February, May, and in the summer, soon after the slough experienced deepwater renewal. Post-freshet EPR remained high until about the time of peak abundance, after which it decreased. This drop in EPR coincided with the decreases in CS and PL of adult females (Figure 5.4). In the model, temporal averages of EPR were linked to days since deepwater renewal (Figure 5.5) in spring and to copepodid abundance in summer (summarized in Table 5.3). EPR estimates did not correlate with any of the chlorophyll variables.

Dimensionless coefficients of the Bĕlehrádek function used to describe the relationship between *E. affinis* development time and temperature (Figure 5.6) were estimated as $a = 13{,}272$ (11,114 – 15,928 95% CI) and $\alpha = 8.72$ (7.58 – 10.06 95% CI). Given an observed temperature range in Deas Slough of roughly 4 – 20 °C, development times would range between a maximum of 72 days and a minimum of 13.6 days. A further increase in temperature of 1.5 °C would reduce these development times by 15 days and 1.3 days, respectively.

Average daily mortality rate estimates increased with life stage. Average ($\pm$ 1 SD) estimates of egg, naupliar, copepodite, and adult female mortality rates were 0.0591 d^{-1} $\pm$ 0.049, 0.0669 d^{-1} $\pm$ 0.077, 0.130 d^{-1} $\pm$ 0.128, and 0.292 d^{-1} $\pm$ 0.200, respectively. Mortality rate estimates suggested lower mortality during winter and early spring for naupliar and copepodid stages (Figure 5.7). High mortality estimates for juvenile stages occurred late in the freshet and the number of days since deepwater renewal was a correlate of mortality rate for juvenile stages (Figure 5.8). During post-freshet abundance peaks, copepodite mortality was positively correlated with copepodid abundance (Figure 5.9). The parameterization of naupliar and copepodite mortality is summarized in Table 5.4. Adult female mortality rate peaked at the end of August, approximately one month after peak temperatures.

5.3.3   Model fitting

Copepodid abundances simulated using the above parameterization with year-specific temperature, river discharge, and tidal heights were realistic when compared to observed vertical tow abundances were able to recreate the population dynamics observed in 2014 and 2015 (Figure 5.10). For 2014, simulated post-freshet abundances increased a few days earlier and abundances in autumn decreased at least 2 weeks earlier than was observed in the field.

The 2013 model run used year-specific river discharge and tidal height and the water column average temperatures used in the base temperature scenarios. When evaluated against observed post-freshet abundances in 2013, simulated abundances rose earlier (~ 2 weeks) and more rapidly and peaked earlier (Figure 5.10). The early post-freshet occurrence of simulated *E. affinis* suggests that additional information may be necessary to predict the timing of salt wedge entry into Deas Slough. The rapid increase in abundance and early peak in the 2013 simulation

were the result of higher resting egg production and post-freshet recruitment than occurred in simulations of either 2014 or 2015.

5.3.4   Subitaneous egg scenarios

E. affinis were able to persist through the freshet without resting eggs in this model. Their recovery post-freshet was slow, however, and female copepodid abundance peaked in November at < 100 individuals m^{-3}, orders of magnitude lower than what has been observed in the field (Figure 5.11). Decreasing mortality rates to match those of the resting egg scenario increased post-freshet abundances compared to the high mortality scenario, but abundances remained far below what was observed in the field.

5.3.5   Influence of warming and changes to the hydrograph on *E. affinis* population abundance and timing

At each level of river discharge, mean annual copepodid abundances were higher (17 – 57%, depending on discharge level) in warm year scenarios when compared to baseline temperature scenarios (Table 5.5). A doubling (~ 2.1x) of abundance during spring led to an ~2.8x increase in resting egg abundance. The hatching of this large pool of eggs in summer led to a sharp post-freshet increase in abundance (Figure 5.12). During cool year scenarios, a smaller (~0.3x) contribution to the resting egg pool resulted in a more gradual increase in abundance and to higher abundances occurring later in the year (Figure 5.12).

When comparing hydrographs at a given temperature, mean annual copepodid abundance was highest in 2070 – 2099 scenarios and lowest in 2010 – 2039 scenarios (Table 5.5). Mean spring abundances of the 2010 – 2039 and median hydrographs were equivalent and resulted in

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similar resting egg abundances. The higher summer river discharge of the 2010 – 2039 hydrograph caused post-freshet deepwater renewal and the resulting hatch of resting eggs to occur in late September, 25 days later than at median river discharge (Fig 5.12). After controlling for the effect of temperature, this late recruitment led to an ~ 56% decrease in summer abundance. Conversely, reductions in summer river discharge in the 2070 – 2099 hydrograph led resting eggs to hatch 7 weeks earlier than in median discharge scenarios and caused mean summer abundance to increase by 900 – 2800%, depending on temperature (Figure 5.12). The increase in summer abundance occurred despite the reduced (by ~ 33%) resting egg abundances that resulted from the early isolation of the slough.

Of greatest interest was the comparison of the R2020-0, R2020+1.5, and R2080+1.5 runs to the baseline, the RMed-0 run (Table 5.5). The R2020-0 run resulted in a 18% decrease in mean annual *E. affinis* abundance, with the greatest decrease occurring in summer (53%). The R2020+1.5 run resulted in a minimal (4%) decrease in mean annual abundance, with increases occurring in the spring (115%) and decreased abundances occurring in autumn (16%). The increase in spring abundance led to a 180% increase in resting egg abundance. The post-freshet abundance peak for both R2020 runs began later than in the RMed-0 run and peak duration was decreased. Mean annual abundance in the R2080+1.5 run was 92% greater than the RMed-0 run. Lower summer river discharge led mean summer abundance to increase almost 3000% and caused the post-freshet high abundance (> 5000 individuals m^{-3}) period to begin 50 days earlier than in the RMed-0 run (Figure 5.12). Resting egg production was increased (95%) and autumn abundances were reduced by 43% compared to the RMed-0 run. Duration of high abundances increased by 25 days in the R2080+1.5 run.

5.3.6 Sensitivity analyses

Model results were sensitive to mortality (Fig 5.13). Increasing mortality rate shifted the post-freshet abundance peak later in the year, which had a large effect on modelled average summer copepodid abundance (Appendix F, Table F.1). Changes to EPR had a similar effect on the timing of post-freshet peak abundance. While higher EPR resulted in earlier peak abundance, modelled abundances were less sensitive to perturbation of EPR than to perturbation of mortality rates (Fig 5.14, Appendix F, Table F.2).

5.4 Discussion

5.4.1 The role of resting egg production in *E. affinis* population dynamics

My model suggests that resting eggs are necessary to explain observed high summer abundances of *E. affinis* in Deas Slough. In order to replicate the rapid increase in abundance that was observed post-freshet in 2015, the addition of a large number of individuals was necessary during the week where resting egg resuspension likely began (Figure 5.11). In the population surface that was generated to calculate mortality estimates for the subitaneous scenario, simulated egg abundance substantially deviated from the input egg abundance during the period in which resuspension likely occurred (~1025 eggs m^{-3} as opposed to the observed egg abundance of 2 m^{-3}). It seems most likely that the influx of individuals to the population was resuspended eggs from the egg bank, which would not have been captured by my sampling. One alternative, that the eggs were produced by the females present in the slough at that time, is not plausible. Given an observed female abundance of 7.6 ± 1.1 individuals m^{-3} and a water temperature of 20.8 $^{\circ}$C, this would have required an EPR of 136 eggs d^{-1}. EPRs reported for *E. affinis* are typically < 10 eggs female^{-1} d^{-1} (Table 2 in Devreker et al. 2009) and the highest EPRs

that I am aware of for *E. affinis* are 38 and 34 eggs female^{-1} d^{-1}, both recorded from lab

populations that were fed in excess (Ban 1994, Devreker et al. 2012). The second alternative

source of individuals, immigration, is also unrealistic because abundances of *E. affinis* in the

channels surrounding Deas Slough are typically orders of magnitude lower than in the slough

(Chapter 2), and, for the period in question, were not detected in channel samples. The presence

of the egg bank may dampen the effects of predicted increases in the variability of river

discharge (Islam et al. 2019a). The egg bank also introduces some uncertainty to modelled post-

freshet *E. affinis* abundances because the number of resting eggs that hatch may be somewhat

independent of how many resting eggs were produced during the previous spring (Appendix F,

Figure F.3). Further research into how long these resting eggs remain viable would help address

this issue.

5.4.2   Proposed mechanistic explanation of *E. affinis* population dynamics

     E. affinis abundance in Deas Slough appears to be primarily temperature-limited during

spring. In February, *E. affinis* EPR increased in response to higher phytoplankton availability;

however, abundances remained low due to cool (~ 6.5 °C) March and April temperatures and

relatively long (~ 50 day) development times. The majority of egg-producing females in

February, March, and April developed under the food limiting conditions of winter and were

heavily infested with ciliate epibionts (Appendix E). That these copepods developed under food

limiting conditions is evidenced by their smaller than expected PL (Figure 5.4, Appendix C).

Because clutch sizes increase with PL (Ban 1994, Lloyd et al. 2013), food limitation that

occurred in winter could therefore restrict spring reproductive output.

By May, Deas Slough was isolated from the salt wedge by high river discharge and salinity had decreased. The reproductive population of *E. affinis* in May was comprised primarily of females that were relatively free of epibionts and had developed during more favourable spring conditions. My largest estimates of PL, CS, EPR, and of resting egg production were from this period (Figure 5.4, Chapter 3). Due to the typically deep distribution of adult females (Chapter 4) and the shallow depth of the slough (~10 m at high tide), dropped eggs would rapidly reach the sediment and encounter low oxygen conditions, which suppresses hatching (Uye et al. 1979, Ban & Minoda 1992). *E. affinis* abundance declined over the summer and adults dominated the population structure by the end of July (Fig 3.2). Reduced recruitment caused by a switch to resting egg production may have been largely responsible for the observed decline in abundance, but estimated mortality rates also increased over this period. Sex ratio for adults became more equal in July and even skewed towards females (Appendix D). Increased mortality of males may be due to natural mortality caused by the physiological stress of very low salinity or perhaps increased predation by non-visual predators. CS and PL of females decreased over this period, which is expected because of increasing temperature. My EPR estimates for early summer are likely underestimates because they were inferred from the egg ratio method and dropped eggs may have been missed.

E. affinis abundance increased later in the summer, soon after the re-entry of saline waters into the slough stimulated the hatching of resting eggs. Abundances increased rapidly because EPR (Figure 5.4) was high and water column average temperature was near its peak (~ 20.5 °C) resulting in development times of ~13 days. As temperature began to decrease, PL of females increased slightly until peak copepodid abundance was reached. Adult females

experienced their heaviest mortality rate during this period and sex ratio became strongly male skewed, suggestive of high female mortality caused by visual predators.

It is likely that the late summer/autumn decline in *E. affinis* copepodid abundance was due to both predation pressure and food limitation. The decline coincided with reductions in EPR, PL, and CS (Fig 5.4). Smaller observed female PL and CS can result from selective predation of large, ovigerous females (Hairston Jr. et al. 1983), and the shift towards a heavily male-dominated adult population that occurred during autumn supports heavy predation by visual predators (Appendix D). If predation pressure was the sole cause of the reduced PL, we would mainly observe the PL decline in later, larger developmental stages (De Robertis et al. 2000, Titelman & Fiksen 2004, Ueda et al. 2010). Instead, PL declined across all copepodid stages through autumn (Appendix C) where PL would be expected to increase due to decreasing temperatures. Such universal decline in PL could have been due to food limitation (Campbell et al. 2001). Chlorophyll levels in the estuary dropped in October (Fig 3.2) and the diet of still abundant *E. affinis* may have been relying more heavily on nano- or microzooplankton, a switch that has been suggested to occur for *E. affinis* in the Charente estuary, France (Modéran et al. 2012). Heterotrophic prey may not meet nutritional requirements of *E. affinis* because phytoplankton prey are preferentially selected when available and phytoplankton based diets can result in higher egg production (Gasparini et al. 1999, David et al. 2006, Modéran et al. 2012, Cabrol et al. 2015).

5.4.3   Population response to warming and changes to the hydrograph

My model results suggest that the positive effect of temperature on *E. affinis* abundance may be either increased or negated by predicted changes to the Fraser River's hydrograph. In the

scenarios using the 2010 – 2039 hydrograph from Morrison et al. (2002), *E. affinis* copepodid abundance was slightly reduced compared to median discharge scenarios. The positive effect of temperature on abundance was offset by the delayed post-freshet deepwater renewal of the slough that occurred in these scenarios. In scenarios using the 2070 – 2099 hydrograph from Islam et al. (2019a), increased copepodid abundances occurred despite the earlier isolation of Deas Slough. Further, a lower reliance on resting eggs to fuel post-freshet abundances was due to an extension of the *E. affinis* growing season into July, when water temperatures are at their highest. In the R2080+1.5 run, mean annual *E. affinis* copepodid abundance almost doubled in comparison the base run (RMed-0). Higher spring abundances resulted in greater resting egg abundance, despite the early isolation of the slough effectively shortening the resting egg production period by ~6 weeks. Having a fixed period of resting egg production in the model was based on reduced photoperiod cueing resting egg production in *E. affinis* (Ban 1992, Glippa et al. 2013). Cues for resting egg production are discussed in greater detail in Section 3.5. To better understand the response of *E. affinis* in the FRE to changes in climate, further study into what governs resting egg production is warranted. The hydrographs used in these scenarios are useful in demonstrating the extent of possible changes in timing on the *E. affinis* population. While these results suggest that the second peak of *E. affinis* density will occur earlier in the year by the end of the century, in the nearer future, there may be years where the post-freshet occurrence of *E. affinis* is substantially delayed as the Fraser's hydrograph flattens.

Modelling the isolation of Deas Slough from the salt wedge and the loss of salinity from the slough based on only Fraser River discharge at Hope, B.C. and tidal height is a simplification. In the model, EPR dropped to 0.4 eggs female^{-1} d^{-1} 90 days after isolation of the slough, which was my rough approximation of when the slough bottom salinity reached zero. In

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reality, salinity loss depends on the absolute salinity reached in the slough, which in turn is

dependent on the magnitude of river discharge in winter and spring. Therefore, with predicted

increases of river discharge in winter and early spring (Morrison et al. 2002, Shrestha et al. 2012,

Islam et al. 2019a), salinity loss from the slough can be expected to occur more rapidly. For

example, in 2015, which had abnormally high late winter and spring discharge (Fig 5.3), the

highest recorded bottom salinity was 9.5 and it took 50 – 77 days of isolation from the salt

wedge for salinity to reach zero. In 2014, it took 88 – 115 days for the bottom salinity of 17.2 to

drop to zero. Salinity intrusion and the timing of slough isolation will also be influenced by river

inputs downstream of Hope (Pawlowicz et al. 2007). As seen in Figure 5.10, I was unable to

fully explain the timing of post-freshet copepodid abundance because resting egg resuspension

appears to have occurred at a lower salinity intrusion in 2013 compared to 2015. Flows at Port

Mann, $Q_{Port\ Mann}$, located just above the delta entrance, can be estimated using equation 3 from

Pawlowicz et al. (2017),

$$Q_{Port\ Mann} = Q_{Hope} + 5.61 Q_{Chilliwack} + 481$$

where Q_{Hope} and $Q_{Chilliwack}$ are measured flows, in $m^{-3}s^{-1}$, from Environment Canada stations

08MF005 and 08MH001, respectively. Based on this calculation, flows downstream of Hope

during the modelled period of resuspension were ~ 20% higher in both 2013 and 2014 than in

2015, which may have resulted in resuspension occurring later than modelled for those years.

Predicting the timing of the isolation of Deas Slough could be improved by incorporating

estimates for river inputs downstream of Hope into predictive equations for salinity intrusion.

Further, sea level rise was not considered in this model. Increased sea level can be expected to

increase the level of river discharge necessary to isolate Deas Slough. For example, a predicted

increase in relative sea level of ~ 50-cm for the Fraser River delta by the end of the century

(Thomson et al. 2008) could increase salinity intrusion along the South Arm of the estuary by 1-km, which would both increase the absolute salinity reached in the slough and reduce its period of isolation during the freshet (Kostaschuk and Atwood 1990, equation (2)).

In this model, *E. affinis* abundance increased in the warm temperature scenarios because of the accelerating effect of temperature on development time, which assumes that development time is not food-limited. Development rate has been found less sensitive to food-limitation than either growth or reproductive rates (Ban 1994, Campbell et al. 2001). However, there is evidence of food-limited reproduction and body size in the population in autumn (Appendix C) that may have extended over winter. Consequently, I cannot entirely exclude the possibility that developmental rate is limited during those periods. Spring is the period where food-limitation would have the largest impact on abundance because spring resting egg production secures the post-freshet abundance peak. At the time of this study, however, there was no indication of food-limitation occurring in spring.

Potential effects of temperature on reproduction and mortality, albeit potentially substantial, are not included in this model due to uncertainty over their magnitude and direction of forcing. That mortality rates are unlikely to remain unchanged with increased temperature is an important caveat given the sensitivity of the model results to variation in mortality (Figure 5.13). Metabolic demands of predators can be expected to be greater at higher temperature (Gillooly et al. 2001), which could result in increased predation pressure. However, there is also the possibility that increases in temperature may exceed the thermal tolerance of some predator populations (Pörtner & Knust 2007, Eliason et al. 2011). Additionally, changes to the timing of *E. affinis* abundance may increase the likelihood of a mismatch with predator populations, particularly predators that

are temporary residents of the estuary (Asch et al. 2019). Potential mismatch is difficult to assess without information on the predators of *E. affinis*, which I did not collect.

Temperature can also influence EPR. Lloyd et al. (2013) found that due to the reduction of ICT with temperature (Vijverberg 1980), EPR of *E. affinis* in the Chesapeake Bay increased with temperature up until ~ 18 °C, above which, EPR declined because of the negative relationship between temperature and CS. When food is not limiting, PL largely controls CS, but CS appears to be very sensitive to food limitation (Ban 1994, Lloyd et al. 2013). I believe that the effect of current food limitation is captured by the estimates of EPR, but the magnitude and timing of food limitation are unlikely to remain unchanged as water temperatures increase. Rising temperatures may increase the likelihood of food limitation given the increased metabolic demands of zooplankton (Gillooly et al. 2001). However, the food landscape that *E. affinis* encounters in warmer conditions may differ to unknown effect. The relationship between phytoplankton phenology and temperature appears weaker than that of heterotrophic populations (Allen & Wolfe 2013, Asch et al. 2019), which may result in a greater match between phytoplankton and protist grazers (Aberle et al. 2012). This scenario was investigated by Aberle et al. (2012) in a mesocosm-based study that included phytoplankton, microzooplankton, and copepods. The authors found that while increased temperatures in the mesocosms resulted in increased match between microzooplankton and phytoplankton and reduced phytoplankton biomass, copepod density was not affected. The authors ascribed this result to the ability of the copepods included in the study to switch from phytoplankton to microzooplankton prey (Aberle et al. 2012), an ability shared by *E. affinis* (Koski et al. 2002, Modéran et al. 2012). Greater study of phytoplankton, microzooplankton, and zooplanktivore populations in the FRE would increase our ability to anticipate potential effects of warming on FRE zooplankton.

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5.4.4 Summary

In summary, this chapter revealed that resting egg production is necessary to explain high post-freshet abundances of *E. affinis* in Deas Slough. The results of this modelling suggest that increases in temperature and changes to the Fraser River's hydrograph have the potential to result in a near doubling of *E. affinis* copepodid abundance and in large (from 50 days earlier to 25 days later, depending on the forecast period) changes in their population phenology, introducing the potential for match/mismatch with predators and prey (Mackas et al. 2012, Aberle et al. 2012, Asch et al. 2019). In conjunction with these changes in abundance and timing, increases in temperature will result in smaller-bodied *E. affinis* (Atkinson 1994, Daufresne et al. 2009, Forster et al. 2012, Rice et al. 2014, Pierson et al. 2016). Potential impacts on the larger food web are dependent on the trophic importance of *E. affinis* in Deas Slough. *E. affinis* is a key species in the food webs of other estuaries (Winkler & Greve 2004, Shoji et al. 2005, Dauvin & Desroy 2005, David et al. 2006) but its role in the FRE is unknown. *E. affinis* in the FRE is currently largely restricted to sloughs (Chapter 2). Future research should address whether projected changes to discharge and temperature, in combination with predicted changes in sea level, could result in an expansion of *E. affinis* populations into the channels of the estuary, where zooplankton abundance has been found to be low year-round (Chapter 2).

5.5 Tables

Table 5.1 Temperature-specific literature estimates of development time (egg to adult) and generation time (egg to egg) in days of *E. affinis*. Values in brackets following temperatures are salinities.

T °C	Egg – egg	Egg – adult	Location	Citation
10	27.2	26.2	Lake Ohnuma, Japan	Ban (1994)
15	14.4	13.4		
20	11.5	10.6		
10	50.2	43.3	Gironde estuary, France	Poli & Castel (1983)
15	31.7	21.6		
20	22.4	17.2		
25	16.1	13.9		
5.5	92.5	80.5	Patuxent River Estuary, USA	Heinle & Flemer (1975)
10	34.1	30.1		
15	21.9	20		
20	16.5	15		
25	11	10		
2.5		101.7	Tjeukemeer, Netherlands	Vijverberg (1980)
5		61.6		
10		33.1		
15		22.5		
10 (S5)	30.1	28.6	Seine Estuary, France	Devreker et al. (2007, 2009)
10 (S15)	31.4	30.2		
15 (S5)	20.0	19.5		
15 (S15)	20.1	19.6		
8		57.6	Westerschelde, Netherlands	Escaravage & Soetaert (1993)
10		26.8		
14		17.4		
17		14.2		
20		13.5		
2	105		Woods Hole, USA	Katona (1970)
9	36.2			
14	21.2			
19.5	15.6			
21.5	12.8			
23.5	9.4			
5	53		Hamble, UK	
10	28			
15	17			
20	12			
10		27		Vuorinen (1982)
15		18.5		
20		15.5		

Table 5. 1. Continued from previous page

T °C	Egg - egg	Egg – adult	Location	Citation
5		71.6	Darß-Zingst estuary, Baltic	Heerkloss et al. (1993)
10		37.6		
15		24.7		
20		18.2		
3.1	60		Schlei, Germany (North Sea)	Hirche (1974)
9.2	33			
12.1	26			
13	26.8			
16.1	22			
18.3	20			
21.4	18			
19.4	20			
10 (S5)	33	32.0	St. Lawrence, Canada	Beyrend-Dur et al. (2009)
10 (S15)	30.3	29.0		
10 (S15)	33.8	31.8		
10 (S5)	31.4	28.4	Seine Estuary, France	
10 (S15)	33.5	30.5		
14 (S1)	20.3	20.0	Chesapeake, USA	Devreker et al. (2012)
14 (S5)	18.9	18.3		
14 (S15)	20.4	20.1		
18 (S5)	12.2	11.9		
18 (S15)	14.1	13.6		

Table 5.2 Proportion of development time spent within a life stage for *E. affinis* based on stage-specific development times from Heinle (1970), Heinle and Flemer (1975), Escaravage and Soetaert (1993), Ban (1994), Devreker et al. (2007, 2009), and Beyrend-Dur et al. (2009).

Stage	Proportion
Egg	0.1201 ± 0.0209
Nauplius	0.3897 ± 0.0588
CI	0.0882 ± 0.0191
CII	0.0786 ± 0.0087
CIII	0.0835 ± 0.00883
CIV	0.1016 ± 0.0329
CV	0.1432 ± 0.0406

Table 5.3 Egg production rate (EPR; eggs female^{-1} day^{-1}) estimates used in model runs. Note that these EPR are halved, as the model is of females. During and prior to the freshet, EPR increased over the spring and was dependent on time since deepwater renewal of the slough. After deepwater renewal, EPR is decreased after the copepodid abundance exceeds 8000 individuals m^{-3} and declined in two steps to the winter rate.

Condition	EPR
< 90 days since renewal	
Nov – Jan	0.25
Feb – Apr 14	2.85
Apr 15 – Apr 31	3.6
May 1 – Jul 15	7.2
> 90 days since renewal	
	0.4
Post-freshet	
Prior to peak abundance	5.35
1st half of period after peak	2.1
2nd half of period after peak	0.5

Table 5.4 Naupliar and copepodite daily mortality rate (*d*) estimates used in model. Date is introduced only to constrain model behaviour. *G* is an estimate of days since deepwater renewal of Deas Slough, which was calculated as the number of days since salinity intrusion at high tide fell below 18-km. $N_{CI\text{-}VI}$ is copepodid abundance (individuals m^{-3}). Calculated mortalities were bounded by minimum and maximum mortality estimates as indicated by min and max values.

Condition	*d*
Nauplii	
Jan – Feb	0.0405
Spring/early summer, $G <= 25$	0.0271
Spring/early summer, $G > 25$	-0.061 + 0.0024G, min 0.027, max 0.400
Renewal – Aug	0.1140
Sep – Dec	0.0440
Copepodites	
Jan – Feb	0.0325
Spring/early summer, $G <= 25$	0.0807
Spring/early summer, $G > 25$	-0.17 + 0.0055G, min 0.067, max 0.620
Renewal – Nov 15	-0.45 + 0.15Log$_{10}$($N_{CI\text{-}VI}$), min 0.020, max 0.330
Nov 15 – Dec	0.109

Table 5.5 Results of climate model run scenarios. Mean seasonal and annual abundances (individuals m^{-3}) of female *E. affinis* copepodids, maximum copepodid abundances, maximum resting egg abundances, Julian day of maximum copepodid abundance, and the number of models days where copepodid abundance > 5000 individuals m^{-3}.

	Median discharge			2020 discharge			2080 discharge		
	T-1.5	T0	T+1.5	T-1.5	T0	T+1.5	T-1.5	T0	T+1.5
Abundance									
Spring	145	331	703	146	336	711	149	346	725
Summer	71	232	704	32	110	269	2060	3626	7136
Autumn	4214	4830	5502	1860	3775	4076	5095	2733	2745
Annual	1199	1401	1756	579	1150	1343	1868	1716	2690
Maximum	7228	14441	19912	4253	9108	21357	14454	13728	30539
Resting eggs	6702	20184	56519	6462	20382	56495	4262	13952	39312
Timing									
Julian day of maximum abundance	270	266	245	307	300	272	253	213	209
Days of abundance > 5000 ind m^{-3}	28	45	44	0	36	28	63	56	70

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5.6   Figures
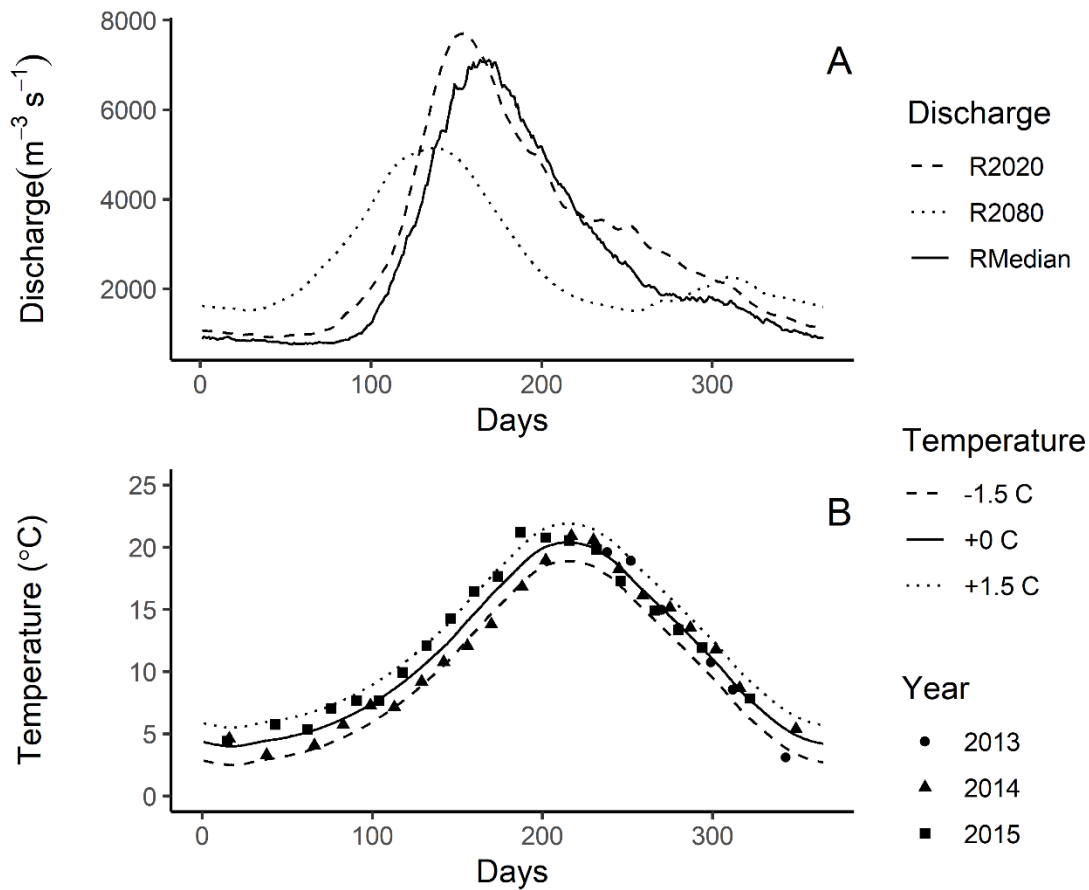
Figure 5.1 Curves are Fraser River discharge (m^{-3} s^{-1}) conditions (A) and temperature (°C) conditions (B) used in model scenarios. Median river discharge (1910 – 2013) was available from wateroffice.eg.gc.ca. R2020 and R2080 discharges were reconstructed, respectively, from Morrison et al. (2002) and Islam et al. (2019a) projections for Fraser River Discharge for the periods 2010 – 2039 and 2070 – 2099, respectively, using WebPlotDigitizer (https://automeris.io/WebPlotDigitizer/). Points in plot B are mean water column temperatures recorded from August 2013 – November 2015 in Deas Slough in the Fraser River Estuary, Canada, that were used to fit temperature curves.
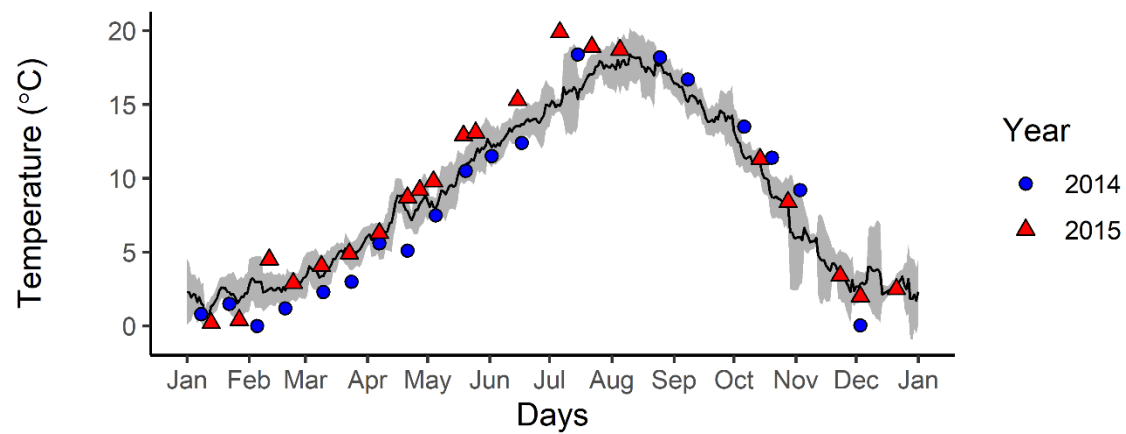
Figure 5.2 Water temperatures (°C) recorded at Hope, British Columbia (08MF005) in 2014 and 2015. The black line with gray shading is a 7-day centered moving average (± 1 standard deviation) of water temperatures recorded for at this location between 1980 and 2009. Data from aquatic.pyr.ec.gc.ca/webdataonlinenational.
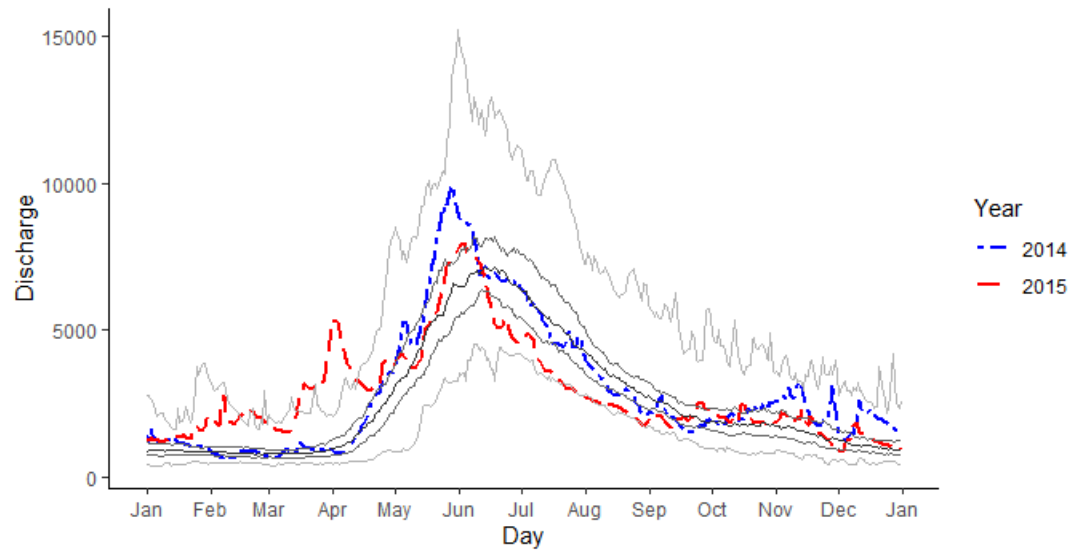
Figure 5.3 River discharge (m^3s^{-1}) at Hope, British Columbia (08MF005) in 2014 and 2015. Median, minimum, maximum, upper, and lower quartiles of river discharge for this location (1912-2013) are plotted in light gray. Data from wateroffice.ec.gc.ca.
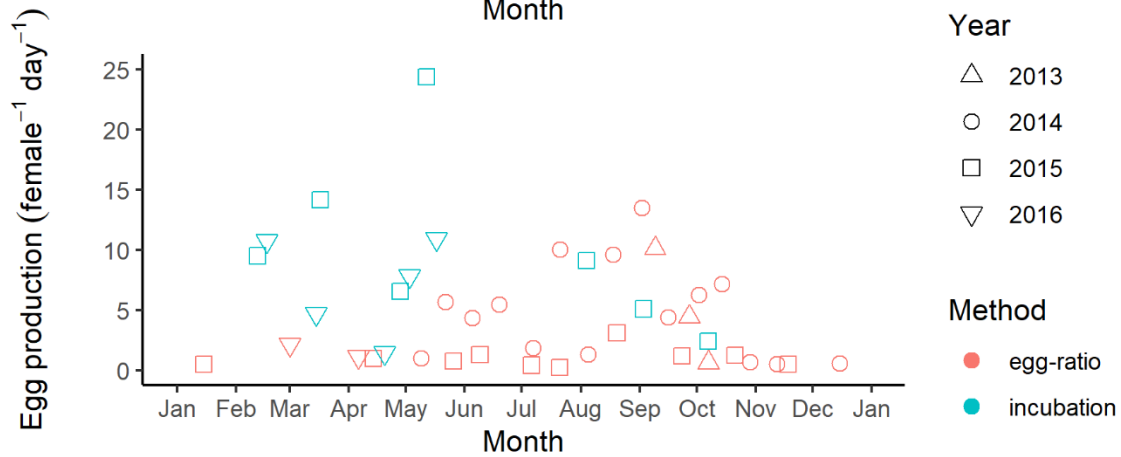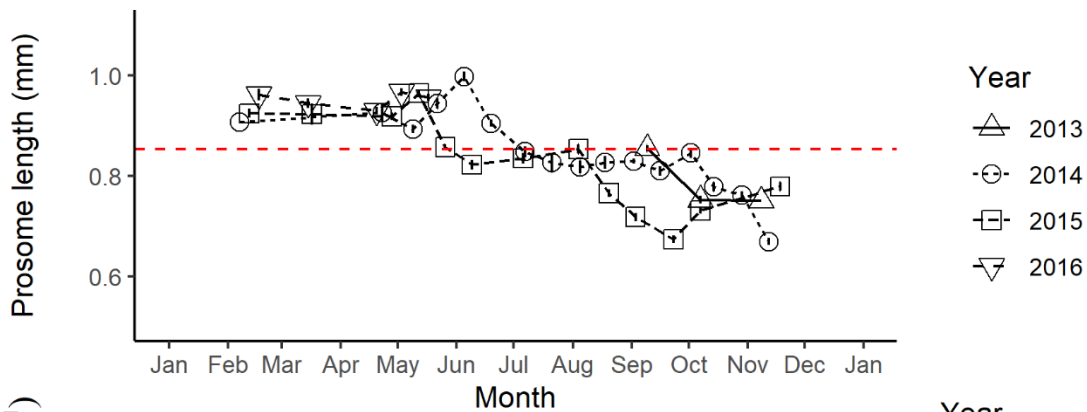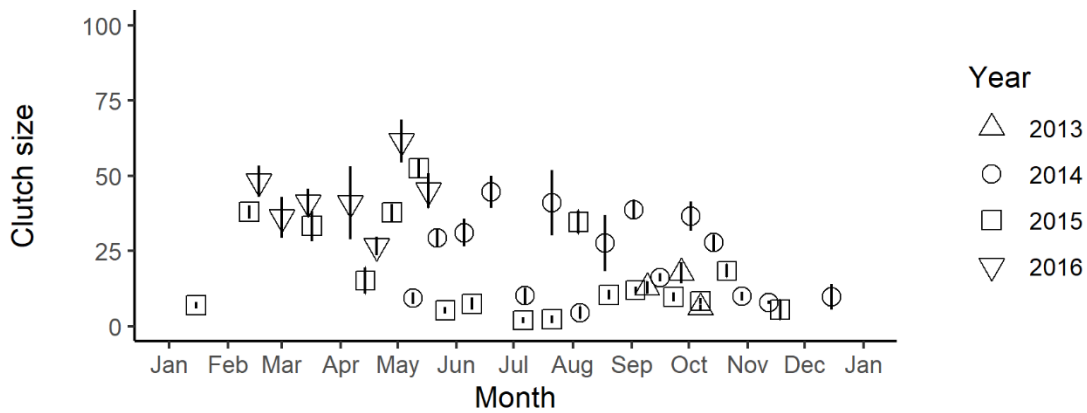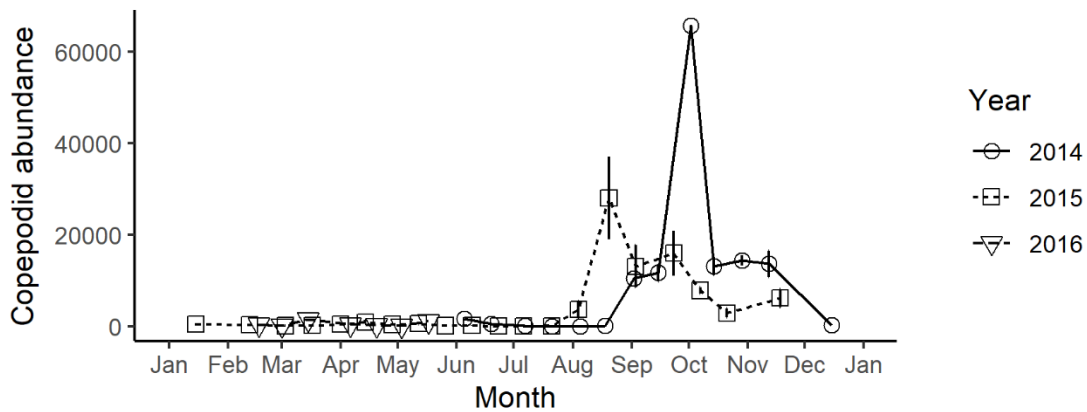
Figure 5.4 Total mean copepodid abundance (A) estimates (individuals m^{-3}) from vertical tows collected from Deas Slough in the Fraser River Estuary, Canada, between June 2014 and May 2016. Clutch sizes (B) and prosome lengths (C) were measured from adult females from Deas Slough collected in both oblique and vertical tows (August 2013 – May 2016), and for incubations (Chapter 3). Clutch size is average number of eggs carried by ovigerous females. Dashed horizontal line is based on the prosome length of adult females raised over the warmest part of the year and indicates expected minimum prosome length for adult females. Error bars are ± 1 standard error of the mean. _E. affinis_ egg production rate (eggs female^{-1} day $^{-1}$, E) estimated between Sep 2013 – May 2016 by incubation and modified egg-ratio method.
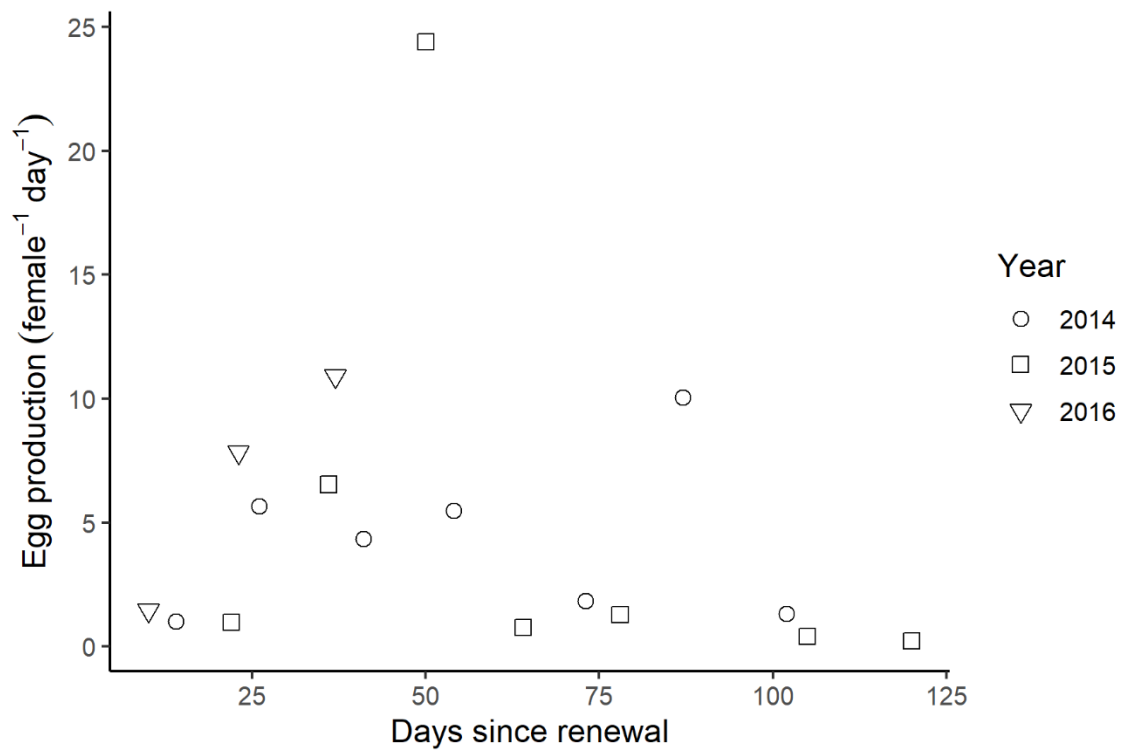
Figure 5.5 Egg production rate (eggs female^{-1} day $^{-1}$) during the period of isolation of Deas Slough from the salt wedge. Days since renewal is the number of days since the salinity intrusion at high water last exceeded 18-km.
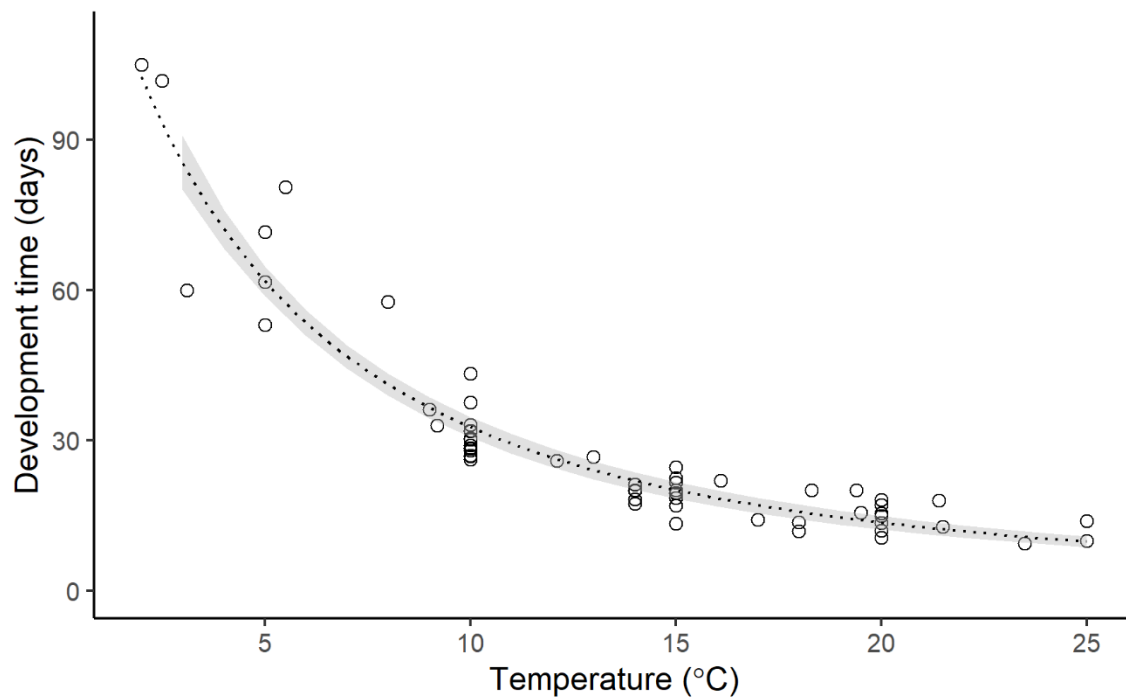
Figure 5.6 Decrease in *E. affinis* development time with increasing temperature. *Dotted line* is a Bĕlehrádek function (1935) that was fitted to temperature-specific estimates (*open circles*) from the studies listed in Table 5.1. The confidence interval (95%) of the curve is shown as a *grey ribbon*. Coefficients were estimated as *a* = 13,272 (11,114 – 15,9298 95%CI) and α = 8.72 (7.58 – 10.06 95%CI).

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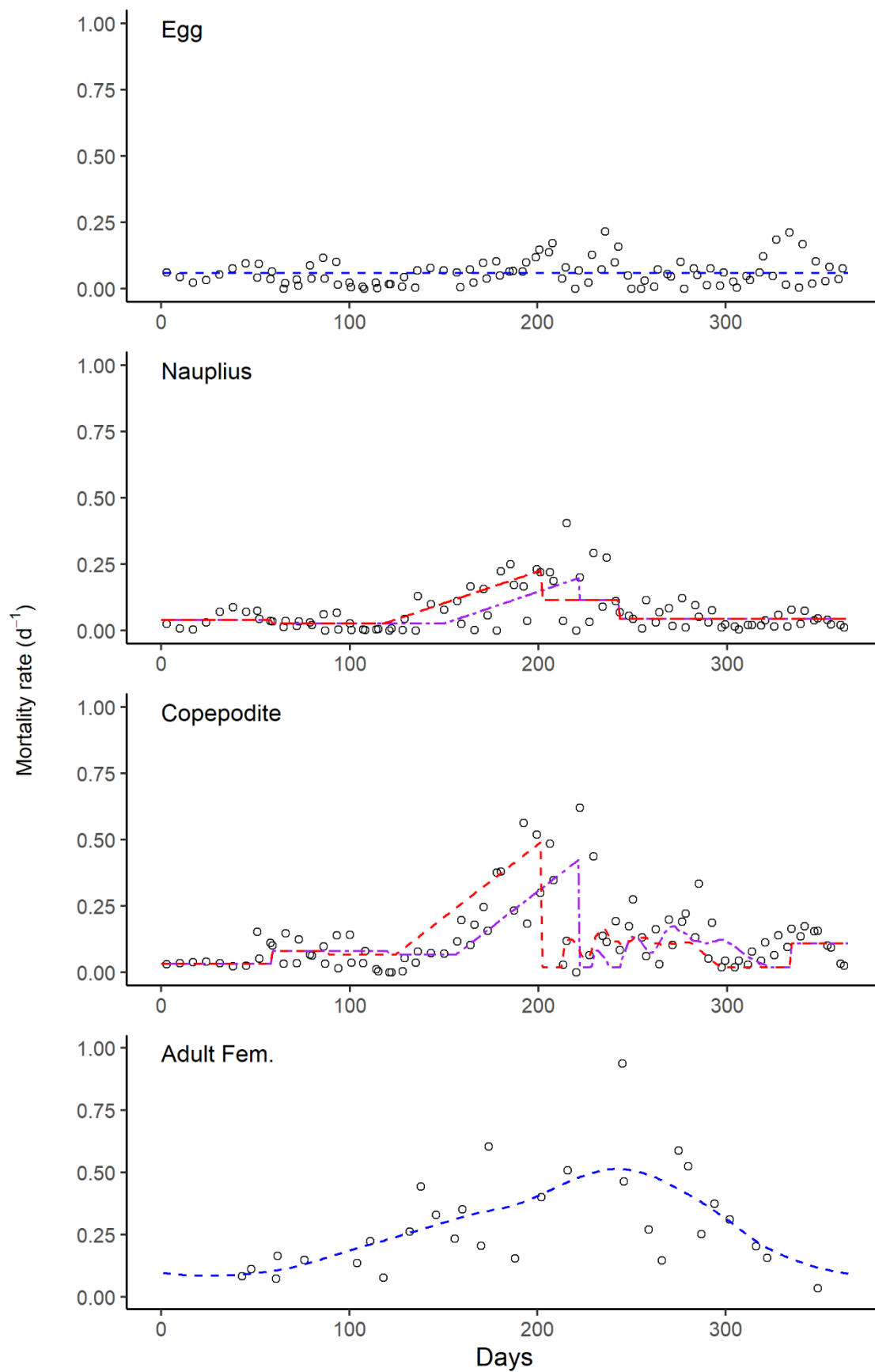
Figure 5.7 (previous page) Mortality rate estimates (*open circles*), by day of the model year, generated using the population surface method (Wood, 1994) for embryonic and juvenile stages and via the VLT approach for adult females. In egg and adult female plots, *dashed lines* show mortality rate for these stages was modelled in my scenarios. In nauplius and copepodite plots, *lines* show how mortality rate can vary between model runs (Shown are mortality rates using river discharge and temperatures from years 2014 (*purple dot-dash line*) and 2015 (*red dashed line*)).
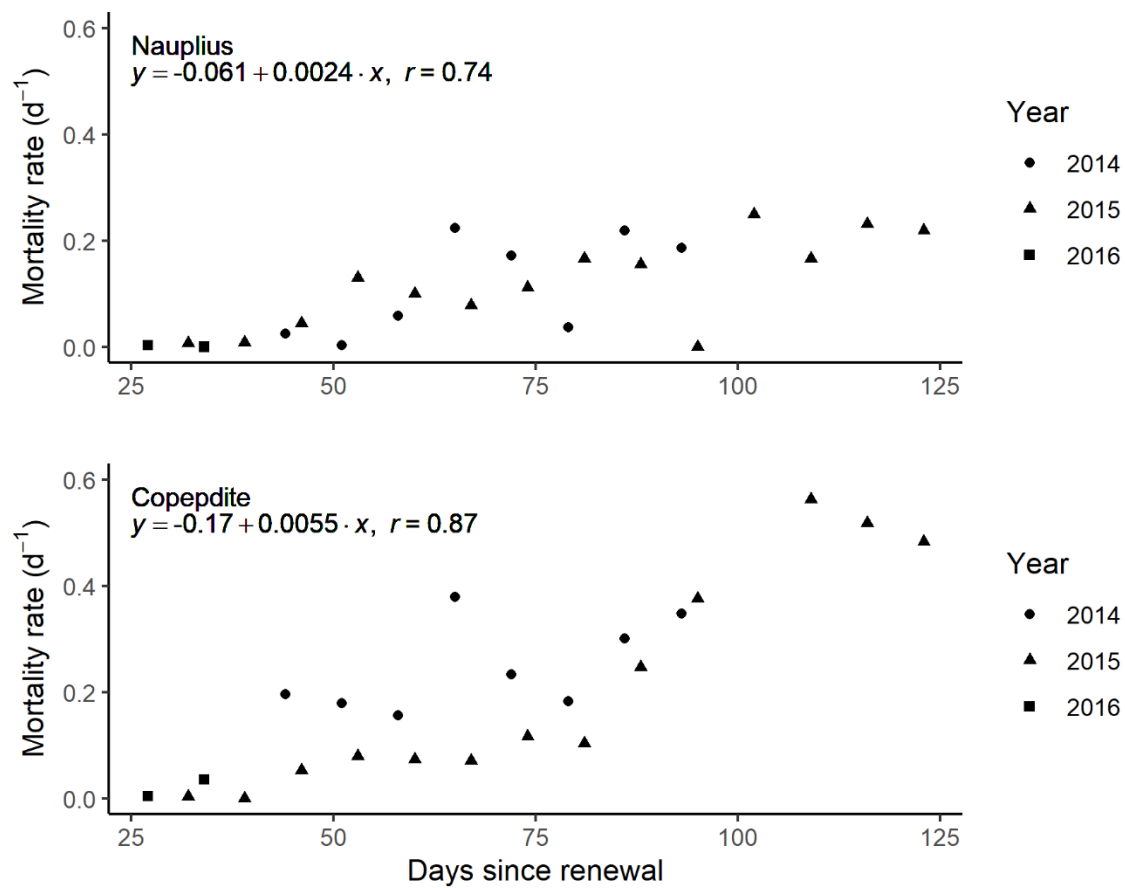
Figure 5.8 Relationship between naupliar and copepodite mortality during the freshet and the number of days since the salt wedge reached the slough (Days since renewal, estimated as the number of days since salinity intrusion at high water fell below 18-km).
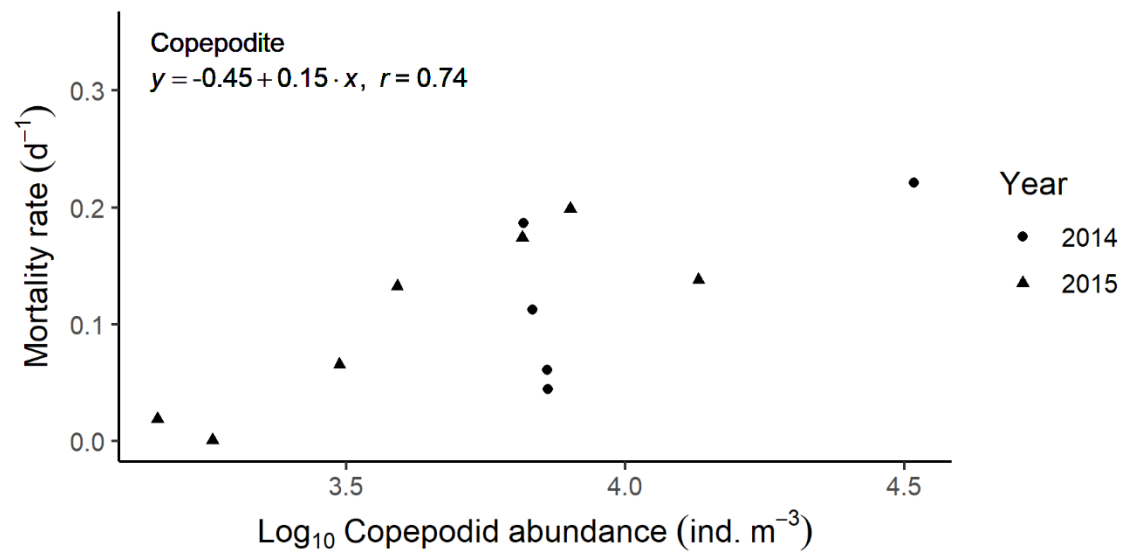
Figure 5.9 Relationship between post-freshet copepodite mortality and log$_{10}$-transformed copepodid abundances (individuals m^{-3}).
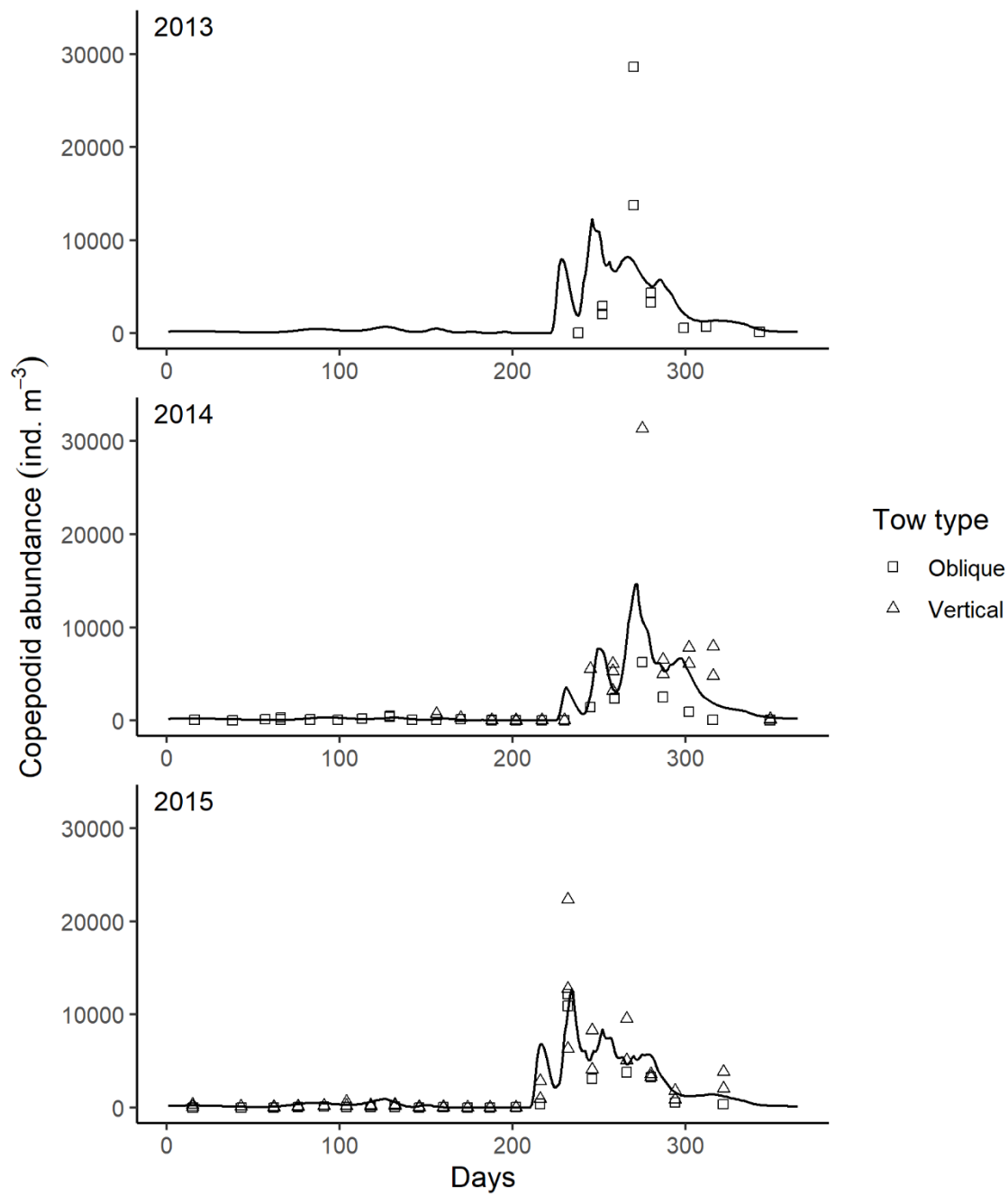
Figure 5.10 Fit of simulated copepodid abundances to abundances estimated from vertical and oblique tows in 2013 - 2015 in Deas Slough, Fraser River Estuary, Canada. Temperature used in simulations of 2014 and 2015 were based on water column average temperatures measurements from that year. Temperature used in simulation of 2013 was that used in the base model, T0.
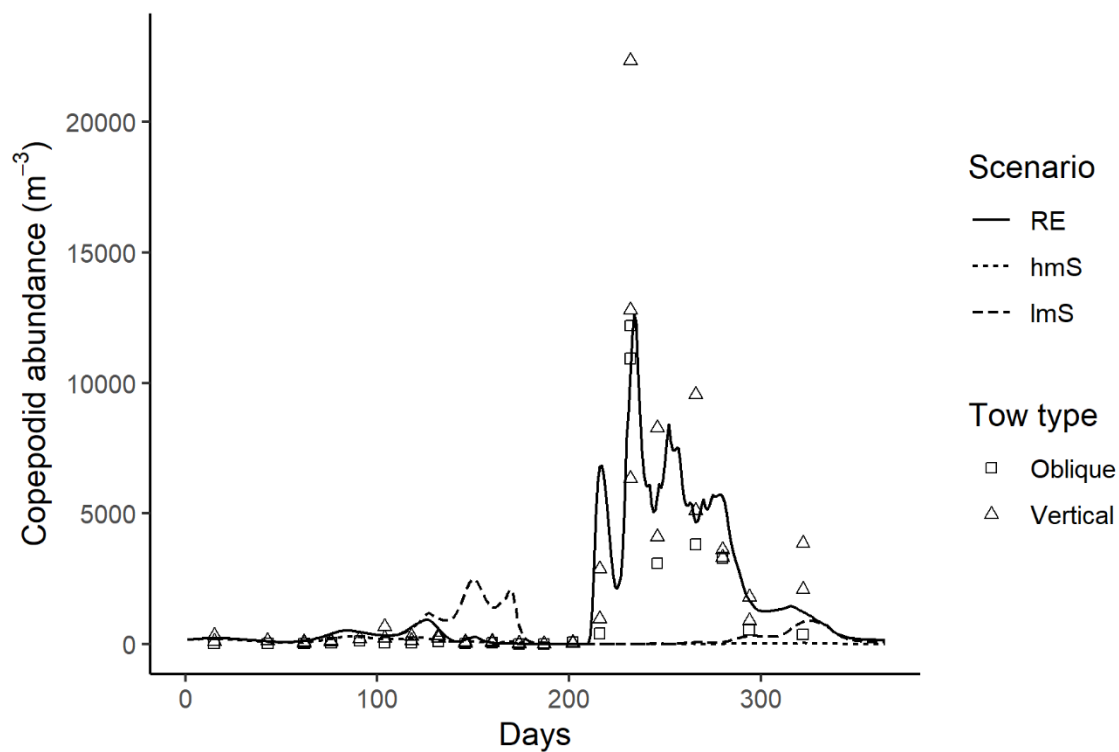
Figure 5.11 Simulated copepodid abundance, by model day, from the fitted 2015 run that included resting egg production (RE) and from high (hmS) and low (lmS) mortality model runs that included only subitaneous egg production. Triangles and squares indicate observed abundances for 2015 from vertical and oblique tows, respectively.
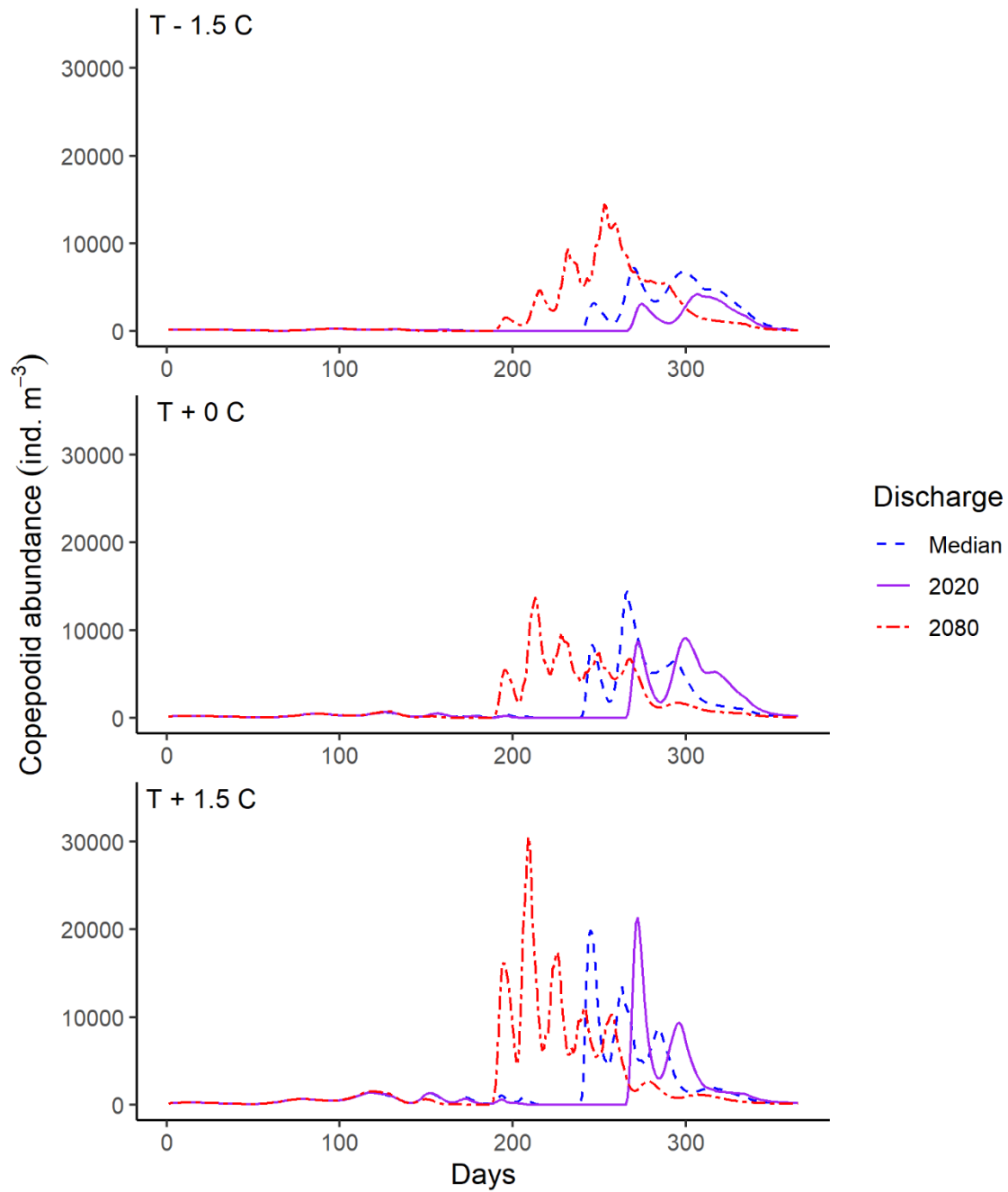
Figure 5.12 Simulated copepodid abundance (individuals m^{-3}), by day of the model year, from temperature and river discharge (m^3 s^{-1}) scenarios. The 2020 and 2080 hydrographs are from Morrison et al. (2020) and Islam et al. (2019a), respectively.
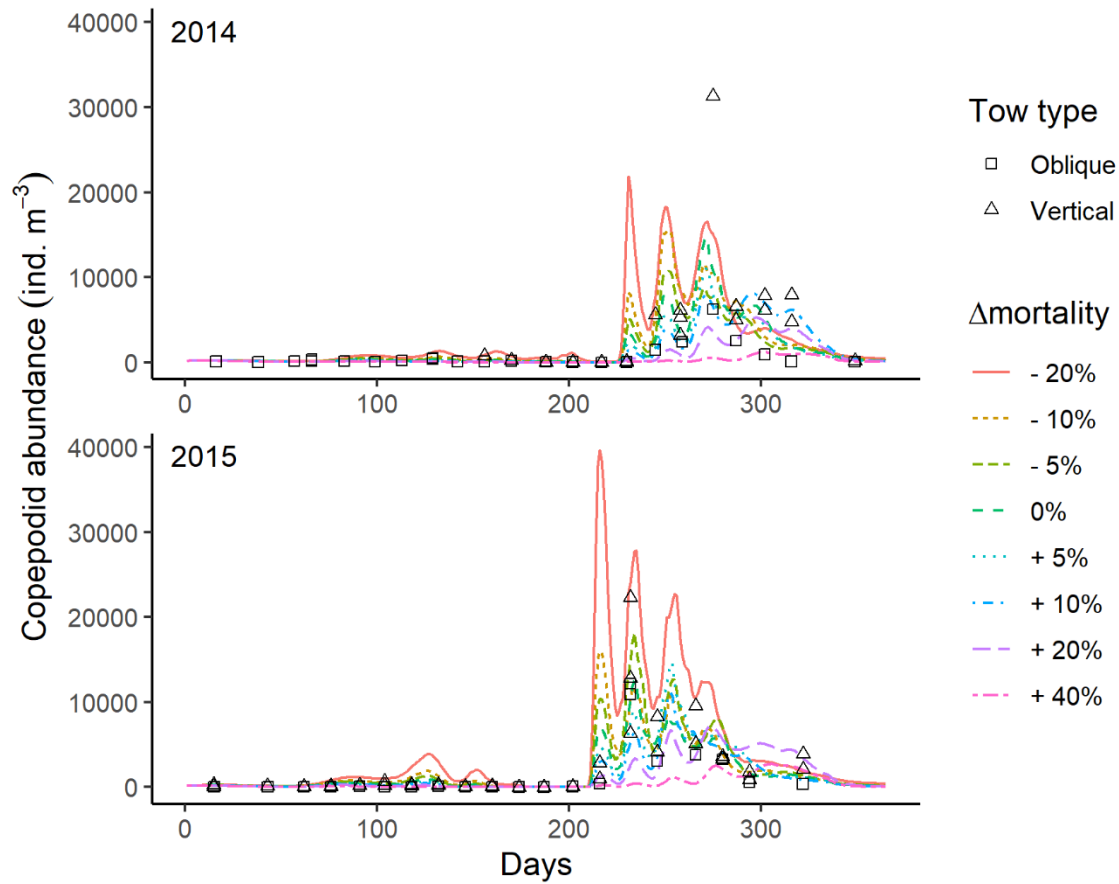
Figure 5.13 Sensitivity of *E. affinis* copepodid abundance (individuals m⁻³) to perturbation in mortality rate. Abundance output for -40% mortality excluded for readability.
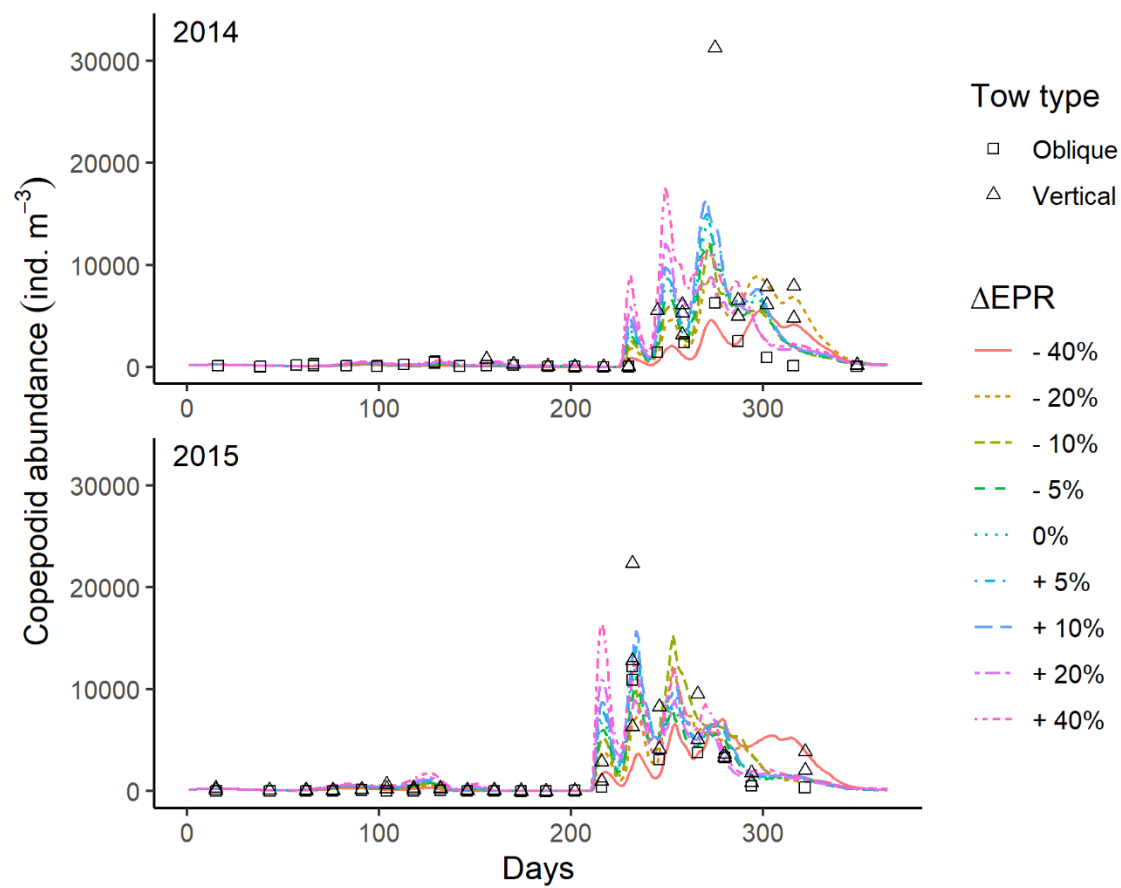
Figure 5.14 Sensitivity of *E. affinis* copepodid abundance (individuals m^{-3}) to perturbation in egg production rate.

Chapter 6: Conclusion

Understanding how predicted changes to climate will influence marine and aquatic ecosystems is among the most pressing tasks facing ecologists today. Predicting the response of estuarine communities is of particular importance, as estuaries are among Earth's most productive environments and support an abundant and diverse megafauna (Nixon 1988, Kennish 2002). This research was motivated by a need to better anticipate how predicted changes in climate would influence the biota residing in or otherwise dependent upon the estuaries of snowmelt-dominated river basins. Zooplankton are important trophic intermediaries in estuarine food webs and their abundance, biomass, and community structure are sensitive to changes in temperature and river discharge (Kimmel & Roman 2004, Costello et al. 2006, Allen et al. 2008, Bollens et al. 2011). My overarching objective with this dissertation was to increase the understanding of zooplankton dynamics in snowmelt-dominated systems and how they will be influenced by predicted changes in water temperature and river discharge through the study of copepods in the Fraser River Estuary (FRE). My specific aims were to (1) describe pelagic copepod dynamics in the FRE, (2) identify environmental drivers of copepod community dynamics in the FRE, (3) identify factors limiting copepod abundance, biomass, and production in the FRE, (4) identify population retention strategies used by *E. affinis* in the FRE, and, finally, to (5) develop a population model able to explore potential effects of projected changes in temperature and Fraser River discharge on the *E. affinis* population.

Chapter 2 presents the results of a 33-month zooplankton monitoring program on the South (Main) Arm of the FRE. This chapter includes the first description of pelagic copepod dynamics in the FRE and provides a useful baseline for future studies. It also provided a record

of the non-indigenous oithonid copepod, identified as *Oithona davisae* on the basis of its morphology, in the FRE. *O. davisae* was at low abundance at the time of my sampling but this species has shown itself capable of becoming a dominant member of the mesozooplankton community in other estuaries on the Pacific Coast (Bollens et al. 2011, Cordell et al. 2015).

Zooplankton abundance was low in the FRE (Figure 2.6) and I suggest that zooplankton production in the FRE is limited by water residence time (Chapter 2). This conclusion was supported by 3 findings: 1) minimum copepod abundance and production occurred in late spring, coinciding with the Fraser's freshet, 2) copepod abundance and production were much higher in areas of the estuary that had higher water residence time, and 3) estuarine copepods were largely restricted to areas of the estuary that had higher water residence time. Unlike what we observed in the FRE, minima of zooplankton and copepod abundance, biomass, and production in temperate estuaries typically occur in winter (Escaravage & Soetaert 1993, David et al. 2006, Islam et al. 2006, Leandro et al. 2007, Bollens et al. 2011), similar to other temperate aquatic systems. The reduced copepod abundances in channels and the restriction of estuarine copepods to sloughs that was observed in the FRE are also atypical findings for an estuary. Variation in zooplankton community composition in an estuary is typically described in terms of salinity and temperature (Bousfield et al. 1975, Miller 1983, Soetaert & Van Rijswijk 1993, Bollens et al. 2011) but in the FRE the greatest determinant of community composition after salinity was whether the sample was taken from a slough or a channel area. In the FRE, water residence times in the channels have been reduced through dredging and channelization. That limitation of zooplankton production likely resulted from, or was exacerbated by, human modifications of the estuary is an important implication of this work. The low zooplankton abundance observed in the FRE may then be a result of physical changes made to the river and estuary rather than a feature

of snowmelt-dominated systems, however this highlights a potentially greater sensitivity of pelagic secondary production to change in hydromorphology in snowmelt-dominated systems.

Mechanisms of population maintenance are central to understanding estuarine zooplankton ecology and to modelling zooplankton dynamics in estuaries. Chapters 3 and 4 address separate strategies for population maintenance in *E. affinis*. In Chapter 3, I investigated the occurrence and timing of resting egg production in *E. affinis*, which is a species which typically carries subitaneous eggs until they hatch, in a series of incubations. *E. affinis* females dropped eggs in May 2015 and again in May 2016, towards the beginning of the freshet. That resting eggs were required to explain observed abundances of *E. affinis* in Deas Slough provides further evidence that these dropped eggs were in fact resting eggs (Chapter 5). Previous authors had speculated on the potential of benthic resting eggs for the maintenance of populations within estuaries (Uye 1980, Runge & Simard 1990, Newton & Mitchell 1999), however, to my knowledge, Chapter 3 presents the first evidence of resting egg production to avoid periods of low salinity and/or rapid flushing in an estuarine species. In Chapter 4, I used vertically discrete sampling to describe the depth distributions of abundant copepods in Deas Slough and compared the distributions of estuarine taxa to those of marine and freshwater taxa. The change in vertical distribution of *E. affinis* over the sampled tidal cycles strongly suggested the presence of vertical migration behaviour that would promote retention within the estuary. This behaviour was largely suppressed during daylight, with *E. affinis* remaining at depth. To my knowledge, this is the first report of an interaction of TVM and DVM behaviours in *E. affinis*. Further, the presence of DVM suggests that selective pressure on *E. affinis* from visual predators is strong in the FRE, despite high turbidity (Bollens & Frost 1991, Hays 2003). Chapters 3 and 4 provide evidence that *E. affinis* in the FRE employ both a behavioural and a life history strategy targeted toward

retention in the estuary. Nonetheless, the near absence of *E. affinis* in channel areas of this estuary suggests that these strategies are insufficient for retention in the larger estuary where residence times are substantially lower.

The importance of resting egg production to *E. affinis* population dynamics in Deas Slough was explored in Chapter 5, as were potential responses of the *E. affinis* population to changes in water temperature and Fraser River discharge. I developed a stage-structured, concentration-based population model, forced by water temperature and Fraser River discharge, that was able to replicate observed population dynamics of *E. affinis* in Deas Slough. Resting eggs were necessary to reproduce the high *E. affinis* abundance observed during early autumn. Model results suggest that predicted changes in water temperature and to the Fraser River's hydrograph have the potential to result in a near doubling (+ 92%) of abundance of *E. affinis* and also in large changes in their phenology. Simulated *E. affinis* abundances increased as a result of more rapid generation times in response to elevated temperature despite an earlier freshet that effectively reduced the period of resting egg production by ~ 6 weeks. Further, the extension of the post-freshet growing season to include July, when temperatures are at a maximum, reduced the reliance of later summer and autumn abundances on the post-freshet hatching of resting eggs. Changes in the timing of *E. affinis* occurrence may alter the degree of match or mismatch with predators and prey (Mackas et al. 2012, Aberle et al. 2012, Asch et al. 2019).

The research presented in this dissertation suggests that zooplankton dynamics in the FRE, and potentially in other snowmelt-dominated systems, may differ from those in temperate estuarine systems fed by pluvial-dominated or highly-regulated rivers. The occurrence of peak river discharge in the middle of the growing season caused abundance minima to occur in late spring in the FRE and maximum abundance to occur to occur in late summer or early autumn.

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Further, the estuarine copepods typically responsible for the high mesozooplankton in estuaries were largely restricted to sheltered sloughs in the FRE. The production of resting eggs by the estuarine specialist *E. affinis* to bridge the period of the freshet (Chapter 3), in addition to tidal vertical migration behaviour (Chapter 4), points to strong selection for population maintenance strategies and highlights how advection risk has shaped the life history of the *E. affinis* population of the FRE. Finally, the importance of advection in the control of copepod abundance, community composition, and phenology in the FRE (Chapters 2 and 5) suggests that that zooplankton production in the FRE, and perhaps other estuaries of snowmelt-dominated river systems, are sensitive to changes in the timing and magnitude of river discharge and, further, may be reduced by estuarine and river channelization.

6.1   Limitations

The abundance data presented in this dissertation, with the exception of Chapter 4, come from net tows and so are subject to a range of methodological issues, such as the possibility of extrusion, clogging, and net avoidance impacting the accuracy of estimates (Sameoto et al. 2000). To reduce the likelihood of extrusion and net avoidance, tows were brought in at a rate of < 1 m s^{-1}. To account for any potential clogging, a flowmeter was mounted in the mouth of the net for more accurate estimates of volume filtered, however progressive clogging of the mesh may have resulted in more accurate sampling at the beginning of the tow than at the end. Because vertical distribution can vary with ontogeny, progressive clogging of the net and not sampling to the bottom of the water column can both affect the accuracy of descriptions of population stage structure. It is not generally advisable to take the mouth of a plankton net to the sediment; however, I did so with the vertical tows in Deas Slough to be able to more accurately

describe changes in population stage structure but that accuracy may still have been reduced by clogging.

Some features of my sampling program may have resulted in an underestimation of mesozooplankton abundance. With the exception of sampling for Chapter 4, zooplankton samples were collected during daylight hours, which increases the likelihood of net avoidance and also of individuals that possess DVM behaviour being beneath the sampled depth. Estuarine zooplankton may maintain a near-bottom depth distribution (Sibert 1981; Ueda et al. 2004; Chapter 4) and my oblique tows necessarily missed the bottom meters of water column. While I tried to minimize this error by sampling on flood tides (where distributions would be shallower due to either vertical migration or resuspension), it is likely that the oblique tows underestimated mesozooplankton abundance. Additionally, with oblique tows it is difficult to be certain of what depth was sampled, this is particularly true when sampling along a salt wedge when the angle of the tow may change rapidly. Nonetheless, these issues are common to most sampling programs in estuaries, and should not preclude comparison to zooplankton abundances in other estuarine systems.

Much the research presented in this dissertation (Chapters 3, 4, & 5) was focused in Deas Slough because of the high mesozooplankton densities observed at that location (Chapter 2). Vertical distributions observed in the slough should not be extended to the channel areas of the estuary as vertical migratory behaviour, while likely still present, may be modified or manifest differently in areas of higher current velocity. Likewise, if an environmental cue is necessary to stimulate the production of resting eggs by *E. afffinis*, it is possible that this cue is not present in the channel areas of the estuary or that the timing of cue differs. Finally, the population model I developed is specific to the slough environment and uses location-specific values of EPR and

mortality. *E. affinis* population dynamics in the channels of the estuary can be expected to be much more directly forced by advection rather than by biological processes.

The emphasis of this dissertation has been on the estuarine calanoid copepod *E. affinis* due to its abundance in the FRE and its importance in other estuarine systems (Simenstad et al. 1990, Winkler et al. 2003, Dauvin & Desroy 2005). *E. affinis* is a species complex comprised of at least 6 genetically distinct clades (Lee 2000, Winkler et al. 2008). By reason of geography, *E. affinis* in the FRE likely belongs to the North Pacific clade, which remains largely unstudied. Alternatively (or additionally), as an international port, it is possible that the FRE is home to non-indigenous populations of *E. affinis*. Populations of the Atlantic clade (recently renamed as *E. carolleea* (Alekseev & Souissi 2011)) are present on the Pacific Coast of the United States in both the San Francisco (California, USA) and Grays Harbor (Washington, USA) estuaries (Lee 2000). Throughout this thesis, I compared the population dynamics, life history strategies, and behaviours observed in *E. affinis* in the FRE to those observed in the much better studied *E. affinis* populations of other regions. In Chapter 5, I used development times from *E. affinis* of other clades to model the effect of temperature on development times, my estimates of EPR used Vijverberg's (1980) empirical equation predicting ICT from temperature, which was derived from a Baltic *E. affinis* population, and I used the relationships between PL and CS from *E. affinis* in Lake Ohnuma, Japan, and the Cheseapeake Bay, USA, to assess potential food limitation. These comparisons are made with caution as evidence exists that the different clades of *E. affinis* are not necessarily interchangeable with respect to either physiology or ecology (Beyrend-Dur et al. 2009, Favier & Winkler 2014). Additionally, I have assumed that a single species of *E. affinis* was present in the FRE, however, multiple clades of *E. affinis* coexist in

other estuaries (Winkler et al. 2008, Alekseev & Souissi 2011) and I cannot preclude that possibility in the FRE.

6.2   Implications and future research

The production of resting eggs by *E. affinis* to bridge periods of high river discharge that is suggested by my results raises the question of how widespread this life history strategy is among *E. affinis* and other estuarine zooplankton. My model results suggest that resting egg production was responsible for the high abundances of E. affinis observed in Deas Slough. *E. affinis* eggs were not the only eggs I observed in the sediments of Deas Slough (pers. obs.) and further study into the locations and composition of egg banks in the estuary could be of interest. In the FRE, channel depth is maintained by dredging and how this practice influences the functioning of egg banks is worthy of study. I did not identify whether the resting eggs produced by *E. affinis* were quiescent or diapausing eggs. This distinction is important, however, because the manner of initiation and termination of the resting period differ between the two egg types as does their period of viability (Drillet et al. 2006, Sichlau et al. 2011, Hansen 2019). Briefly, diapause eggs are typically produced in anticipation of adverse conditions and the stimulus for production acts on the female copepod (Dahms 1995, Marcus 1996). Diapause eggs must undergo a refractory period, the duration of which can vary substantially in length and be dependent the on environment, prior to hatching (Marcus 1996). In contrast, quiescent eggs are subitaneous eggs whose development is arrested in direct response to adverse conditions and whose development resumes when conditions improve (Danks 1987, Marcus 1996). Diapause eggs may remain viable for decades, whereas the hatching rate of quiescent eggs may decrease after only a year (Hairston et al. 1995, Drillet et al. 2006, Sichlau et al. 2011). Further effort to

characterize the resting eggs produced by *E. affinis* would help us better understand flexibility of timing of resting egg production and hatching and the role egg banks may play in the population's response to changes in climate.

In addition to changes in abundance and phenology, changes in climate may bring about a reduction of copepod size and also a change in species composition by altering the temperature-salinity conditions available within the estuary (Atkinson 1994, Rice et al. 2014, Pierson et al. 2016). Notably, this project had originally intended to model the dynamics of a second *Eurytemora* species, *E. americana*, that resides in a niche that is higher salinity and lower temperature than that of *E. affinis*. I had to drop the species from the project because it was virtually absent in spring 2015, likely due to reduced salinities in the estuary. Further changes in species composition can result from species introductions. I only found one non-indigenous copepod species in the FRE; however, increases in water temperature might increase the likelihood that non-indigenous copepods become established and increase in abundance within the estuary. Indeed, prevalence of non-indigenous copepods is greater in the warm season in both the Columbia River and San Francisco Bay estuaries (Bollens et al. 2011, Breckenridge et al. 2015).

What impact changes to the timing, abundance, size, or composition of the mesozooplankton may have on the larger FRE ecosystem largely depends on trophic ramifications. While mesozooplankton made up a large portion to the diet of juvenile sockeye rearing in Deas Slough (Birtwell et al. 1987a), the importance of mesozooplankton in the larger FRE food web is not well understood. Mesozooplankton, and *E. affinis* in particular, are considered an important part of the food web in many studied estuaries, typically serving as a link from phytoplankton and detritus to juvenile fish and *Neomysis* spp. and/or other

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malacostracan species (Winkler et al. 2003, Dauvin & Desroy 2005, David et al. 2006).

Neomysis spp., including *N. mercedis*, are considered a major predator of *E. affinis* in other estuaries (Siegfried & Kopache 1980, Fockedey & Mees 1999, Winkler et al. 2003), but in a diet investigation of *N. mercedis* collected at Woodward Island in the FRE, *E. affinis* were not found, though authors noted significant predation on estuarine harpacticoids (Johnston & Lasenby 1982). It would be interesting to compare diets of *N. mercedis* and other zooplanktivorous species collected in slough and channel areas. Both the highly male-skewed sex ratio (Appendix D) and the effect of light on tidal vertical migratory behaviour in *E. affinis* (Chapter 4) suggest strong pressure from visual predators, which are typically fish.

I began my PhD with an interest in how changes in climate would affect the Fraser River Estuary ecosystem, but over the course of my research, I've become increasingly interested in how past physical modifications have altered this system and its productivity. In the present-day estuary, water residence times and current velocity are largely coupled to river discharge. When the floodplain of the Fraser River was intact, waters would have spilled over the banks of the channels during the freshet, creating large areas of relatively shallow, slow-moving water. Prior to the construction of the Iona and Steveston jetties, the Fraser's plume would have remained nearer the delta, instead of being jetted across the Strait of Georgia. The effect of the freshet on water residence times (and therefore mesozooplankton) in the estuary would have been muted. Mesozooplankton production in the present-day estuary is thus more sensitive to changes in the timing and magnitude of river discharge than it would have been prior to European settlement, which raises the possibility that the physical modifications made to the estuary have decreased its resilience in face of climate change. A most interesting avenue of research would be to pursue this line of thinking and attempt to reconstruct zooplankton production in the historical estuary.

The reconstruction would require modelling both current and historical water residence times. Not only would such a retrospective study be valuable to inform potential restoration efforts but could provide important lessons on the potential consequences of development within estuaries.

Finally, the research I present in this dissertation suggests that zooplankton production in the FRE is very sensitive to the changes in hydrology and hydromorphology that can occur as a result of climate-induced alteration of river discharge or of physical modification to the estuary or river. The sensitivity to the timing of peak river discharge may be a result of human-made changes to the hydromorphology of the FRE rather than a feature of snowmelt-dominated estuarine systems, which suggests that river training modifications may negatively impact the resilience of these systems. Given the large change that is occurring to their hydrologic cycles (Nijssen et al. 2001, Wu et al. 2012), more study of snowmelt-dominated estuaries is warranted.

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Appendices

Appendix A : Supplementary information for Chapter 2

Table A. 1 Mean abundance (individuals m^{-3}) by station of copepod taxa present in > 10% of samples over the study period (August 2013 – May 2016). Abundances of adults are listed separately where I could not identify copepodite stages to species.

Taxon	Stations							
	S1	S2	C1	C2	C3	C4	R1	M1
Copepod nauplii	8109	8649	900	1089	629	2353	509	14391
Calanoida								
Acartia spp.	17	--	< 1	1	1	3	--	59
Acartia hudsonica	10	< 1	--	< 1	< 1	2	--	1
Acartia longiremis	< 1	--	1	< 1	< 1	3	--	66
Calanoida spp.	5	1	1	14	10	71	< 1	2286
Epischura nevadensis	13	12	2	20	23	2	28	--
Eurytemora spp. CI-CV	2343	388	3	35	21	2	--	--
Eurytemora affinis CVI	211	13	1	3	< 1	< 1	--	--
Eurytemora americana CVI	2	< 1	--	2	< 1	< 1	--	--
Diaptomidae CI-CV	83	96	138	76	82	47	106	--
Leptodiaptomus ashlandi CVI	20	24	74	65	58	26	13	--
Paracalanus spp.	--	--	16	5	17	904	--	2828
Pseudocalanus spp.	12	--	20	20	20	137	--	258
Skistodiaptomus spp. CVI	3	3	6	8	7	1	20	--

Table A.1 (con't)

Taxon	S1	S2	C1	C2	C3	C4	R1	M1
Cyclopoida								
Acanthocyclops spp.	1	19	1	< 1	1	< 1	< 1	--
Diacyclops thomasi	2081	339	21	35	16	12	70	--
Corycaeidae spp.	--	< 1	5	3	7	86	--	414
Cyclops spp.	< 1	< 1	2	3	< 1	2	--	--
Cyclopidae spp.	107	144	46	22	35	19	7	--
Oithona davisae	4	14	4	2	2	4	--	--
Oithona similis	< 1	--	57	21	11	885	--	1827
Oncaeidae	--	1	20	9	1	61	--	223
Harpacticoida								
Coullana canadensis	222	96	47	26	2	6	< 1	3
Halicyclops spp.	23	10	1	1	< 1	< 1	--	--
Harpacticoida spp.	88	301	31	72	208	67	8	2
Huntemannia jadensis	0	0	1	< 1	< 1	0	0	0
Microsetella spp.	< 1	0	3	2	< 1	9	0	3
Pseudobradya spp.	1046	1216	83	163	108	11	26	21

Table A. 2 List of copepod taxa identified over the course of this study by habitat category. Genus level identifications omitted where their categorization did not differ from that of species level identifications. Order level identifications represent individuals that I was not able to identify to a finer resolution.

Estuarine	Freshwater	Marine	Uncategorized
Acartia hudsonica	*Acanthocyclops robustus*	*Acartia longiremis*	*Acartia* spp.
Coullana canadensis	*Cyclops scutifer scutifer*	*Aetideus armatus*	*Ergasilus* spp.
Eurytemora affinis	*Diacyclops thomasi*	*Calanus marshallae*	Calanoida
Eurytemora americana	*Epischura nevadensis*	*Calanus pacificus*	Caligidae
Euterpina acutifrons	*Eucyclops agilis*	*Candacia* sp.	Cyclopidae
Diarthrodes spp.	*Eucyclops elegans/speratus*	*Centropages abdominalis*	Cyclopoida
Halicyclops spp.	*Leptodiaptomus ashlandi*	*Ditrichocorycaeus anglicus*	
Harpacticoida	*Macrocyclops albidus*	*Onychocorycaeus catus*	
Harpacticus spp.	*Mesocyclops edax*	*Epiladocera* spp.	
Huntemannia jadensis	*Microcyclops* spp.	*Eucalanus bungii*	
Leimia vaga	*Paracyclops chiltoni*	Euchaetidae	
Mesochra alaskana	*Paracyclops poppei*	*Gaetanus* spp.	
Microarthridion littorale	*Skistodiaptomus oregonensis*	*Paracalanus parvus*	
Neotachidius triangularis	*Skistodiaptomus pallidus*	*Paracalanus quasimodo*	
Nitokra spp.		*Pseudocalanus mimus*	
Oithona davisae		*Pseudocalanus minutus*	
Onychocamptus spp.		*Pseudocalanus moultoni*	
Pseudobraya spp.		*Pseudocalanus newmani*	
Schizopera spp.		*Scolecithricella minor*	
Tachidius discipes		*Tortanus discaudatus*	
Tisbe spp.		*Metridia pacifica*	
		Microcalanus pusillus	
		Microsetella norvegica	
		Microsetella rosea	
		Monothula subtilis	
		Neocalanus sp.	
		*Oithona (Paroithona) s*pp.	
		Oithona atlantica	
		Oithona similis	
		Oithona spinirostris	
		Oncaeidae	
		Pontellidae	
		Triconia borealis	
		Triconia conifera	
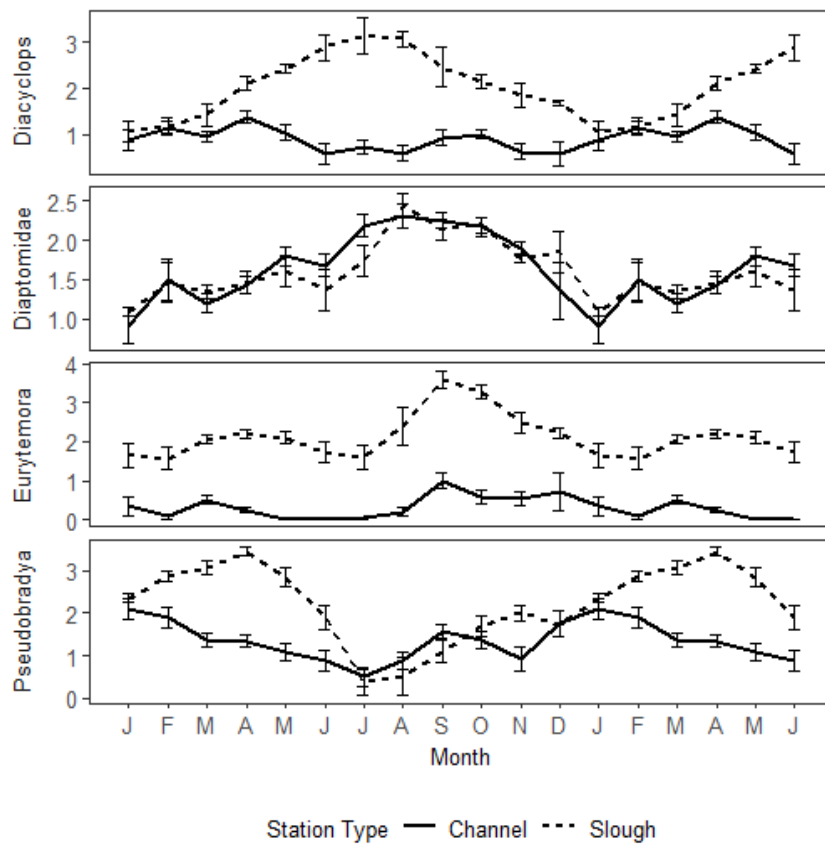
Figure A. 1 Mean annual variation in the log abundance (individuals m⁻³) of *Diacyclops thomasi*, freshwater

diaptomids (Adults of *Leptodiaptomus ashlandi* and of *Skistodiaptomus* spp. + diaptomid copepodites),

***Eurytemora affinis* (*E. affinis* adults + *Eurytemora* spp. copepodites), and *Pseudobradya* spp. for channel and**

slough stations from August 2013 – May 2016, in the Fraser River Estuary, B.C., Canada. Annual monthly

averages have been extended over an 18-month period to improve interpretability. Data for graphs were

weighted to ensure that each year had equal influence on mean values, despite differing sampling effort

between years. Bootstrapping (1000 interactions) was used to estimate standard error because means were

weighted

Table A. 3 Pearson's *r* correlations of environmental variables to NMS ordination axes. Variables with *r* > 0.3 are listed

Variable	Axis 1	Axis 2	Axis 3
Day of year	--	--	-0.561
Temperature			
Maximum	-0.349	--	-0.594
Minimum	-0.469	--	-0.565
Mean	-0.406	--	-0.594
Salinity			
Maximum	0.699	--	--
Mean	0.823	--	--
Minimum	0.465	--	--
Stratification	0.661	--	--
Discharge (m^3s^{-1})			
Maximum during previous 2 weeks	-0.397	--	--
2-day lag	-0.383	--	--

Table A. 4 Mean abundances (individuals m^{-3}), by station, of non-copepod taxa collected in oblique tows. Rare taxa excluded or, where available, added into higher taxonomic grouping.

	Patullo (R1)	Deas Slough (S1)	Ladner Slough (S2)	Massey (C1)	Wellington (C2)	Cannery Channel (C3)	Jetty (C4)	Sand Heads (C5)
Arthropoda								
Bosmina spp. (mostly *B. longirostris*)	50	27	91	60	26	32	21	
Camptocercus spp.		< 1		2	< 1	< 1		
Chydoridae (includes *Chydorus* and *Leydigia*)	5	3	3	8	4	2	2	
Monospilus dispar		< 1	< 1				< 1	
Eurycercus spp.	< 1			< 1	< 1	< 0.1	< 1	
Alona spp.	< 1	< 1	3	< 1			< 1	
Daphnia spp. (*D. ambigua, D. pulex, D. mendotae* group, *D. longiremus*)	6	2	4	4	4	2	1	
Ceriodaphnia spp.	< 1	< 1	6	8	3	7	1	
Leptodora kindtii	< 1	2	< 0.1	< 1	< 1	< 0.1		
Holopedium gibberum	1	< 1		1	< 1	< 1	< 1	
Moina spp.			< 0.1	< 0.1		< 0.1		
Diaphanosoma spp.	1	24	4	< 1	1	< 1	< 1	
Sida crystallina		< 0.1		< 0.1	< 0.1		< 0.1	
Podonidae (*Podon leuckarti + Pleopsis polyphemoides*)		< 0.1		< 0.1		< 0.1	6	240
Evadne nordmani						< 0.1	< 0.1	10
Polyphemus pediculus	< 0.1			< 0.1		< 0.1		

	Patullo (R1)	Deas Slough (S1)	Ladner Slough (S2)	Massey (C1)	Wellington (C2)	Cannery Channel (C3)	Jetty (C4)	Sand Heads (C5)
Brachyura			< 1		< 0.1		< 1	< 0.1
Cancridae (mostly *Cancer* spp.)				< 0.1	< 1	< 0.1	< 0.1	2
Caridea				< 0.1		< 0.1	< 1	< 1
Neotrypaea californiensis						< 0.1	< 1	4
Cirripedia	< 1	2	< 1	7	8	4	159	108
Ostracoda		< 1	28	1	4	< 1	3	2
Amphipoda				< 0.1		< 0.1	< 0.1	16
Gammaridae	< 0.1	< 0.1		< 1	< 1	< 0.1	< 0.1	< 0.1
Corophium spp.		< 0.1	< 1		< 0.1	< 0.1	< 0.1	2
Hyperiidae				< 0.1	< 0.1	< 0.1	6	< 1
Cumacea				< 0.1	< 0.1	< 0.1	< 1	
Euphausiacea				< 0.1			16	77
Isopoda				< 1	< 1	< 1	3	7
Mysidae (mostly *Neomysis mercedis* + *Alienacanthomysis macropsis*)		< 0.1	< 1	< 0.1	< 0.1	< 0.1	< 0.1	
Insecta	25	< 1	6	5	5	< 1	2	
Acarina	1	< 1	< 1	< 1	< 1	< 0.1	< 0.1	
Tardigrada	5			< 1	< 1			

Table A. 4. Con't

	Patullo (R1)	Deas Slough (S1)	Ladner Slough (S2)	Massey (C1)	Wellington (C2)	Cannery Channel (C3)	Jetty (C4)	Sand Heads (C5)
Annelida		< 0.1		< 1	2	< 1	< 0.1	
Hirudinea			4	< 1			< 0.1	
Oligochaeta	2	< 1	30	9	8	< 1	2	< 0.1
Polychaeta	1	24	8	13	50	18	83	350
Nematoda	84	7	174	108	46	9	63	2
Platyhelminthes - Turbellaria	< 1	< 1	15	2	2	< 1	2	
Bryozoa	1.	< 0.1	< 1	2	< 1	3	51	117
Chaetognatha					< 0.1		4	6
Chordata								
Oikopleura.dioica				< 1	< 1	< 1	160	2275
Other larvacean				1			< 1	< 0.1
Fish	< 1	< 1	< 1	< 1	< 1	< 1	< 1	< 0.1

Table A. 4. Con't

	Patullo (R1)	Deas Slough (S1)	Ladner Slough (S2)	Massey (C1)	Wellington (C2)	Cannery Channel (C3)	Jetty (C4)	Sand Heads (C5)
Hydrozoa	< 1	< 0.1	< 1	< 1	< 1	< 1	< 1	14
Hydroidolina							< 0.1	6
Campanulariidae							< 0.1	3
Siphonophora							< 0.1	2
Ctenophora							< 1	20
Mollusca								
Bivalvia	< 1	1	1	14	3	5	91	1510
Pteropoda				< 0.1	< 1	1		114
Gastropoda		< 1	< 0.1	8	6	2	74	47
Rotifera	72	923	1415	188	112	81	98	924
Asplanchna spp.	4	20	69	14	19	18	5	8
Brachionidae	10	4	133	6	2	3	33	
Kellicottia spp.	125	200	455	134	114	207	86	

Appendix B : Calculation of individual copepod biomass

Where local estimates were available of individual biomass, these were used in calculations of total biomass and copepod production. If local estimates were not available, literature estimates of individual biomass, prosome length (PL), or total length (TL) were used, except in the case of *Eurytemora affinis*, for which prosome length was measured directly. Where biomass was not expressed in ug C, it was converted using the relationship presented in Wiebe (1988). Estimation of individual biomass from prosome or total length was done according to the taxon, as detailed below. Where male length or weight was not reported, it was assumed to be the same as that of the adult female. During counting, copepodite stages were most often separated into CI-V or CI-III and CIV-V. These were assigned biomass values of CIII, CII, or CIV, respectively. Where estimates for these stages were not available, estimates were taken from the nearest stage for which they were available. Biomass of copepod eggs was ignored.

B.1   Calanoida

Stage-specific total length and dry weight (DW) for most marine calanoids in coastal British Columbia were provided by Moira Galbraith. Estimates were not available for *Paracalanus* copepodites, which were abundant in many of my samples. To estimate the PL of *Paracalanus* copepodites, I applied the proportional change in PL during development reported for the genus by Conway (2006) to the adult female PL reported by Galbraith. Individual biomass was calculated according to Uye (1991), where $\mu g\ C = 10^{(-8.451+3.128*\log(PL))}$. For freshwater calanoids, DWs were taken from Hawkins & Evans (1979) and Culver et al. (1985).

As the focal species of this thesis and one of the most abundant species in the estuary, the greatest care was taken with respect to *Eurytemora affinis*. I was unable to find estimates of individual biomass or PL for *E. affinis* of the Pacific clade. I directly measured PL of more than 650 *Eurytemora* spp. individuals collected across a range of environmental conditions (Table B.1). Measured copepodids were grouped into 4 temperature bins, according to bottom temperature* measured at the time of sampling: $< 5.99°C$, $6-11.99°C$, $12.0-17.99°C$, and $> 18.0°C$ (Table B.2). Individual biomass was estimated using the relationship derived by Kankaala and Johansson (1986) for *E. affinis*, ug C = $6.25*PL(mm)^{2.83}$. Individual biomass was averaged across temperature bins (Table B.3); however, measurements do suggest that PL, and therefore biomass, varies seasonally with temperature.

Table B.1 Number of *Eurytemora* spp. measured by instar and temperature bin.

Instar	≤ 5.9°C	6-11.9°C	12-17.9°C	≥18°C	n
CI	11	32	12	12	67
CII	14	27	11	10	62
CIII	13	31	11	10	65
CIV	6	34	12	6	58
CV female	5	10	10	5	30
CV male	6	15	6	3	30
CVI female	86	145	62	30	323
CVI male	3	23	18	5	49
n	144	317	142	81	684

Table B. 2 Mean prosome lengths (mm) ± SD for *Eurytemora* spp. by instar and bottom temperature at the time of sampling.

Instar	≤ 5.9°C	6-11.9°C	12-17.9°C	≥18°C
CI	0.35±0.04	0.35±0.03	0.29±0.03	0.30±0.04
CII	0.44±0.03	0.41±0.04	0.39±0.03	0.37±0.05
CIII	0.54±0.05	0.51±0.04	0.44±0.02	0.44±0.05
CIV	0.61±0.09	0.58±0.07	0.53±0.04	0.50±0.04
CV female	0.81±0.10	0.78±0.07	0.64±0.05	0.60±0.06
CV male	0.65±0.03	0.61±0.05	0.63±0.04	0.51±0.02
CVI female	0.94±0.06	0.94±0.05	0.73±0.04	0.83±0.16
CVI male	0.64±0.09	0.71±0.05	0.63±0.03	0.56±0.02

Table B. 3 Mean individual biomass (ug C) of instars of *Eurytemora affinis* estimated from the relationship derived by Kankaala and Johansson (1986) for *E. affinis*, ug C = 6.25*PL$^{2.83}$. Column headers indicate bottom temperature at the time of sampling.

Instar	≤ 5.9°C	6-11.9°C	12-17.9°C	≥18°C
CI	0.314	0.320	0.187	0.202
CII	0.595	0.519	0.433	0.386
CIII	1.087	0.910	0.608	0.623
CIV	1.536	1.362	1.028	0.870
CV female	3.422	3.140	1.806	1.474
CV male	1.810	1.553	1.654	0.920
CVI female	5.246	5.246	2.565	3.689
CVI male	1.778	2.383	1.669	1.235

B.2   Cyclopoida

For the Cyclopidae, DW estimates of Hawkins & Evans (1979), Culver et al. (1985), and Maier (1994) were used. For life stages where DW values were unavailable, the DW of similarly-sized cyclopoid copepods were substituted. *Diacyclops thomasi* was overwhelmingly the dominant member of the Cyclopidae. As I was unable to find an appropriate empirical equation to estimate individual biomass from either PL or TL, DW estimates of Culver et al. (1985) were used for CI-CV and for CVI females and Hawkins & Evans (1979) DW estimates were used for CVI males (See note on the measurement of body lengths in Cyclopoida below). Fifty *D. thomasi* were

measured from samples where bottom temperatures were 4 °C, 15 °C, and 19 °C. PL did not vary strongly across the samples.

For the Oithonidae, biomass (mg DW) for *Oithona atlantica* adult females and for *Oithona similis* were provided by Moira Galbraith of Fisheries and Oceans Canada. The values for *O. similis* were extended to *O. spinirostris* and other marine *Oithona*. *Oithona* spp. copepodites collected were primarily from later stages so DW values used are from CV. Where copepodids CI-III were recorded, the PL for *O. similis* CII from Conway (2006) was used. PL was not scaled to local adults as was done for *Oncaea* spp. and *Paracalanus* spp. for reasons noted below. For *O. davisae*, prosome length and biomass in ug C were estimated according to Uye and Sano (1998).

For the 'poecilostomes' *Corycaeus* spp. and adult *Oncaea* spp., DW values were provided by Moira Galbraith of Fisheries and Oceans Canada. DW was not available for *Oncaea* copepodites and was estimated using Conway (2006) and local values for CVI females as described above. Dumont's (1975) relationship of total length to individual DW was used to estimate DW as PL was not available. Values for *Corycaeus* spp. were extended to unidentified 'poecilostomes' and *Ergasilus* spp.

Note: Some ambiguity exists in the measurement of body lengths in cyclopoids. The standard definition of 'total length' is length from the anterior end of the prosome to the end of the caudal rami. In some cases, however, and notably in the case of Culver's measurements of *Diacyclops thomasi*, total length measurements are taken to the beginning of the caudal rami. In the case of *Oithona* spp., cephalothorax length is sometimes measured rather than prosome length (Conway

2006), where the cephalothorax is considered to be the prosome and the first urosomal segment combined (Sabatini & Kiørboe 1994), the cephalosome and the first pedigerous segment (Conway 2006), or the same thing as the prosome (Dvoretsky & Dvoretsky 2009).

B.3   Harpacticoida

Local estimates of DW were available for *Pseudobradya* spp. and *Coullana canadensis*, and *Microsetella* spp. (Johnston 1981, Galbraith, pers. comm.). *Pseudobradya* spp. biomass estimates were used for other Ectinosomatidae (excluding *Microsetella* spp.). *Pseudobradya* spp. and *Coullana canadensis* accounted for > 81% of the average abundance of Harpacticoida. A further 11% was attributed to 'harpacticoid spp.' Due to the effort required to identify harpacticoid taxa to species, in most samples, many were not identified to species. For this reason, I lumped all Harpacticoida that were not *C. canadensis, Pseudobradya* spp., *Huntemannia jadensis*, and *Microsetella* spp. into 'harpacticoid spp.'. Based on the species identification that were done, I believe that 'harpacticoid spp.' was primarily comprised of multiple members of the family Tachidiidae and *Leimia vaga* of the family Harpacticidae. 'Harpacticoid spp.' were assigned the average of the total length reported by Reid and Williamson (2009) for *Tachidius discipes* and the total length reported by Willey (1923) for *Leimia vaga*. TL for copepodite stages was not available. Where copepodid stage CI-CV was indicated, or was not specified, TL was assumed to be ¾ that of the adult female. This method is not perfect, but I believe it introduces less error than would the assumption that all individuals were adult-sized. Individual biomass was estimated using the relationship derived by Dumont et al. (1975).

Pseudobradya spp. was one of the most abundant taxa in the estuary. To ensure the accuracy of the literature biomass estimate used, I measured the TL of 20 individuals collected at 2 temperatures (3°C and 20°C) and estimated biomass, in ug C, using the relationship derived by Uye et al. (2002) for a similarly-shaped ectinosomatid, *Microsetella norvegica*. Measured individuals ranged in biomass from 0.25 – 0.91 ug C and individuals known to be adult females ranged from 0.50 – 0.91 ug C. Given this, Johnston's estimate of 0.41 ug C (after conversion from DW using Wiebe (1988)) seemed reasonable.

B.4   Siphonostomatoida

Sea lice were extremely rare in my samples (3 individuals were counted). Individual biomass values for *Corycaeus* used for these taxa are likely inaccurate but represent my best approximation. Due to their rarity, the associated error is unlikely to have a perceptible impact on the summarized biomass data or the resulting production estimates.

Appendix C : Annual variation in prosome length of *E. affinis* copepodids and the relationship between prosome length and clutch size: Evidence for food limitation.

PL of *Eurytemora* copepodids were measured from samples collected at a range of temperatures in order to estimate biomass (Appendix B). Additional measurements were done haphazardly from a range of samples, with an emphasis on adult females, and not all stages were necessarily measured on every date.

Across all measured stages, *Eurytemora* copepodids were largest in the spring and smallest in autumn (Fig C.1). Because *E. affinis* that develop at cooler temperatures should grow to a larger size, we would predict that copepodids would be at their largest in late winter and early spring and at their smallest in late July and August. The smaller than expected size of copepodids in late winter, early spring, and in autumn suggests that these individuals developed under food-limited conditions.

To further investigate possible food limitation, I compared the relationship of *E. affinis* CS and PL to that found by Ban (1994) and Lloyd et al. (2013) for *E. affinis* under food replete conditions. As the PL – CS relationships determined by Ban (1994) and Lloyd et al. (2013) were likely based on complete clutches, the average CS plotted here was calculated using only the largest 25% of recorded clutches. Comparison to the relationship determined by Lloyd et al. (2013), suggests that food-limitation of *E. affinis* reproduction occurs over most of the year (Figure C.2). This is plausible, and chronic food limitation has also been suggested for *E. affinis* in the San Francisco Estuary (Kimmerer et al. 2014b). The sampling dates where CS approached the prediction of Lloyd et al. (2013) are those that occurred soon after the freshet, during the period of most rapid population growth, and one date from late spring. The clutch sizes predicted

by Ban (1994) were smaller and lead to a more conservative estimate for the period of food limitation – autumn (again with the caveat that I don't have sufficient data to assess food-limitation in Dec – Jan). Note some dates during the freshet also had lower than expected CS, but this is confounded by the dropping of eggs.
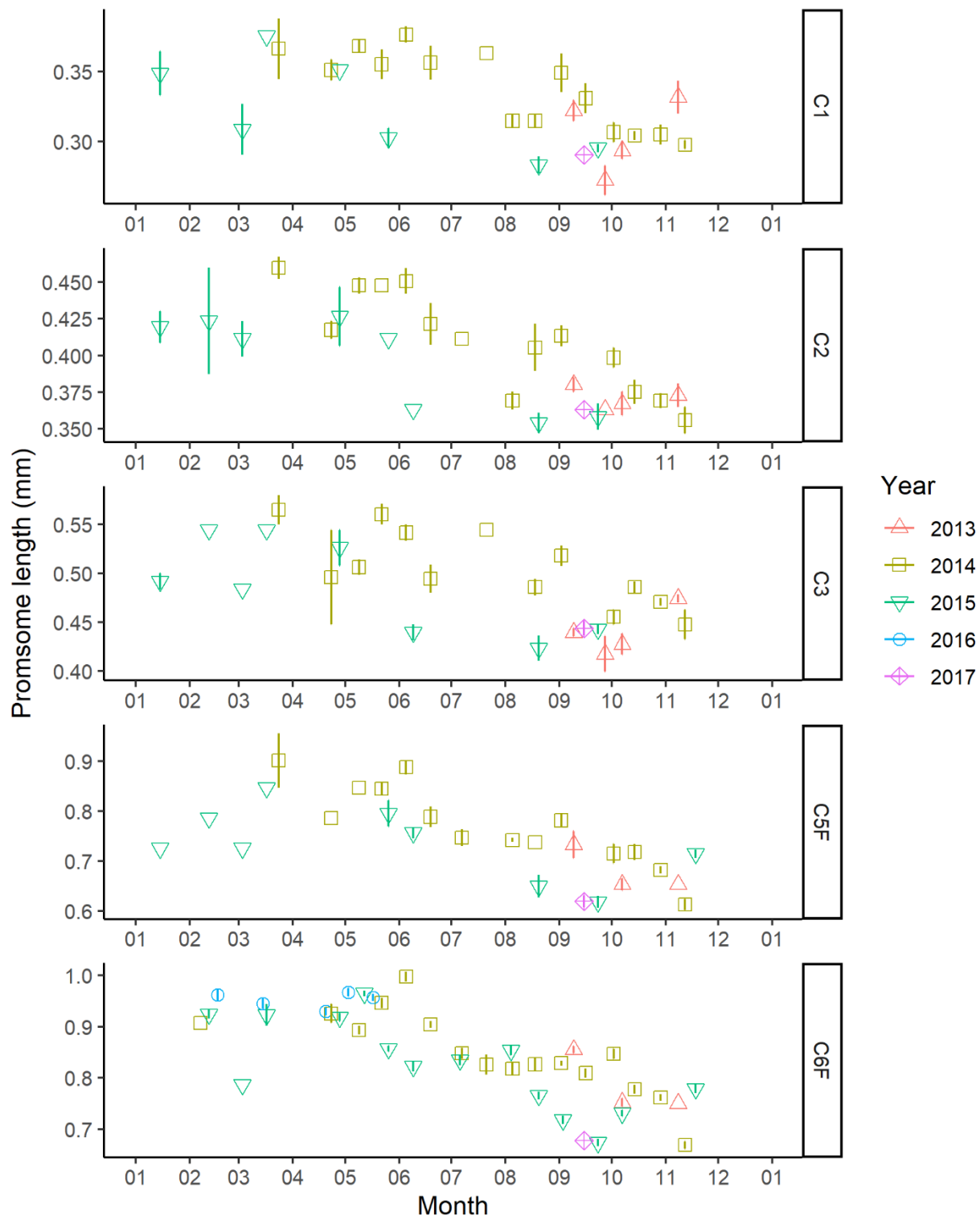
Figure C. 1 (previous page) Mean prosome lengths (mm) of copepodid stages CI-CIII and CV and CVI females. Error bars represent ± 1 standard error of the mean. Where no error bar is present, only a single individual at that stage was measured. Note that scales of y-axes differ.
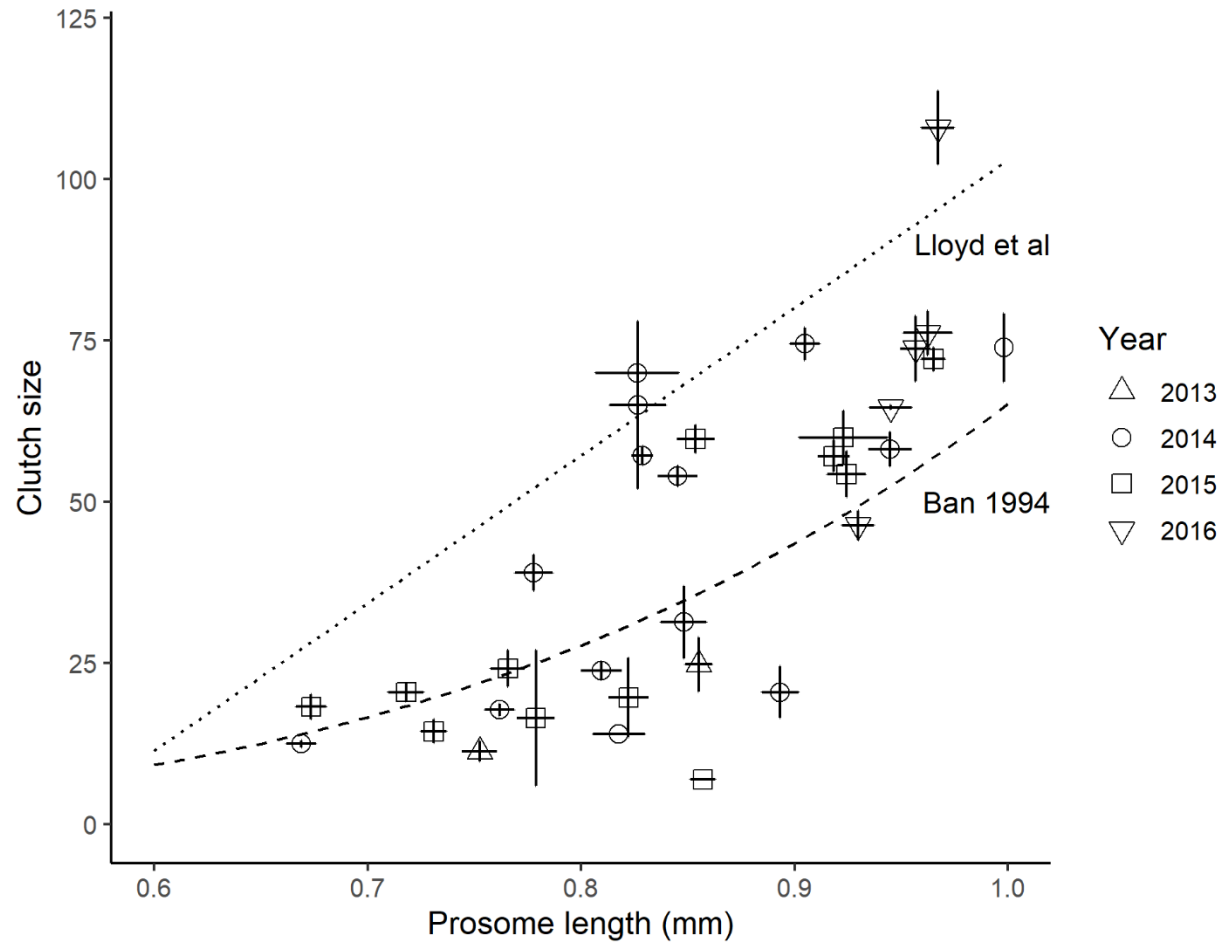
Figure C. 2 Relationship of clutch size and prosome length (mm) in the FRE compared to the empirically-derived relationships of Ban (1994) and Lloyd et al. (2013) for populations of *E. affinis* in Lake Ohnuma, Japan, and the Chesapeake Estuary, USA, respectively. Because I counted the size of all clutches, irrespective of fullness, clutch sizes plotted here are the largest 25% of recorded clutches. Error bars are ± 1 standard error of the mean. Year of sample collection is indicated by shape.

Appendix D : Annual variation in *E. affinis* sex ratio

Sex ratio was calculated as the proportion of the adult population that is female, $N_f / (N_m + N_f)$.
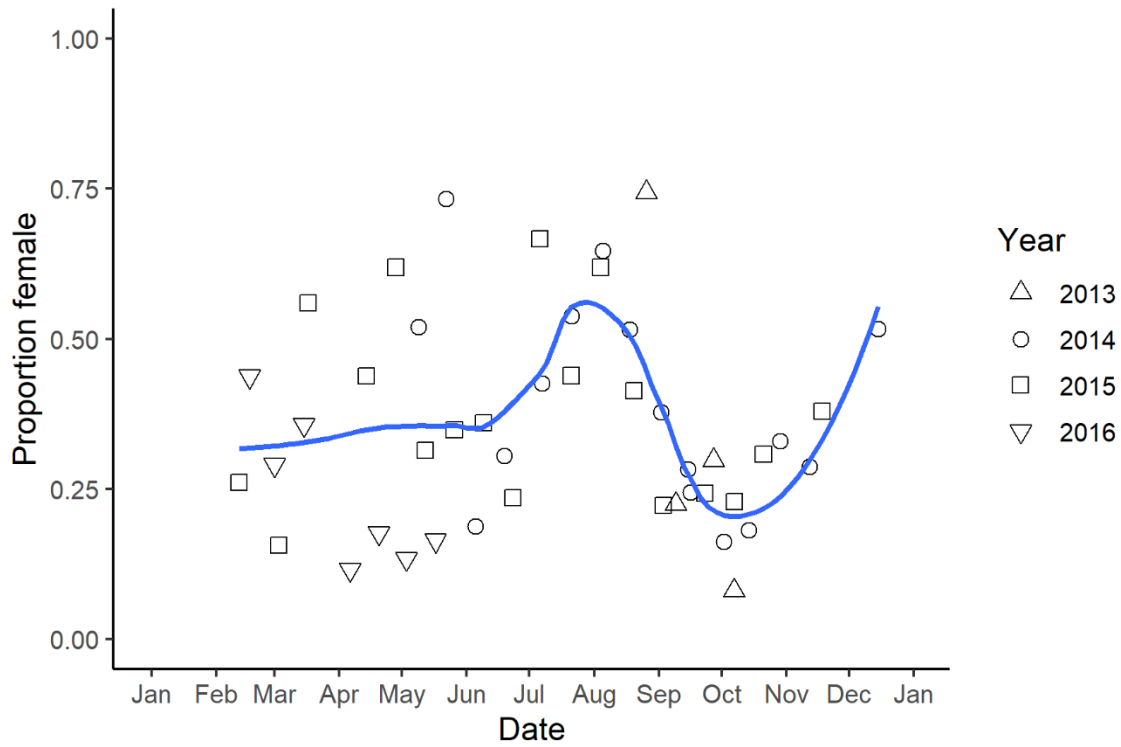

Figure D. 1 Annual variation in the sex ratio of *E. affinis* adults. Data plotted are female proportion of the adult population, averaged within a sampling date. Proportions based on counts < 10 were excluded. Year of sample collection is indicated by shape. Trend in sex ratio is highlighted with a *blue line* (LOESS smooth, span = 0.5).

Appendix E : The occurrence of ciliate epibionts on *E. affinis* in Deas Slough

E. affinis copepodids collected from the FRE were frequently densely covered in epibionts, which were tentatively identified as peritrich ciliates. Infestation was most severe on adult *E. affinis* but was observed on all copepodid stages and, on rare occasion, nauplii. While ciliate epibionts were occasionally observed on other copepods, they appeared to primarily infest *E. affinis*. Heavy infestation by ciliate epibionts has been linked with increased mortality, decreased body size and reduced EPR of the copepod host (Burris & Dam 2014, Jones et al. 2016). For *E. affinis*, specifically, results of behavioural studies conducted by Souissi et al. (2013) suggest that heavy infestation by *Zoothamnium* spp. increased mortality in *E. affinis* and negatively affected swimming activity. Heavy infestation also reduced mating frequency and clutch sizes produced by females were very small (≤ 4 eggs).

The prevalence of infestation (proportion of *E. affinis* copepods carrying epibionts) was recorded rather haphazardly over the course of sample processing, but a seasonality in infestation is nonetheless apparent (Figure E. 1). In Deas Slough, infestation peaked in the winter and decreased with increasing water temperature (Figure E. 2). In the Seine, infestation also occurred primarily in winter, though levels of infestation were described as low, and authors hypothesized that *E. affinis* may be more vulnerable to infestation in winter due to an aging and physiologically weaker population (Souissi et al. 2013).
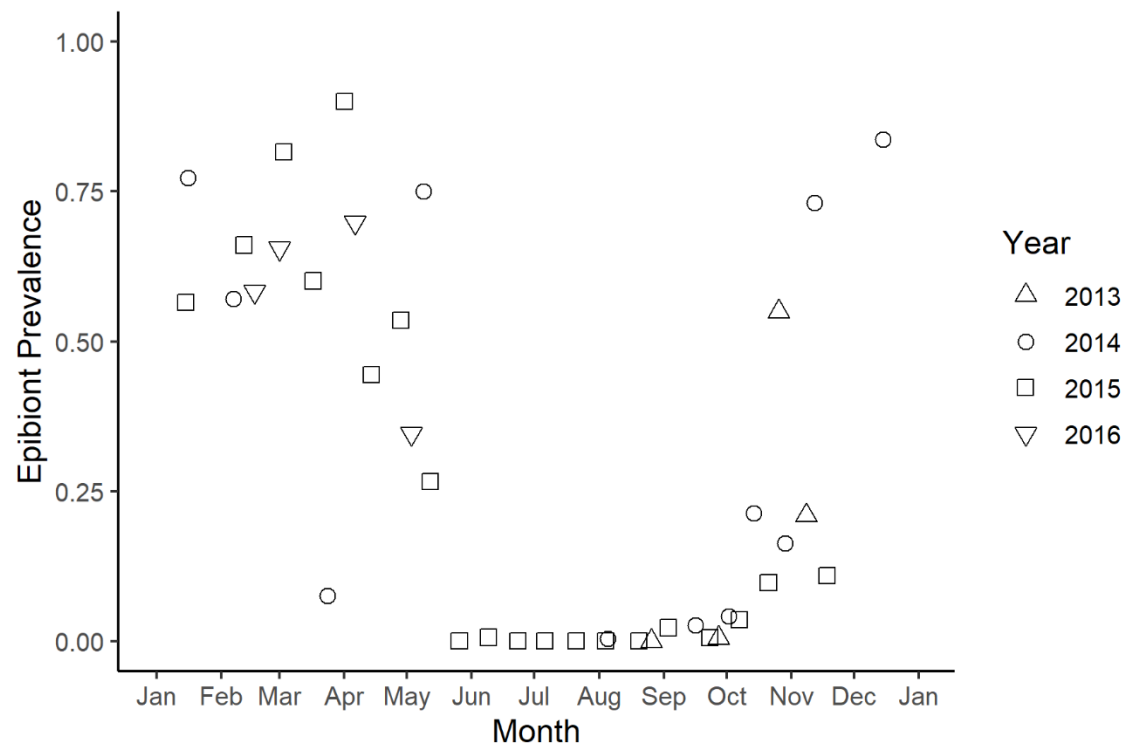
Figure E. 1 Annual variation in the proportion of *Eurytemora affinis* copepodids infested with ciliate epibionts in Deas Slough, FRE, BC. *Shape* indicates year of collection.
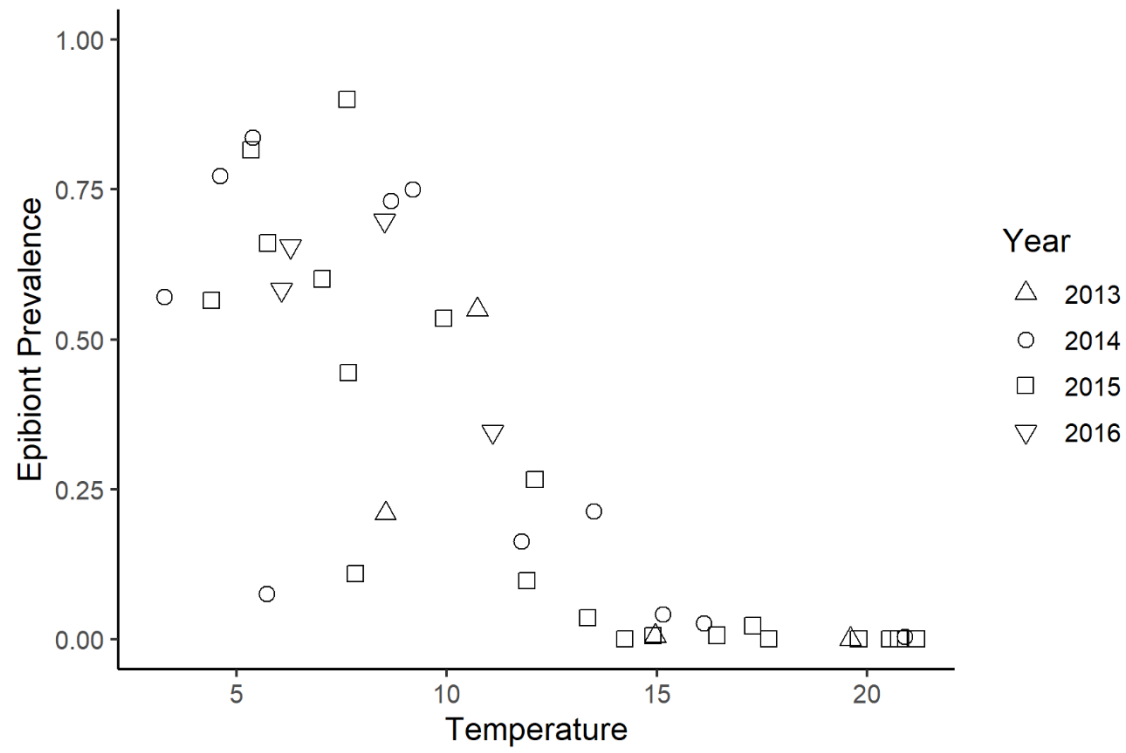
Figure E. 2 Variation in epibiont prevalence on *Eurytemora affinis* copepodids (proportion infested) with mean water column temperature (°C) in Deas Slough, FRE, BC. *Shape* indicates year of collection.
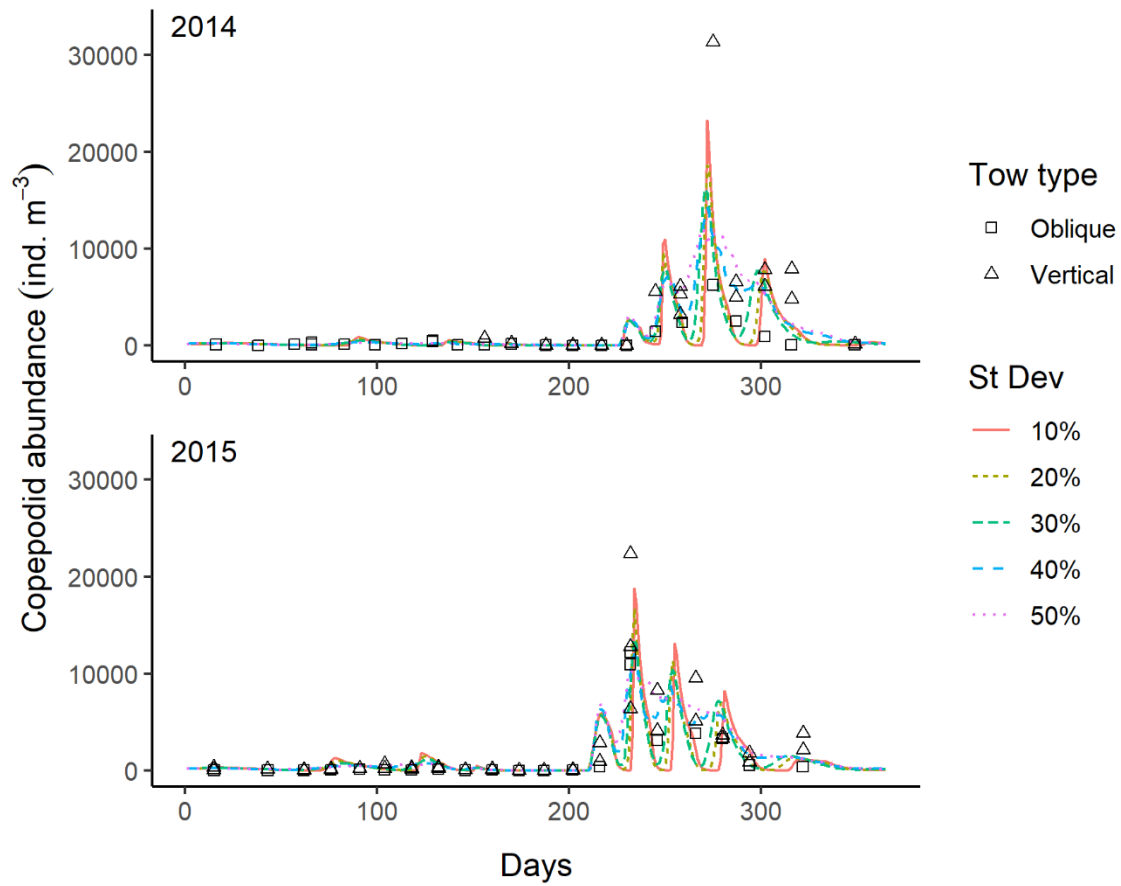
Figure F. 1 Determination of standard deviation, as percentage of stage duration, used in naupliar and copepodite molting rate probability density functions.
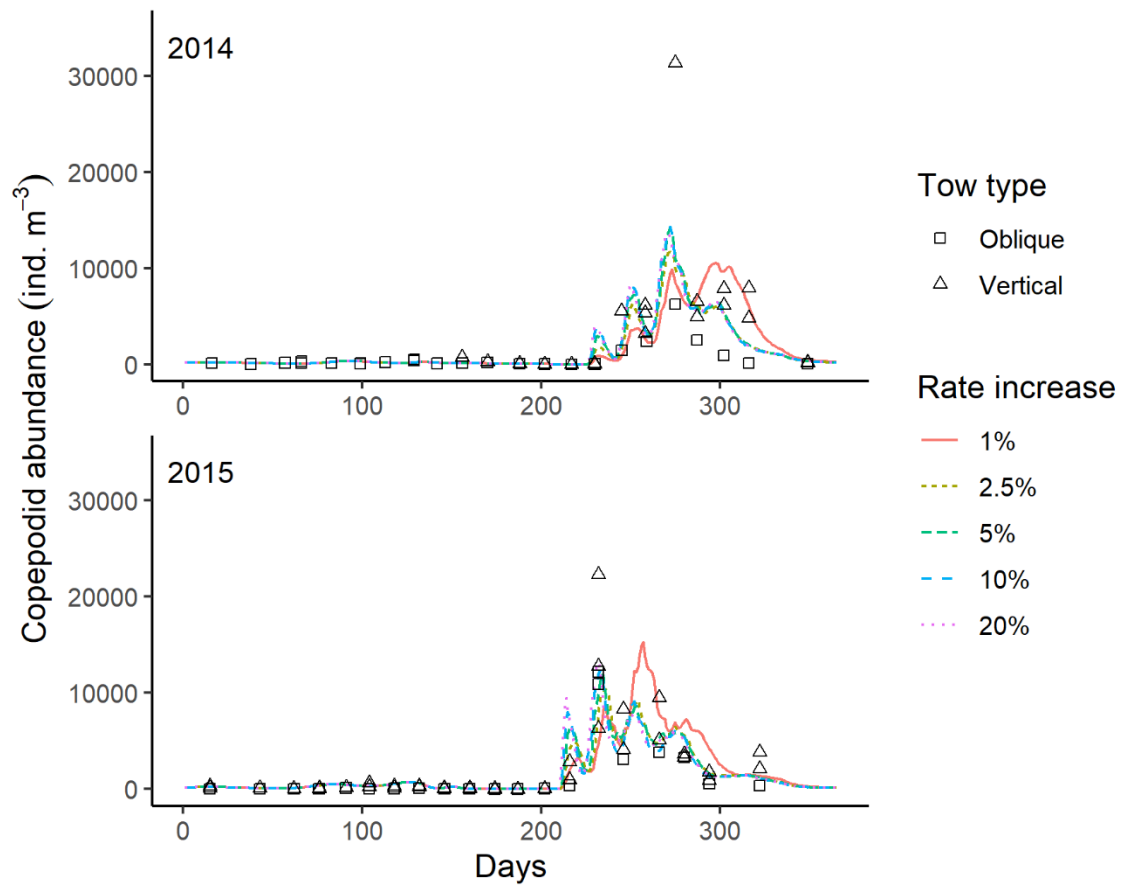
Figure F. 2 Determination of rate of increase in hatching rate of resting eggs. Hatching rates were increased by 1%, 2.5%, 5%, 10%, and 20% per day over period of resting hatching.
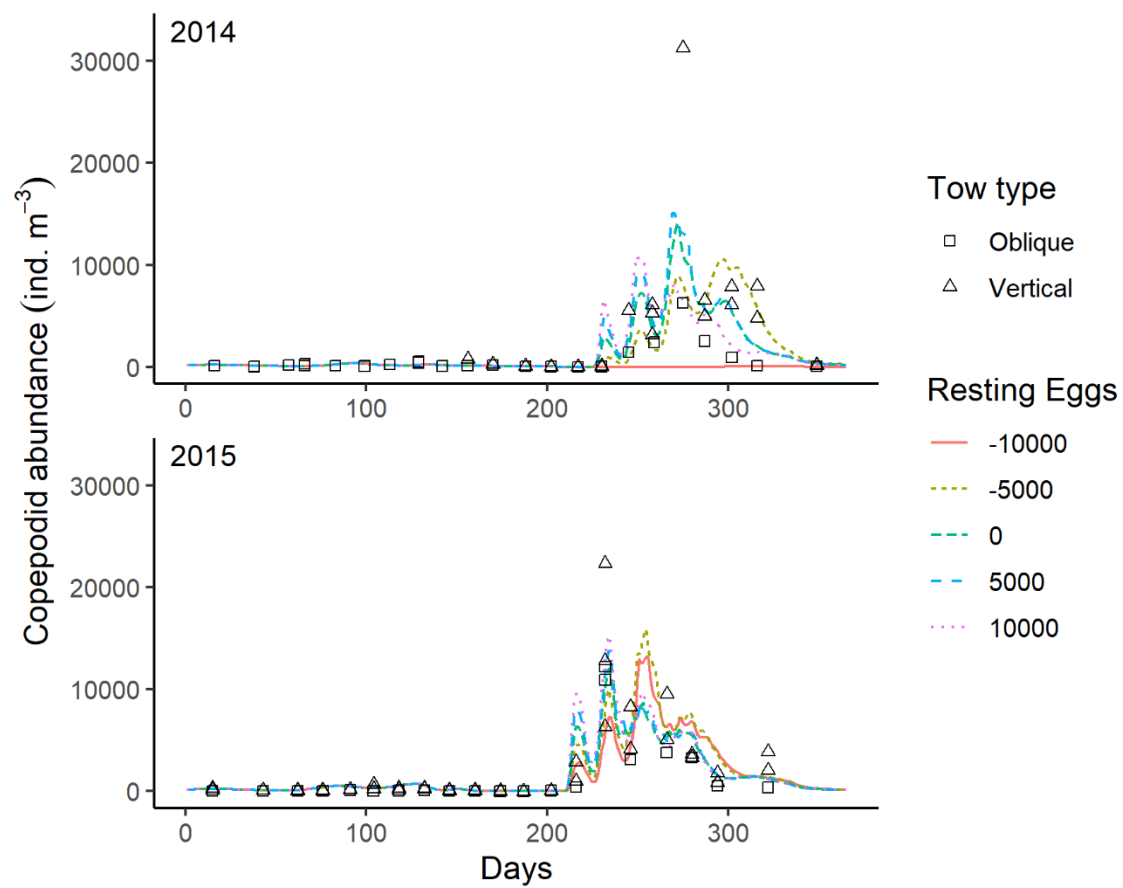
Figure F. 3 Exploring the impacts of contributions to and from an egg bank on post-freshet copepodid abundance dynamics. Resting eggs were added at t = 200.
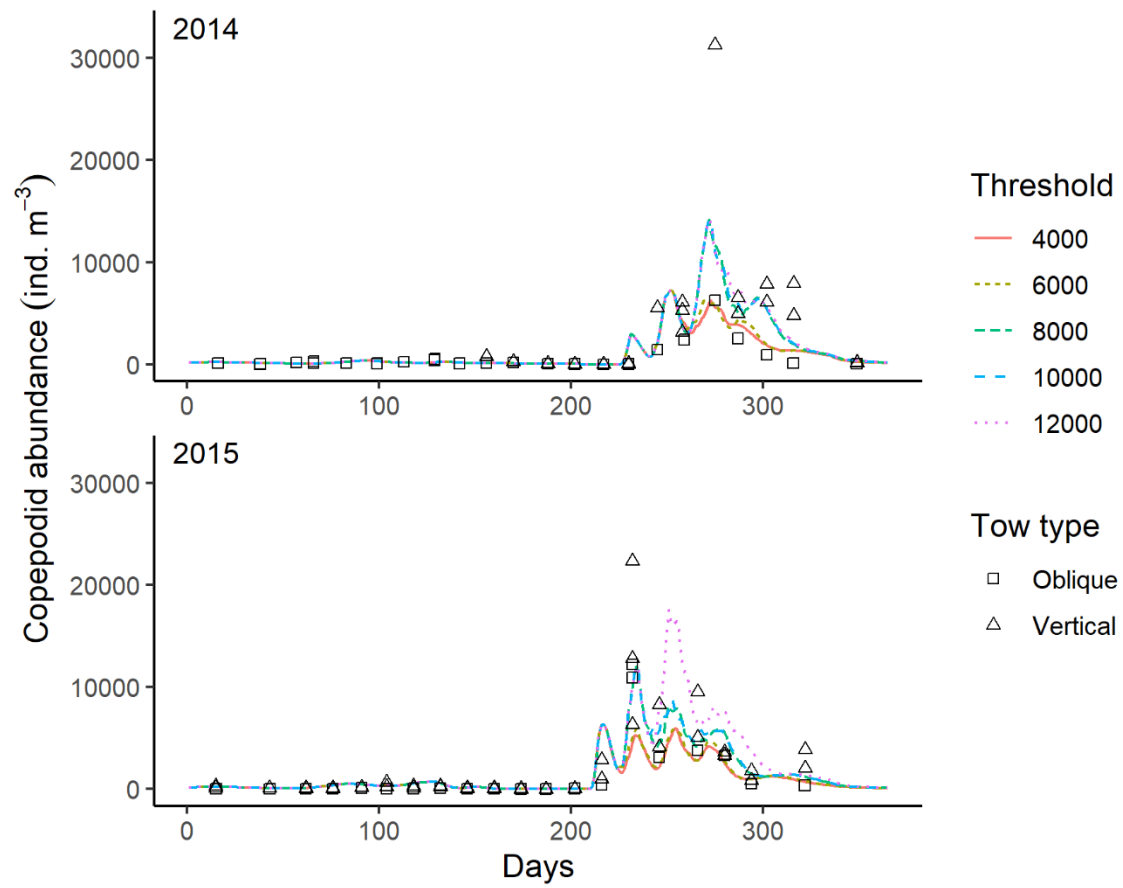
Figure F. 4 Determination of abundance threshold used to trigger decrease in egg production rate.

Table F. 1 Sensitivity of simulated *E. affinis* copepodid abundance to perturbation of mortality rate. Changes to abundance metrics are reported as percentages and changes to timing are reported in days.

	Perturbation to mortality rate, all life stages							
	-40%	-20%	-10%	-5%	+5%	+10%	+20%	+40%
2014 Abundance change (%)								
Spring	1090	227	79	33	-24	-42	-66	-87
Summer	5821	478	122	42	-35	-58	-85	-98
Autumn	539	34	18	-12	-20	-6	-47	-89
Annual	882	68	26	-7	-20	-10	-49	-88
Maximum	1125	49	7	-27	-24	-45	-64	-92
Resting eggs	5377	587	157	60	-37	-60	-83	-97
2014 Timing change (days)								
Julian day of max abundance	-41	-41	-20	-20	0	23	26	29
# days > 5000 ind. m^{-3}	120	6	10	0	-8	0	-43	-48
2015 Abundance change (%)								
Spring	1300	249	84	35	-25	-44	-67	-88
Summer	1682	232	42	45	-31	-52	-76	-97
Autumn	167	106	8	19	28	6	24	-55
Annual	773	159	26	29	4	-17	-16	-70
Maximum	2123	213	27	44	15	-11	-43	-78
Resting eggs	4126	506	143	55	-35	-58	-82	-96
2015 Timing change (days)								
Julian day of max abundance	-18	-18	-18	0	19	19	40	71
# days > 5000 ind. m^{-3}	90	16	0	0	-10	-24	-29	-56

Table F. 2 Sensitivity of simulated *E. affinis* copepodid abundance to perturbation of egg production rate.

Changes to abundance metrics are reported as percentages and changes to timing are reported in days.

	Perturbation to EPR							
	-40%	-20%	-10%	-5%	+5%	+10%	+20%	+40%
2014 Abundance change (%)								
Spring	-48	-26	-13	-6	7	14	29	59
Summer	-74	-46	-27	-12	13	27	58	135
Autumn	-42	4	-14	-7	10	19	-8	21
Annual	-42	2	-15	-7	10	18	-2	28
Maximum	-62	-40	-17	-18	2	12	-18	19
Resting eggs	-77	-48	-27	-14	16	33	72	175
2014 Timing change (days)								
Julian day of max abundance	27	25	0	-1	-1	-2	-23	-23
# days > 5000 ind. m^{-3}	-40	7	-6	-3	2	5	4	9
2015 Abundance change (%)								
Spring	-54	-29	-15	-8	8	17	34	73
Summer	-71	-41	-21	-11	13	25	5	47
Autumn	30	15	41	-6	6	13	-10	16
Annual	-9	-7	15	-8	9	17	-1	31
Maximum	-43	-2	21	-11	12	24	-13	30
Resting eggs	-78	-48	-27	-14	16	33	72	172
2015 Timing change (days)								
Julian day of max abundance	45	19	19	0	0	0	-18	-18
# days > 5000 ind. m^{-3}	-15	-17	2	-10	3	7	-11	2