2005

Larval dynamics of brachyuran crabs in a high latitude fjord, southeast Alaska

Jennifer L. Fisher
San Jose State University

Follow this and additional works at: https://scholarworks.sjsu.edu/etd_theses

Recommended Citation

Fisher, Jennifer L., "Larval dynamics of brachyuran crabs in a high latitude fjord, southeast Alaska" (2005). *Master's Theses*. 2757.

DOI: <https://doi.org/10.31979/etd.rkpg-d3tg>

https://scholarworks.sjsu.edu/etd_theses/2757

This Thesis is brought to you for free and open access by the Master's Theses and Graduate Research at SJSU ScholarWorks. It has been accepted for inclusion in Master's Theses by an authorized administrator of SJSU ScholarWorks. For more information, please contact scholarworks@sjsu.edu.

NOTE TO USERS

This reproduction is the best copy available.

UMI[®]

LARVAL DYNAMICS OF BRACHYURAN CRABS IN A HIGH LATITUDE
FJORD, SOUTHEAST ALASKA

A Thesis

Presented to

The Faculty of Moss Landing Marine Laboratories

and the Department of Marine Science

San Jose State University

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

by

Jennifer L. Fisher

August 2005

UMI Number: 1429420

INFORMATION TO USERS

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleed-through, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

UMI Microform 1429420

Copyright 2006 by ProQuest Information and Learning Company.

All rights reserved. This microform edition is protected against unauthorized copying under Title 17, United States Code.

ProQuest Information and Learning Company
300 North Zeeb Road
P.O. Box 1346
Ann Arbor, MI 48106-1346

© 2005

Jennifer L. Fisher

ALL RIGHTS RESERVED

APPROVED FOR THE DEPARTMENT OF MARINE SCIENCE

Dr. Stacy Kim
Adjunct Professor of Benthic Ecology

Dr. Jonathan Geller
Associate Professor of Invertebrate Zoology

Dr. William Broenkow
Emeritus Professor of Physical Oceanography

Dr. Steven G. Morgan
Professor of Environmental Science & Policy
University of California Davis

APPROVED FOR THE UNIVERSITY

08/11/05

ABSTRACT

LARVAL DYNAMICS OF BRACHYURAN CRABS IN A HIGH LATITUDE FJORD, SOUTHEAST ALASKA

by Jennifer L. Fisher

The seasonal abundance and the horizontal and vertical distribution of seven species of brachyuran larvae are described from lower Glacier Bay (Southeast Alaska, USA) to determine larval export or retention. The importance of lunar phase on larval vertical position and the effect of day/night and tide cycles on megalopal vertical distribution are addressed. The larvae of most species exhibited a highly seasonal pattern of abundance, which in their first appearance coincided with the onset of oceanographic conditions favorable to survival (increasing water temperature and abundant food supply). Embryo hatch times were delayed and larval durations were longer compared to lower latitudes. With the exception of *Cancer magister*, all larval stages of each species were persistent throughout the study, suggesting that these species are retained. Although the dispersal patterns for *C. magister* were less clear, Glacier Bay acted as a settling area for this species and five others.

THIS THESIS IS DEDICATED TO NIVA
FOR HER UNCONDITIONAL AND UNDYING LOVE; AND FOR ALWAYS
GETTING ME OUT OF THE HOUSE NO MATTER HOW FOCUSED I WAS

ACKNOWLEDGEMENTS

This work would not have been possible if it were not for the support of Mary Beth Moss, the Chief of Resource Management at Glacier Bay National Park, during the inception of this project. I appreciate her vision for the need for this work and for her insightfulness and steadfastness in assisting with the acquisition of the resources needed to complete this demanding field study. Additionally, Dr. Stacy Kim and Dr. Steven Morgan offered advice that greatly enhanced this project and the written thesis. I would also like to thank my committee members, and Lewis Sharman of the National Park Service, for their constructive criticism on drafts of this written thesis.

I would like to thank the staff at Glacier Bay National Park for their logistical support. I owe a special thanks to Justin Smith, Erika Kean, and Kristen Wulff for their upbeat attitude during tedious and tiresome operations both in the field and behind a microscope. This work could not have been completed in the time frame that it did without their dedication and support.

I would like to thank my friends, family, and the people at Moss Landing Marine Laboratories for their moral support. I would especially like to thank Michael Donnellan for always being there when I needed him, and for his guidance during all facets of this epic journey.

Finally, I would like to graciously thank the National Park Service Challenge Cost-Share program and the PADI AWARE Foundation for their gracious financial support.

TABLE OF CONTENTS

List of Tables	
Chapter 1	ix
Chapter 2	x
List of Figures	
Chapter 1	xi
Chapter 2	xii
 Chapter 1: SEASONAL TIMING AND DURATION OF BRACHYURAN LARVAE IN A HIGH-LATITUDE FJORD	 1
Abstract	2
Introduction	3
Methods	
Study Site	8
Plankton Sampling	8
Sample Processing	10
Larval Duration	11
Results	
Species Abundance and Temporal Distributions	12
Family Cancridae	13
Family Majidae	14
Family Pinnotheridae	15
Family Atelecyclidae	15
Family Xanthidae	16
Larval Duration	16
Discussion	17
Literature Cited	22
Figure Legends	28
 Chapter 2: RETENTION OF BRACHYURAN LARVAE IN A NEWLY DESIGNATED MARINE RESERVE IN SOUTHEAST ALASKA	 41
Abstract	42
Introduction	43
Methods	
Study Site	47
Plankton Sampling	48
Sample Processing	49
Larval Flux	49
Statistical Analysis	51

Results	
Larval Density (zoeae stage I-V)	53
Daytime Megalopal Density	55
Night Tows	56
Water Velocity Estimates	56
Larval Flux and Net Transport	57
Discussion	57
Literature Cited	64
Figure Legends	72

CHAPTER 1 LIST OF TABLES

Table 1. The total abundance (percent abundance) of all species observed.	26
Table 2. Seasonal timing of stage I zoeae and larval duration times ($\pm$ minimum and maximum) compared to published studies from other geographic regions.	27

CHAPTER 2 LIST OF TABLES

Table 1. Results of a harmonic equation that predicts the difference in water velocity (m/s) from Acoustic Doppler Current Profiler data from modeled data (Tide and Currents v2.0a, Nautical Software Inc.).	68
Table 2. Statistical results for each species and stage observed comparing the effects of tide, sampling depth, and site on larval abundance (larvae/100m ³).	69
Table 3. Statistical results for the effects of tide cycle, day/night, sampling depth (surface, midwater, bottom), and region (BC, West, Middle, East) on megalopal abundance.	70
Table 4. Average time between succeeding slack tides (hours) for each site sampled in Sitakaday Narrows ($\pm$ SD) from corrected modeled data.	71

CHAPTER 1 LIST OF FIGURES

Figure 1. Study area depicting the sampling sites in Sitakaday Narrows.	30
Figure 2. Seasonal patterns of temperature and chlorophyll- <i>a</i> in Sitakaday Narrows from 1993-2002 averaged over the entire water column.	31
Figure 3. Seasonal distribution of all larvae observed.	32
Figure 4. Mean larval abundance (± 1 SE) of <i>Cancer oregonensis</i> .	33
Figure 5. Mean larval abundance (± 1 SE) of <i>Cancer magister</i> .	34
Figure 6. Mean larval abundance (± 1 SE) of the group Majidae (<i>Chinoecetes bairdi</i> , <i>Hyas lyratus</i> , and <i>Oregonia gracilis</i>).	35
Figure 7. Mean larval abundance (± 1 SE) of <i>Pugettia</i> spp.	36
Figure 8. Mean larval abundance (± 1 SE) of group <i>Hyas lyratus/Oregonia gracilis</i> .	37
Figure 9. Mean larval abundance (± 1 SE) of <i>Fabia subquadrata</i> .	38
Figure 10. Mean larval abundance (± 1 SE) of <i>Telmessus cheiragonus</i> .	39
Figure 11. Estimated larval duration (days) $\pm$ minimum and maximum of <i>Cancer magister</i> from this study and published field studies.	40

CHAPTER 2 LIST OF FIGURES

Figure 1. Study area depicting the sampling sites in Sitakaday Narrows.	74
Figure 2. Harmonic regression curves fit to the differences between modeled current velocity (Tide and Currents v 2.0a, Nautical Software Inc.) and measured velocity from an Acoustic Doppler Current Profiler for each site and depth sampled.	75
Figure 3. Vertical distribution of stage I and II-V zoeae of <i>Cancer oregonensis</i> between tides for each date sampled.	76
Figure 4. Vertical distribution of stage I and II-V zoeae of <i>Telmessus cheiragonus</i> between tides for each date sampled.	77
Figure 5. Vertical distribution of stage I and II zoeae of <i>Majidae</i> between tides for each date sampled.	78
Figure 6. Vertical distribution of stage I and II zoeae of <i>Pugettia</i> spp. between tides for each date sampled.	79
Figure 7. Vertical distribution of stage I and II zoeae of <i>Cancer magister</i> between tides for each date sampled.	80
Figure 8. Larval abundance (larvae/100m ²) with relation to lunar phase (full moon, first quarter, new moon, third quarter).	81
Figure 9. Vertical distribution of stage I and II-V zoeae of <i>Fabia subquadrata</i> between tides for each date sampled.	82
Figure 10. Vertical distribution of megalopae between tides.	83
Figure 11. Mean larval abundance (± 1 SE) of <i>Cancer oregonensis</i> , <i>C. magister</i> , and <i>C. gracilis</i> megalopae in surface tows conducted during the night and day during consecutive tidal cycles.	84
Figure 12. Predicted water velocity (m/s) in Sitakaday Narrows versus the predicted time (hours) from the beginning of ebb tide from Tides and Currents (Nautical Software, v 2.0a).	85
Figure 13. Larval density ($\text{Log}_{10} \text{larvae}/100\text{m}^3 + 1$) of all stages of <i>Cancer magister</i> and <i>Cancer oregonensis</i> versus depth averaged water velocity (m/s) for each tide, site, and depth sampled.	86

CHAPTER 1

SEASONAL TIMING AND DURATION OF BRACHYURAN LARVAE IN A HIGH-LATITUDE FJORD

ABSTRACT

This paper describes the seasonal distribution and abundance of brachyuran crab larvae from 5 families in lower Glacier Bay (Southeast Alaska, USA). This is one of the few field studies describing the entire pelagic phase of brachyuran larvae in Alaska. I compared the seasonal timing and larval duration of *Cancer magister* and four other species in Glacier Bay and at lower latitudes to assess the hypothesis that larval release time and duration are later and longer with increasing latitude. The larvae of most brachyuran species observed in Glacier Bay exhibited a highly seasonal pattern of abundance, which in their first appearance coincided with the onset of oceanographic conditions favorable to survival (increasing water temperature and abundant food supply). During the month of May, larval abundance of *Cancer magister* increased 63%, *Cancer oregonensis* 92%, *Fabia subquadrata* 69%, *Pugettia* spp. 73%, and Majidae 77%. The initial occurrence of larvae is delayed approximately 3-4 months relative to published release times in California, Oregon, and Washington for these species. Further, the pelagic larval duration for *Cancer magister* is approximately 30 days longer than published larval durations in lower latitudes, which I suggest is a function of water temperature.

INTRODUCTION

Most studies of population dynamics, recruitment patterns, and settlement timing of brachyuran larvae in the Northeast Pacific have focused on the commercially important species, *Cancer magister*, from California (Reilly 1983), Oregon (Lough 1974), Washington (Stevens and Armstrong 1984), and British Columbia (Jamieson and Phillips 1988; Jamieson et al. 1989; Jamieson and Armstrong 1991; McConnaughey et al. 1992; Dinnel et al. 1993; Jamieson and Phillips 1993). Like many marine invertebrates, brachyurans exhibit broadcast reproductive strategies. After brooding eggs beneath their abdomen, they release planktotrophic larvae that spend months in the plankton before metamorphosing and settling to the bottom as juveniles. Studies conducted on the pelagic larval phase of *C. magister* suggest that the timing and larval duration generally vary with latitude. Along the outer coast of California, Oregon, and Washington, larval timing and duration are similar; larvae occur in the plankton from mid-January to May/June, translating to a larval duration of approximately 120 days. In the Georgia, Haro, and Rosario Strait complex (Jamieson and Phillips 1993) of British Columbia, larvae occur in highest abundance in the plankton from March-August, translating to a larval duration of approximately 150 days. As *C. magister* larvae develop along the outer coast, there is a shift in larval abundance with relation to distance from shore. Early-stage larvae are found in closest proximity to shore, while late-stage larvae have been found up to 200 kilometers offshore (Lough 1976; Reilly 1983; Jamieson and Phillips 1988). In the GHRS, *C. magister* megalopae are retained by vertically migrating into deep inward-flowing

bottom currents during the day, resulting in little to no exchange of megalopae to outer coast areas (Jamieson and Phillips 1993). Jamieson and Phillips (1993) partly attribute the longer development time of larvae in GHRS to the extreme temperature fluctuations encountered during these vertical migrations.

The temporal distribution and larval duration of *Cancer magister* have not been studied in Alaska, and few studies have been conducted on other decapod larvae, despite the commercial importance of many other species in this area, including red king crab (*Paralithodes camtschatica*) and Tanner crab (*Chionoecetes bairdi*). In part, this is attributable to the logistical difficulty of working in remote areas, in addition to the relatively short field season. Glacier Bay National Park and Preserve (58°25'N, 136°00'W), in Southeast Alaska, provides an ideal location to investigate the seasonal timing and duration of crab larvae in a high-latitude system. Glacier Bay is relatively protected from adverse weather and sea conditions, and is accessible from the National Park Service headquarters. Further, in 1999, the commercial harvest of fish and crabs in Glacier Bay began to be phased out, thereby creating one of the largest marine reserves in the United States (1,255 km²). The entire bay was closed immediately to commercial harvest of Dungeness crab and red king crab, while parts of the bay were closed to the harvest of Tanner crab (Figure 1). Prior to the fishing closure, Glacier Bay supported a highly productive fishery for these species.

Several studies have investigated the distribution and relative abundance of adult *Cancer magister* and other commercially important species in Glacier Bay, both before and after the fishing closure (O'Clair et al. 1990; O'Clair et al. 1995; O'Clair et

al. 1996; Scheduling et al. 2001; Swiney and Shirley 2001; Taggart et al. 2003b). However, patterns of larval distribution and abundance have not been addressed, despite the importance of larval dispersal for adult populations. Likewise, little research prior to this study has been conducted on non-commercially important crab species. This paper describes the seasonal distribution and abundance of brachyuran larvae from five families in lower Glacier Bay. Understanding the seasonal timing of larvae in a specific geographic area can help determine the natal origin of cohorts and is the first step in understanding dispersal patterns and population connectivity.

Adults from the family Cancridae release larvae that undergo five zoeal stages and a megalopa stage (Shanks 2001). *Cancer magister* adults inhabit sandy substrata in lower Glacier Bay and are largely absent from the upper Bay (Taggart et al. 2003b). While hypotheses of limited larval supply (hydrographic isolation), decreased larval and juvenile survival (from temperature and salinity stresses), and post-settlement mortality (from predation, or temperature and salinity stress) have been proposed as factors explaining the limited abundance of adults in the upper Bay (Taggart et al. 2003b), no direct evidence was given to support these claims. Adults of *C. oregonensis* inhabit complex, pebbly substrate from the intertidal to at least 436 m (O'Clair and O'Clair 1998), but little is known about their adult distribution in Glacier Bay. Much of Glacier Bay is steep-walled with unstable substrata, so adults could be highly abundant and widely distributed. On the few occasions they have been observed *in situ* using SCUBA, they were common in these pebbly, unstable habitats (0.57/m², Donnellan et al. 2004). Although *C. productus* adults have been found in calm bays and estuaries in

Southeast Alaska, very few have been observed in Glacier Bay (Streveler, pers. com.). In Southeast Alaska, *C. gracilis* adults inhabit eelgrass (*Zostera*) beds and are found from the intertidal to 174 m, but they have never been recorded in Glacier Bay.

The Majidae are commonly called the spider or decorator crabs and are distributed worldwide, except in Antarctica. Their larvae undergo three pelagic stages, two zoeae and a megalopa, before metamorphosis and settlement to the bottom as juveniles (Shanks 2001). Currently there is a productive commercial fishery for *Chionoectes bairdi* in Glacier Bay, and ongoing studies of the adult distributions and movements are in progress (Taggart et al. 2003a). The adult distributions of the non-commercial majid species (*Pugettia* spp., *Hyas lyratus*, and *Oregonia gracilis*) are largely unknown.

Many other species of abundant brachyuran crabs exist in Glacier Bay where adult distributions are largely unknown. Pea crabs of the family Pinnotheridae undergo six larval stages (five zoea and a megalopa) (Shanks 2001). As adults, these crabs live parasitically or commensally within the mantle of bivalves, which are very abundant (236/m², Bodkin and Kloecker 1999) in soft-bottom habitats of Glacier Bay. *Fabia subquadrata* is especially found in the horse mussel, *Modiolus modiolus*. Large, multi-layered reefs composed completely of horse mussels have been observed in Glacier Bay (Etherington, USGS, unpublished data). Therefore, it is possible that crabs from this family are very abundant in Glacier Bay. The crabs in the family Atelecyclidae are commonly referred to as the horse crabs. Their larvae undergo six stages (five zoeae and 1 megalopa) before metamorphosing and settling to the benthos as juveniles

(Shanks 2001). *Telmessus cheiragonus* is the sole member of this family observed during this study. *Telmessus cheiragonus* adults range from the Bering Sea to California and to Hokkaido Japan and Korea, and are found from the intertidal to 110 m on various substrata (O'Clair and O'Clair 1998). Although the family Xanthidae contains more genera than any other brachyuran family, only one species (*Lophopanopeus bellus*) occurs in Alaska. Xanthid larvae undergo four zoeal and a megalopal stage before metamorphosing into juveniles (Shanks 2001). The adults inhabit the intertidal to 80 m from Alaska to central California.

This paper describes the temporal distribution and abundance of brachyuran larvae in lower Glacier Bay. This is one of the few field studies describing the entire pelagic phase of brachyuran larvae in Alaska (see Incze et al. 1987) for *Chinoecetes bairdi* and *C. opilio*). The abundance estimates in this study can be used as a baseline for future studies in this area, which is rapidly changing due to the commercial fishing closure, sea-otter recolonization, and increased photic depth from terrestrial stabilization following glacial retreat. I also compared the seasonal timing and larval duration of *Cancer magister* and other species observed in Glacier Bay to the same species found at lower latitudes to assess the hypothesis that larval release time and duration are later and longer with increasing latitude.

METHODS

Study Site

Glacier Bay is a recently (< 250 years ago), partially de-glaciated fjord. The Bay is approximately 100 km long from the entrance sill (30 m) to the northern reaches and varies in width from approximately 15 km to 4 km (Sitakaday Narrows) (Figure 1). There is significant freshwater input, mainly from run-off and glacial meltwater in the upper bay, which contributes to a net down-bay flow of water. The mixed semi-diurnal average tidal range is approximately 3.7 m at Bartlett Cove in the lower bay and 4.2 m in upper bay locations. Oceanographic research in Glacier Bay by the United States Geological Survey (USGS) from 1993-2002 suggests that Glacier Bay sustains high primary productivity (chlorophyll-*a* levels) throughout the summer months (May-October) (Figure 2), and that the amount of available sunlight (day length) is the most influential factor describing the onset of the spring phytoplankton bloom in the lower bay region (Etherington et al. 2004).

Plankton Sampling

Discrete depth and surface plankton samples were collected approximately weekly ($n = 22$ sampling days) from a 9.6 m vessel during April 26-October 5, 2002. Discrete depth tows were conducted using a General Oceanics double-trip opening and closing mechanism with 0.5 m diameter ring nets fitted with 500- μ m mesh netting modified with a choke band. Each net had a time-depth recording device to determine whether the net sampled the intended depth. Surface tows were conducted with a 0.5 m

by 0.75 m neuston net fitted with 500- μ m mesh. Each net was equipped with a General Oceanics flowmeter (Model 2030) so that the volume of water sampled could be calculated. All nets were towed at approximately two knots relative water speed, against the prevailing current. The discrete depth and surface nets were towed for approximately twelve and eight minutes, respectively (sampling time was reduced for surface tows to minimize clogging of the net with phytoplankton), resulting in an average water volume sampled of 186 m³ (SD 72 m³) for tows at depth and 132 m³ (SD 51 m³) for surface tows.

Within each tide cycle (ebb and flood), three sites were sampled in Sitakaday Narrows (West, Middle, East) (Figure 1). These sites were located in water of approximately 50 m depth and were systematically chosen to represent a spatial distribution across the Narrows. In order to avoid large vessel traffic (i.e., cruise ships), the center station was not located directly in the center of the channel. Three discrete depths were sampled at each site resulting in a total of 18 samples per sampling outing, and 395 samples total. Depths were initially chosen systematically to represent areas of potential vertical flow differences such as benthic boundary layers and areas of potential water stratification (surface, midwater, and bottom). Due to logistical constraints (e.g., small vessel size, limited net retrieval system, and strong current speeds encountered in the Narrows), the greatest depth that could be consistently sampled was 30 m, which was not influenced by the benthic boundary layer. Therefore, the surface, midwater, and bottom tows were located at water depths of 1 m,

10 m, and 30 m respectively. All depths, sites, and tides were averaged for ease of presentation.

Sample Processing

Each sample was preserved in a buffered 4% formalin solution in seawater. Based on the abundance of larvae and zooplankton present, samples were split using a Folsom plankton splitter in the laboratory, and all densities were standardized to a constant volume (# larvae/100m³). The presence or absence and relative abundance of zooplankton and anomuran larvae was qualitatively noted. All brachyuran larvae were picked by hand using a dissecting microscope (10X-40X) and identified to stage and species whenever possible using a variety of larval keys (Hart 1935; Knudsen 1959; Hart 1960; Kurata 1963; Poole 1966; Trask 1970; Lough 1974; Ally 1975; Haynes 1981; Iwata and Konishi 1981; Debrosse et al. 1990a; Debrosse et al. 1990b). If larvae could not be identified to species, they were identified to genus or family.

Three species within the Family Majidae (*Hyas lyratus*, *Oregonia gracilis*, and *Chinoecetes bairdi*) have zoeal stages that are difficult to separate morphologically and therefore I treated these zoeae collectively as Majidae. Megalopae of *C. bairdi* were conspicuous and easily distinguishable by numerous carapace and rostral spines, and *H. lyratus* and *O. gracilis* megalopae were distinguishable by the presence or absence of lateral carapace spines. However, these lateral carapace spines are easily damaged and could have been missed during identification. Therefore, *H. lyratus* and *O. gracilis* megalopae were pooled. The species grouping *Pugettia* spp. possibly includes both

Pugettia gracilis and *Pugettia producta* because it is difficult to separate these species using external morphological features. Nevertheless, it is likely that the larvae observed were *P. gracilis*, since *P. gracilis* adults have been observed in Glacier Bay and *P. producta* has not. The published northern limit of *P. producta* is Prince of Wales Island, Alaska, 600 km to the south, but this species has been observed off Chichagof Island, 20 km to the south of Glacier Bay (O'Clair and O'Clair 1998, Donnellan pers obs.). *Pinnixa* spp. was most likely *Pinnixa littoralis* or *Pinnixa occidentalis*. *P. littoralis* is generally found as a symbiont in bivalves, which are abundant in Glacier Bay, but its presence in the Bay would be beyond the published northern range of Sitka, Alaska. However, *P. occidentalis* inhabits the spoonworm, *Echiurus echiurus alaskamus*, who is widely distributed throughout Glacier Bay (Sharman et al. 2003).

Larval Duration

For comparison with previous studies, larval duration is reported in two ways; development time for the zoeal stages and the development time for the entire pelagic phase (from larval release through the megalopal stage). The development time for the zoeal stages is reported as the time from which the stage I zoeae were first observed in the plankton to the time that the megalopae were first observed. The development time for the entire pelagic phase is reported as the average time between the minimum and maximum duration, with the *minimum* duration defined as the time from the first zoeae to the first peak in megalopal abundance, and the *maximum* duration as the time from

the first zoeae to the time the last megalopae was observed. Reilly (1983) defined larval duration for the entire pelagic phase as the period from the first collection of stage I zoeae to the time “post-larvae” were first collected on the benthos. Because I did not monitor settlement, Reilly’s (1983) development time is assumed to be longer than my estimated pelagic phase. Lough (1974) apparently estimated larval duration as the time from the peak occurrence of stage I zoeae to the time that megalopae were generally absent from the plankton, which is comparable to my estimated *minimum* duration. Further, both Lough (1974) and Reilly (1983) sampled approximately monthly, resulting in an uncertainty of ± 30 days. This research began April 26, but stage I zoeae of most species were already present in the plankton, and the study ended on October 5, prior to the last occurrence of megalopae for some species. Therefore, the estimates of larval duration reported are minimums for most species.

RESULTS

Species Abundance and Temporal Distribution

Various larval stages of twelve species were collected, representing five families of brachyuran crabs (Table 1). All species exhibited a strong seasonal pattern in larval abundance with first stage larvae (zoeae stage I) most abundant in May (Figures 4-9). During this month, larval abundance of *Cancer magister* increased 63%, *Cancer oregonensis* 92%, Majidae 77%, *Pugettia* spp. 73%, and *Fabia subquadrata* 69%. This first peak of stage I zoeae is approximately 3-4 months later than the times reported by Lough (1976) for *Cancer magister*, *C. oregonensis*, and *Fabia subquadrata*

in central Oregon. However, the timing of *C. magister* and *Chionoecetes bairdi* is comparable to studies conducted in Canada and the Bering Sea (Incze et al. 1987) (Table 2). Following the May peak, abundance of stage I zoeae declined precipitously throughout the season. The abundance of subsequent larval stages of all species was generally much lower, and peaks occurred later in the season, with megalopae of some species present in the plankton (albeit in very low numbers) only during the end of the sampling season in early October (Figures 4-9).

With the exception of *Telmessus cheiragonus* and the Majidae group, stage I zoeae of most species were present in the plankton for approximately 12 to 16 weeks (Figure 3). Although larval abundance was highly variable, multiple peaks of stage I zoeae coupled with the protracted larval release time indicated non-synchronous release and/or the possibility of multiple cohorts. *T. cheiragonus* and the group Majidae stage I zoeae were already present in the plankton in relatively large numbers at the onset of sampling, so the minimum estimated time that first stage larvae were present in the plankton was approximately four weeks.

Family Cancridae

Cancer oregonensis were the most abundant larvae observed, comprising 69% of the total (Table 1). Abundance peaked on June 24 with a mean larval density of 1,085 stage I zoeae/100 m³ and a maximum density of 5,218 zoeae/100 m³ on that day (Figure 4). Although the abundance of subsequent zoeal stages was substantially lower, stage III and IV zoeal abundance was comparable to that of peak stage I on July 22,

which indicates an influx of these stages from outlying areas. Megalopae were first collected July 29 and occurred at low densities until October 4.

Three peaks in the abundance of *C. magister* stage I zoeae were collected on May 11, 31 and June 24. Although abundance was low ($< 10/100 \text{ m}^3$), two peaks in zoeae stage II were observed on June 24 and August 22, while stage III-V zoeae were rarely collected ($< 3/100 \text{ m}^3$) throughout the sampling period (Figure 5). A single megalopa was collected July 10, but most were collected from September 19 until sampling ended on October 5.

Zoeal stages of *Cancer productus* were collected in low numbers, and stage V zoeae were not observed (Table 1). Stage II zoeae were collected prior to stage I, indicating that the larval hatching period was earlier than the first observed date of stage I zoeae on July 29 (Figure 3). Furthermore, abundance of stage I zoeae in October was similar to that observed in July, suggesting that the larval hatching period for *C. productus* may be more protracted than for the other species. Megalopae peaked in abundance over three subsequent dates, September 29 and October 4 and 5. *Cancer gracilis* were the least abundant larvae collected, with only one stage III zoea observed (Table 1).

Family Majidae

The stage I zoeae of the majids (*Hyas lyratus*, *Oregonia gracilis*, and *Chinoecetes bairdi*) were second in abundance after *Cancer oregonensis* (Table 1). This may have been attributable, in part, to combining three distinct species. However,

even if each species was represented equally (~4% of total larvae observed), they would be the third most abundant, with *Pugettia* spp. as second (5.1% of total larvae observed). At least one larval stage from the genus *Pugettia* was observed on almost every sampling date. Peak abundance occurs later with each subsequent larval stage of this species, indicating a single cohort was followed through the sampling season (Figure 7). Megalopae of *Hyas lyratus* and *Oregonia gracilis* were collected from June 24 through August 22 in moderate numbers and peaked on July 22 with 47 megalopae/100 m³ collected on the surface at one site (Figure 8). *C. bairdi* zoeae were not distinguished, and megalopae were very rare; only three individuals were collected (August 22 and 29, and October 6).

Family Pinnotheridae

Abundance of *Fabia subquadrata* stage I zoeae peaked on May 25 and then declined precipitously. Later stage larvae (zoeae II-V) were never collected at densities > 10 larvae/100 m³. Megalopae were collected from July 29 until October 4, but never in great numbers (16 total over the entire sampling period) (Figure 9). A total of 100 larvae of *Pinnixa* spp. were collected throughout the sampling period (Table 1), 70% of which were zoeae stage I. Zoeae stage IV-V and megalopae were not collected.

Family Atelecyclidae

Stage I-IV of *Telmessus cheiragonus* zoeae all peaked in abundance on May 11, indicating that hatching occurred considerably earlier than the onset of sampling

(Figure 10). Megalopae were collected continuously in low numbers (< 6 megalopae/100m³) May 13 through June 24.

Family Xanthidae

Lophopanopeus bellus larvae were collected at low densities throughout the study (Table 1). Stage I zoeae were collected during every sampling event from May 31 through August 22, and zoeae stage II and III were collected occasionally throughout August. Megalopae were observed on May 25 and then again in September and October (Figure 3). The occurrence of megalopae on two separate dates indicates that this species released two broods spaced seasonally in the spring and fall, which has been documented in Puget Sound (O'Clair and O'Clair 1998).

Larval Duration

The larval durations were estimated for the most abundant species and are summarized in Table 2. The low abundances of *Cancer gracilis* and *Lophopanopeus bellus* zoeae and *Chinoecetes bairdi* megalopae precluded an accurate estimate of larval duration for those species. *Cancer magister*, *C. oregonensis*, *Fabia subquadrata*, and *Pugettia* spp. had the longest larval durations, spanning the entire length of the study (approximately 119-154 days). For all species, the larval durations reported here are longer than those reported by Lough (1974). The larval duration of *C. magister* is longer than the durations reported for the outer coast of California to Washington and

comparable to durations of *C. magister* in the inside waters of Washington (Jamieson and Phillips 1993) (Figure 11).

DISCUSSION

Larval release is generally triggered by physical and/or biological cues such as tidal fluctuations and light/dark regimes (see Morgan 1995 for review), temperature increases (Shirley and Shirley 1989a), phytoplankton blooms (Starr et al. 1990), or a combination of any of the above. In high latitude regions, crabs are subjected to dramatic seasonal fluctuations and environmental forces. In Glacier Bay, tidal changes are great (~4m daily, on average), and seasonal variations in temperature, salinity, and light/dark regimes are dramatic. The larvae of most brachyuran species observed in Glacier Bay exhibited a highly seasonal pattern of abundance, which in their first appearance coincided with the onset of oceanographic conditions favorable to survival (increasing water temperature and abundant food supply). Larval abundance increased dramatically in May concurrent with an increase in water temperature of almost 2°C (from 4.4°C in March to 6.2°C in May) and the seasonal peak in chlorophyll-*a* values (Figure 2). If larvae were released in Glacier Bay prior to May, the water temperature would have been approximately 5°C. From model simulations based on known temperature tolerances of *Cancer magister* by Moloney et al. (1994), 100% larval mortality would occur at 5.1°C. Further, their models predicted that larvae would have the highest rates of survival to metamorphosis when they were released during periods of rising temperature and when temperatures were the warmest (15°C).

While it is important that larvae are released during times of favorable water temperatures and abundant food resources, hatching may also be a function of embryo development time. Shirley and Shirley (1989b) found that the embryo hatch time of *Paralithodes camtschaticus* was not correlated with the phytoplankton bloom in Southeast Alaska, but was instead dependent on embryo development time. The delayed hatching time of brachyuran larvae in Glacier Bay relative to many of the same species from field studies at lower latitudes (Lough 1976; Reilly 1983), may in part be explained by prolonged embryo development time. From laboratory studies, Shirley et al. (1987) found that the duration of *Cancer magister* embryo incubation was inversely proportional to water temperature. Indeed, during a year of cooler sea surface temperatures (10.6°C), Reilly (1983) observed first stage zoeae of *C. magister* in the plankton almost one month later than during years of warmer temperatures (12.8-13.1°C). In Glacier Bay, *C. magister* adults extrude eggs in September through November (Swiney and Shirley 2001). At 5°C, embryo developmental time in the laboratory, from extrusion to hatch, was estimated at 160 days (Shirley et al. 1987). With average water temperatures over this period in Glacier Bay of approximately 5°C (Figure 2), the estimated earliest hatching period would occur March through May. This estimate coincides with the timeframe when hatching did occur in 2002 (May-August), and may in part explain the delayed larval release time compared to release times documented in lower latitudes (at least for *C. magister*).

The prolonged hatching period observed for some species indicates that there was no single bay-wide event that the adults tracked to release larvae. Long release

times could be sustained by high phytoplankton abundance or could be the result of delayed development due to cool water temperatures during embryo incubation time. Shirley et al. (1987) found that larval hatching duration was inversely proportional to water temperature. Female *Cancer magister* reared at 5°C released larvae over a 25-day period. However, during this study, stage I zoeae of *C. magister* were observed in the plankton for 146 days indicating that factors other than water temperature were probably influencing larval hatching. Extended larval release time by the population could also be the result of multiple cohorts being released in a season, or the continual release of larvae. Once their embryos are developed, crabs may be releasing larvae as long as temperatures permit larval survivorship. However, at some point it becomes disadvantageous to release larvae. Stage I *C. magister* zoeae released in August during this study would be estimated to settle in January when primary productivity, and thus food resources, are at their lowest, and water temperatures are approximately 5°C where larval mortality is estimate to be 100% (Moloney et al. 1994). Thus, larvae released this late would probably face very low survivorship to metamorphosis because of minimal food and critically low water temperatures.

Environmental factors (e.g., temperature) have been suggested as determinants influencing larval duration times (Pechenik 1987). Overall, shorter larval durations minimize the time that larvae are susceptible to predation in the plankton. Temperature (Sulkin and McKeen 1994) and increased food availability (Paulay et al. 1985) are inversely related to larval development time due to rapid growth in optimal conditions (abundant food and warm water). Therefore, the prolonged larval durations observed

during this study, compared to field studies in lower latitudes, may be attributed to the cooler water temperatures experienced. Moloney et al. (1994) predicted that at 6.1°C, the larval duration (from hatch to settlement) of *Cancer magister* would be 260 days. Therefore, at an average temperature of 6.8°C from April 26-Oct 17 (averaged over the entire water column, n=5 sampling periods, SE 0.05°C, at an oceanographic sampling station near the study area, USGS data Glacier Bay Field Station), the estimated larval duration of 154 days for *Cancer magister* was much shorter than that predicted by Moloney et al. (1994), but comparable to observations made by Jamieson and Philips (1993) of *C. magister* larval durations in the inside waters of British Columbia. This apparent contradiction might be explained by high primary productivity in Glacier Bay. Although, it appears that food abundance alone was not compensatory enough to reduce the larval duration time relative to lower latitudes.

To ensure viable offspring, it is imperative that adults couple larval hatching rhythms with times of favorable environmental conditions (Giese and Pearse 1974). This could be especially problematic at high latitudes, where the window of favorable water temperatures and abundant food resources can be narrow. Further, decreased temperatures significantly increase larval duration (Shirley et al. 1987; Moloney et al. 1994; Sulkin and McKeen 1994) which can increase vulnerability to mortality from predation. For a family such as the cancrids that has the longest known larval development time of all the brachyurans (Hines 1986), delayed larval hatching could mean the failure of an entire cohort. On the other hand, premature larval hatching could have a large impact on overall survival to metamorphosis if larvae are released

during unfavorable oceanographic conditions (cooler water temperatures and decreased food sources). In Glacier Bay, multiple factors appear to play a role in determining the timing and duration of larval release and overall larval development time. There appears to be a temperature threshold coupling embryo development time and favorable oceanographic conditions for larval release and subsequent development. Once this threshold is exceeded, it appears that release occurs until all larvae are released, or until conditions become unfavorable to release. This window occurs during the summer months when water temperatures are at their maximum and is later than that for similar species in lower latitudes.

LITERATURE CITED

- Ally R (1975) A description of the laboratory-reared larvae of *Cancer gracilis* Dana, 1852 (Decapoda, Brachyura). *Crustaceana* 28
- Bodkin J, Kloecker K (1999) Intertidal clam diversity, size, abundance and biomass in Glacier Bay National Park and Preserve- 1999 Annual Report. US Geological Survey, Alaska Science Center, Anchorage, AK
- Debrosse G, Sulkin S, Jamieson G (1990a) Intraspecific morphological variability in megalopae of three sympatric species of the genus *Cancer* Brachyura Cancridae. *Journal of Crustacean Biology* 10: 315-329
- Debrosse GA, Baldinger AJ, McLaughlin PA (1990b) A comparative-study of the megalopal stages of *Cancer oregonensis* Dana and *Cancer productus* Randall (Decapoda, Brachyura, Cancridae) from the Northeastern Pacific. *Fishery Bulletin* 88: 39-49
- Dinnel PA, Armstrong DA, McMillan RO (1993) Evidence for multiple recruitment-cohorts of Puget Sound Dungeness crab, *Cancer magister*. *Marine Biology* (Berlin) 115: 53-63
- Donnellan M, Fisher J, Barber J (2004) The ecological effects of sea otters on shallow benthic communities in Glacier Bay National Park and inventory and monitoring of shallow subtidal communities in lower/mid Glacier Bay. National Park Service, Glacier Bay National Park, pp 52
- Etherington L, Hooge P, Hooge E (2004) Factors affecting seasonal and regional patterns of surface water oceanographic properties within a fjord estuarine system: Glacier Bay, Alaska. USGS, Alaska Science Center, Anchorage, AK, pp 79
- Giese A, Pearse J (1974) Reproduction of Marine Invertebrates. Academic Press Inc., New York and London
- Hart J (1935) The larval development of British Colombia Brachyura: I. Xanthidae, Pinnotheridae (in part) and Grapsidae. *Canadian Journal of Research* 12
- Hart J (1960) The larval development of British Colombia Brachyura: II. Majidae, Subfamily Oregonidae. *Canadian Journal of Research* 38
- Haynes E (1981) Description of stage-I zoeae of Snow Crab, *Chionoecetes bairdi*, (Oxyrhyncha, Majidae) from plankton of lower Cook Inlet, Alaska. *Fishery Bulletin* 79: 177-182
- Hines A (1986) Larval patterns in the life histories of brachyuran crabs (Crustacea, Decapoda, Brachyura) Proceedings of the invertebrate larval biology workshop held at Friday Harbor Marine Laboratories. *Bulletin of Marine Science*, University of Washington, pp 444-466
- Incze L, Armstrong David A, Smith S (1987) Abundance of larval Tanner crabs (*Chionoecetes* spp.) in relation to adult females and regional oceanography of the southeastern Bering Sea. *Can J Fish Aquat Sci* 44: 1143-1156
- Iwata F, Konishi K (1981) Larval development in laboratory of *Cancer amphioetus* Rathburn, in comparison with those of seven other species of *Cancer* (Decapoda, Brachyura). *Publ Seto Mar Biol Lab* 27: 369-391

- Jamieson G, Armstrong D (1991) Spatial and temporal recruitment patterns of Dungeness crab in the northeast Pacific. *Memoirs of the Queensland Museum* 31: 365-381
- Jamieson G, Phillips A, Huggett W (1989) Effects of ocean variability on the abundance of Dungeness crab (*Cancer magister*) megalopae. In: Beamish R, McFarlane G (eds) Effects of ocean variability on recruitment and an evaluation of parameters used in stock assessment models. *Can Spec Publ Fish Aquat Sci*, pp 305-325
- Jamieson GS, Phillips A (1993) Megalopal spatial distribution and stock separation in dungeness crab (*Cancer magister*). *Canadian Journal of Fisheries & Aquatic Sciences* 50: 416-429
- Jamieson GS, Phillips AC (1988) Occurrence of Cancer crab (*Cancer magister* and *Cancer oregonensis*) megalopae off the west-coast of Vancouver Island, British-Columbia. *Fish Bul* 86: 525-542
- Knudsen J (1959) Life cycle studies of the Brachyura of Western North America, II. The life cycle of *Lophopanopeus bellus* diegenesis Rathburn. *Bulletin, Southern California Academy of Sciences* 58
- Kurata H (1963) Larvae of Decapoda Crustacea of Hokkaido 1. Atelecyclidae (Atelecyclinae). *Bull Hokkaido Reg Fish Lab Board Can Trans Series* 1124
- Lough RG (1974) Dynamics of crab larvae (Anomura, Brachyura) off the central Oregon coast. PhD
- Lough RG (1976) Larval dynamics of Dungeness Crab, *Cancer magister*, off Central Oregon Coast, 1970-71. *Fish. Bull.* 74: 353-376
- McConnaughey R, A., Armstrong D, A., Hickey B, M., Gunderson D, R. (1992) Juvenile dungeness crab (*Cancer magister*) recruitment variability and oceanic transport during the pelagic larval phase. *Canadian Journal of Fisheries & Aquatic Sciences* 49: 2028-2044
- Moloney C, Botsford L, Largier J (1994) Development, survival and timing of metamorphosis of planktonic larvae in a variable environment: The Dungeness crab as an example. *Marine Ecology Progress Series* 113: 61-79
- Morgan SG (1995) The timing of larval release. CRC Press, Boca Raton, FL
- O'Clair C, Shirley T, Taggart S (1996) Dispersion of adult *Cancer magister* at Glacier Bay, Alaska: variation with spatial scale, sex, and reproductive status High Latitude Crabs: Biology, Management, and Economics. Alaska Sea Grant College Program, pp 209-227
- O'Clair CE, Stone R, Freese J (1990) Movements and habitat use of Dungeness crabs in Glacier Bay fishery Glacier Bay Science Symposium. US National Park Service, Glacier Bay National Park and Preserve, AK
- O'Clair R, M., O'Clair C, E. (1998) Southeast Alaska's Rocky Shores: Animals. Plant Press, Auke Bay, AK
- O'Clair C, Freese J, Stone R, Shirley T, Leder E, Taggart S, Kruse G (1995) Nearshore distribution and abundance of Dungeness crabs in Glacier Bay National Park, Alaska. In: Engstrom (ed) Proceedings of the Third Glacier Bay Science Symposium, National Park Service, Anchorage, Alaska, pp 196-202

- Paulay G, Boring L, Strathmann RR (1985) Food limited growth and development of larvae: Experiments with natural seawater. *Journal of Experimental Marine Biology and Ecology* 93: 1-10
- Pechenik J (1987) Environmental influences on larval survival and development. In: Giese A, Pearse J, Pearse V (eds) *Reproduction of Marine Invertebrates*. Blackwell Scientific Publications and The Boxwood Press, Palo Alto, CA and Pacific Grove, CA
- Poole R (1966) A description of laboratory-reared zoeae of *Cancer magister* Dana, and megalopae taken under natural conditions (Decapoda Brachyura). *Crustaceana* 11: 83-97
- Reilly PN (1983) Dynamics of Dungeness crab, *Cancer magister*, larvae off Central and Northern California. In: Wild PW, Tasto RN (eds) *Life history, environment, and mariculture studies of the Dungeness crab, (Cancer magister)*, with emphasis on the central California fishery resource. California Department of Fish and Game, pp 57-84
- Scheduling K, Shirley T, O'Clair C, Taggart S (2001) Critical habitat for ovigerous Dungeness crabs Kruse, Gordon H.; Bez, Nicolas; Booth, Anthony; Dorn, Martin W.; Hills, Sue; Lipcius, Romuald N.; Pelletier, Dominique; Roy, Claude; Smith, Stephen J.; Witherell, David: Eds. University of Alaska Sea Grant College Program Report. Spatial processes and management of marine populations. [print] (Ak-SG-01-02). 2001. 431-445. University of Alaska Sea Grant College Program, Fairbanks, Alaska, 99775-5040
- Shanks A, L. (2001) An identification guide to the larval invertebrates of the Pacific Northwest. Oregon State Univeristy Press, Corvalis
- Sharman L, Eichenlaub B, Van Leeuwen D, Croll S, Grover J, Lenhart G, Hoope P (2003) NPS Alaska Coastal Resources Inventory and Mapping Field Protocol - The Polygon Method - Developed at Glacier Bay National Park and Preserve 1997-1998. National Park Service, Glacier Bay National Park
- Shirley S, Shirley T (1989a) Interannual variability in density, timing and survival of Alaskan red king crab *Paralithodes camtschatica* larvae. *Mar Ecol Prog Ser* 54: 51-59
- Shirley SM, Shirley TC (1989b) Interannual Variability In Density Timing And Survival Of Alaskan Usa Red King Crab Paralithodes-Camtschatica Larvae. *Marine Ecology Progress Series* 54: 51-59
- Shirley SM, Shirley TC, Rice SD (1987) Latitudinal variation in The Dungeness crab, *Cancer magister*, zoeal morphology explained by incubation temperature. *Marine Biology* 95: 371-376
- Starr M, Himmelman J, Therriault J (1990) Direct coupling of marine invertebrate spawning with phytoplankton blooms. *Science* 247: 1071-1074
- Stevens B, Armstrong D (1984) Distribution, abundance and growth of juvenile Dungeness crabs, *Cancer magister*, in Grays Harbor estuary, Washington. *Washington Fish Bull* 82: 469-483

- Sulkin SD, McKeen G (1994) Influence of temperature on larval development of four co-occurring species of the brachyuran genus *Cancer*. *Marine Biology* (Berlin) 118: 593-600
- Swiney KM, Shirley TC (2001) Gonad development of southeastern Alaskan Dungeness crab, *Cancer magister*, under laboratory conditions. *Journal of Crustacean Biology* 21: 897-904
- Taggart S, Mondragon J, Andrews A, Nielsen J, de La Bruere L (2003a) Testing the effectiveness of a high latitude marine reserve network. Phase 1: Distribution of king and Tanner crabs in Glacier Bay, Alaska. In: US Geological Survey ASC, Anchorage, AK (ed), pp 26
- Taggart SJ, Hooge PN, Mondragon J, Hooge ER, Andrews AG (2003b) Living on the edge: distribution of Dungeness crab *Cancer magister* in a recently deglaciated fjord. *Mar. Ecol. Prog. Ser.* 246: 241-252
- Trask T (1970) A description of laboratory-reared larvae of *Cancer productus* Randall (Decapoda, Brachyura) and a comparison to larvae of *Cancer magister* Dana. *Crustaceana* 18: 133-146

Table 1. The total abundance (percent abundance) of all species observed. “*”=<0.1%, “n.o.”= species/stage combinations that were not observed or were not identified using external morphological features, “-”=stages that are not produced by that species or species group.

Family	# of Larval Stages	Species	Larval Stage						Total
			1	2	3	4	5	PL	
Cancridae	5 zoeae 1 megalopa	<i>Cancer oregonensis</i>	55,258 (34.5)	11,282 (7.0)	22,571 (14.2)	19,473 (12.2)	2,432 (1.5)	77 *	111,093 (69.4)
		<i>Cancer magister</i>	2,022 (1.0)	135 *	70 *	5 *	7 *	98 (0.1)	2,337 (1.3)
		<i>Cancer productus</i>	41 *	11 *	2 *	2 *	n.o.	58 *	114 *
		<i>Cancer gracilis</i>	n.o.	n.o.	1 *	n.o.	n.o.	25 *	26 *
		Unidentified Cancer	48 *	38 *	3 *	n.o.	n.o.	n.o.	89 *
Majidae	2 zoeae 1 megalopa	Majidae	19,645 (12.3)	1,045 (0.7)	-	-	-	n.o.	20,779 (13.0)
		<i>Pugettia</i> spp.	8,103 (5.1)	2,033 (1.3)	-	-	-	890 (0.6)	11,026 (7.0)
		<i>Oregonia gracilis</i>	n.o.	n.o.	-	-	-	49 *	49 *
		<i>Hyas lyratus</i>	n.o.	n.o.	-	-	-	135 (0.1)	135 (0.1)
		<i>Chinoecetes bairdi</i>	n.o.	n.o.	-	-	-	4 *	4 *
Pinnotheridae	5 zoeae 1 megalopa	<i>Fabia subquadrata</i>	6,236 (3.9)	556 (0.3)	137 (0.1)	85 (0.1)	236 (0.1)	16 *	7,266 (4.5)
		<i>Pinnixa</i> spp.	70 *	17 *	13 *	n.o.	n.o.	n.o.	100 *
Atelecyclidae	5 zoeae 1 megalopa	<i>Telmessus cheiragonus</i>	2,014 (1.3)	1,859 (1.2)	1,459 (0.9)	838 (0.5)	577 (0.4)	237 (0.1)	6,984 (4.4)
Xanthidae	4 zoeae 1 megalopa	<i>Lophopanopeus bellus</i>	23 *	4 *	1 *	n.o.	-	53 *	81 *

Table 2. Seasonal timing of stage I zoeae and larval duration times ($\pm$ minimum and maximum) compared to published studies from other geographic regions. “*” highlights larval durations that were estimated from published opportunistic observations of stage I zoeae and megalopae in the field.

Species	Region	Date of First Occurrence Zoeae Stage I	Development Time (days)		Reference
			Zoeal Stages	Hatch to Megalopae	
<i>Cancer magister</i>	Southeast AK	26-Apr	146	154 (146-162)	this study
	Inside waters, WA	March-April		150*	Orensanz & Gallucci (1988) Jamieson & Phillips (1993)
	Outer coast, WA	Jan-Feb		120*	Armstrong et al. (1987) Dinnel et al. (1993)
	Central OR	29-Jan	105 (94-130)	130 (89-143)	Lough (1976)
	Central CA	12-Dec	80-95	115 (105-125)	Reilly (1983)
	Lab 10°C (No. CA)		69		Sulkin and McKeen (1994)
<i>Cancer oregonensis</i>	Southeast AK	26-Apr	94	133 (105-161)	this study
	Central OR	Jan	na	120 (105-140)	Lough (1976)
	Lab 10°C (No. CA)		72		Sulkin and McKeen 1994
<i>Cancer productus</i>	Southeast AK	14-Jul	74	83	this study
	Puget Sound	March-June			O'Clair
	Lab 11°C (No. CA)		97		Trask (1969)
	Lab 10°C (No. CA)		59		Sulkin and McKeen 1994
<i>Fabia subquadrata</i>	Southeast AK	26-Apr	118	125 (118-132)	this study
	Central OR	Feb		90 (63-200)	Lough (1976)
	Lab 11-13°C (WA)			54	Irvine and Coffin (1960)
<i>Pugettia</i> spp.	Southeast AK	26-Apr	51	121 (79-163)	this study
	Central OR	All year		49 (45-53)	Lough (1976)
Majidae zoeae	Southeast AK	26-Apr	59	103 (87-118)	this study
<i>C. bairdi</i> zoeae	Bering Sea	April-June			Incze et al. (1987)
<i>H. lyratius</i> / <i>O. gracilis</i> megalopae	Southeast AK			31	this study
<i>Telmessus cheiragonus</i>	Southeast AK	26-Apr	29	47 (35-59)	this study

FIGURE LEGENDS

Figure 1. Study area depicting the sampling sites in Sitakaday Narrows (West, Middle, East). The entire Bay is closed to the commercial harvest of *Cancer magister* and *Paralithodes camtschaticus*. The shaded area depicts the part of the Bay open to the commercial harvest of *Chionoecetes bairdi*.

Figure 2. Seasonal patterns of temperature and chlorophyll-*a* in Sitakaday Narrows from 1993-2002 averaged over the entire water column (± 1 SE) (data from USGS Glacier Bay Field Station, Gustavus, AK). The arrow indicates average larval release time for many species observed during the study.

Figure 3. Seasonal distribution of all larvae observed. Z1-Z5 represents zoeal stage 1-5 and PL represents megalopae. "Stars" depict occurrences over one day.

Figure 4. Mean larval abundance (± 1 SE) of *Cancer oregonensis*. All data are averaged for all sites, depths, and tides sampled from April 26-October 5, 2002.

Figure 5. Mean larval abundance (± 1 SE) of *Cancer magister*. All data are averaged for all sites, depths, and tides sampled from April 26-October 5, 2002.

Figure 6. Mean larval abundance (± 1 SE) of the group Majidae (*Chionoecetes bairdi*, *Hyas lyratus*, and *Oregonia gracilis*). All data are averaged for all sites, depths, and tides sampled from April 26-October 5, 2002.

Figure 7. Mean larval abundance (± 1 SE) of *Pugettia* spp. All data are averaged for all sites, depths, and tides sampled from April 26-October 5, 2002.

Figure 8. Mean larval abundance (± 1 SE) of group *Hyas lyratus/Oregonia gracilis*. All data are averaged for all sites, depths, and tides sampled from April 26-October 5, 2002.

Figure 9. Mean larval abundance (± 1 SE) of *Fabia subquadrata*. All data are averaged for all sites, depths, and tides sampled from April 26-October 5, 2002.

Figure 10. Mean larval abundance (± 1 SE) of *Telmessus cheiragonus*. All data are averaged for all sites, depths, and tides sampled from April 26-October 5, 2002.

Figure 11. Estimated larval duration (days) $\pm$ minimum and maximum of *Cancer magister* from this study and published field studies (California, Reilly 1983; Oregon, Lough 1976; outer coast Washington, Armstrong et al. 1987 and Dinnel et al. 1993;

Strait of Georgia Washington, Orensanz and Gallucci 1988 and Jamieson and Phillips 1993; Southeast AK, this study).

Figure 1.

Figure 2.

Figure 3.

Figure 4.

Figure 5.

Figure 6.

Figure 7.

Figure 8.

Figure 9.

Figure 10.

Figure 11.

CHAPTER 2

RETENTION OF BRACHYURAN LARVAE IN A NEWLY DESIGNATED MARINE RESERVE IN SOUTHEAST ALASKA

ABSTRACT

The horizontal and vertical distributions of seven species of larval brachyurans were measured during ebb and flood tides at three sites across the mouth of Glacier Bay (Southeast Alaska, USA) to determine whether larvae were retained or exported. The importance of lunar phase on larval vertical position and the effect of day/night and tide cycles on megalopal vertical distribution are addressed. There was no effect of tide or site on larval abundance. However, with the exception of *Cancer magister*, all larval stages of each species were persistent throughout the study, suggesting that these species are retained. Although the dispersal patterns for *C. magister* were less clear, Glacier Bay acted as a settling area for this species and five others. Megalopae were more abundant during nighttime flood tides at the surface, and most species were more abundant at the surface during spring tides. Active vertical migration has been well documented as an explanation for variable vertical distributions. In this tidally driven fjord system, however, I suggest that turbulent flow during high amplitudes tides forces larvae to the surface. The flow across the inlet (4 km wide) is reported and a model relating measured water velocity to local tide predictions was produced, which allowed the calculation of the volume of water flowing through the inlet.

INTRODUCTION

Marine reserves have been proposed and implemented as an alternate strategy to conventional fisheries management techniques (e.g., catch limits, seasonal closures, altering fishing methods) for sustaining adult populations of commercially important species. It is hypothesized that marine reserves will help sustain fisheries by protecting adult populations within the reserve, and increasing adjacent populations by a direct spillover of adults or recruits to the fished areas (“spillover effect” and “recruitment effect” respectively) (Halpern 2003). In a review of 89 studies conducted on marine reserves, Halpern (2003) concluded that “no-take” marine reserves increased overall species abundance, size, biomass, and diversity relative to adjacent areas that were fished. Studies have shown that the “spillover effect” does increase both fish (Russ et al. 2004) and invertebrate (Davis & Dodrill 1980) abundance in adjacently fished areas. However, because it is difficult to measure the number of larvae leaving a marine reserve, it is much more difficult to directly measure the “recruitment effect” of marine reserves. Therefore, most studies have reported on the theory alone (Rogers-Bennett et al. 1995, Crowder et al. 2000, Botsford et al. 2001) or have relied on mathematical models (Demartini 1993, Stockhausen et al. 2000, Lockwood 2002, Gerber et al. 2003) to determine the number of recruits produced from a marine reserve. The lack of field studies to directly measure the “recruitment effect” of a marine reserve can partially be attributed to the difficulty in directly quantifying the numbers of larvae leaving a marine reserve, a poor understanding of larval dispersal distances, and a poor knowledge of connectivity between populations (Botsford et al. 2001, Gaines et al.

2003, Largier 2003, Palumbi 2003, Shanks et al. 2003). Based on population models and studies conducted on advection, cross-shelf transport, and hydrographic influences on larval dispersal and recruitment (Quinn et al. 1993, Wing et al. 1995, Alexander & Roughgarden 1996, Bjorkstedt et al. 1997, Botsford et al. 1998) arguments have been presented to place marine reserves in areas of major eddies or countercurrents that would have a positive effect on the dispersal and subsequent recruitment of target species (Murray et al. 1999). If marine reserves are placed in areas of considerable offshore transport, then larvae may not return to repopulate the reserve or adjacent areas, making the reserve unsustainable and useless as a source population. Therefore, an understanding of species-specific larval dispersal to and from adjacent areas is pivotal in the design of successful marine reserves for the protection of species with complex life stages. The next logical step is to measure reproductive output from a marine reserve to determine whether the “recruitment effect” is working.

Laboratory and field studies suggest that larval dispersal is not a passive phenomenon. Examples demonstrate that brachyuran larvae and zooplankton are able to regulate their vertical position in the water column in tidally influenced estuaries (Cronin & Forward 1979, Epifanio 1988, McConaugha 1988, DiBacco & Chadwick 2001). Although the larvae might not be adept at swimming against strong tidal forces (Young 1995), by controlling their vertical position they can be effectively transported upstream or downstream in an estuary (see Epifanio 1988 for review). By vertically migrating, or simply by sinking during low flow and being re-suspended during high flow (de Wolf 1973), a larva has the capability to utilize tidal stream transport and

various flow fields. This can result in larval export, retention, or a combination of both in an estuary. For example, fiddler crab (*Uca* spp.) and blue crab (*Callinectes sapidus*) larvae have been observed dispersing as early-stage larvae and reinvading parent estuaries as late-stage larvae or juveniles for settlement (Wheeler 1978, Christy 1982, Christy & Stancyk 1982, Dittel & Epifanio 1982, Epifanio et al. 1984). Conversely, all stages of the xanthid crab, *Rithropanopeus harrissii*, are retained in the parent estuary (Cronin & Forward 1982). In San Diego Bay, California, DiBacco et al. (2001) observed all stages of *Lophopanopeus* spp. larvae retained in the bay while *Pachygrapsus crassipes* were exported from the estuary as early-stage larvae. These variable results suggest that a species-specific understanding of larval export versus retention is necessary.

In 1999, one of the largest marine reserves in the United States (1,255 km²) was created in Glacier Bay National Park and Preserve (Southeast Alaska), providing an opportunity to study the dispersal or retention of decapod larvae from a marine reserve system. Because Glacier Bay is a semi-closed system with a narrow entrance, the number of larvae entering and leaving the estuary can be quantified. To obtain an accurate measure of larval flux, continuous sampling of larval abundance and water velocity are needed over a known area. Studies measuring larval exchange from an estuary have generally focused on species that are already known to be imported or exported during a certain larval stage (Emmerson 1983, Dittel et al. 1991, Lago 1993, Rowe & Epifanio 1994). Further, studies estimating larval flux have focused on areas with shallow and narrow entrances so that the cross-sectional area requiring sampling to

yield an accurate estimate can be minimized (above references and Christy and Staneyck 1982; DiBacco and Chadwick 2001). Continuous samples are generally collected at a single station over multiple depths for a determined number of tidal cycles, and then abundance is extrapolated across the entire cross-sectional area of the estuary. The assumption is that larval abundance is homogenous across the estuary. DiBacco and Chadwick (2001), however, found that larval abundances of *Lophopanopeus* spp. and *Pachygrapsus crassipes* were variable across the San Diego Bay estuary. Therefore, to obtain the most accurate estimate of larval flux, abundance should be measured at multiple stations across the mouth of an inlet, bay, or estuary. Prior to the present study, estimating larval flux on the scale of Glacier Bay (approximately 4 km wide 50 meters water depth at the entrance) had not been done.

To determine whether brachyuran larvae were retained or exported, I measured their vertical and horizontal distributions, along with current speed and direction, during ebb and flood tides throughout most of the larval season. To measure the “recruitment effect” of this newly designated marine reserve, larval flux (a product of larval density and water volume transport) was calculated for each species and stage. Larval retention is understood if all stages are observed throughout the study period. Further, it might be expected that there would be no difference in larval abundance between tides, indicating that larvae are not being transported into or out of the estuary. On the other hand, if larvae were exported, late-stage larvae might be absent, or in very low numbers, and larvae would be expected to be more abundant during outgoing tides. Additionally, I addressed the importance of lunar phase on larval vertical position, and

the effect of night vs. day and vertical position relative to tide cycle on larval abundance. Assuming a net outflow of water from Glacier Bay (due to freshwater input from streams and glaciers), passive dispersal would result in a net outflow of larvae, resulting in larval export. If larvae were retained, however, variable vertical position, indicating behaviorally regulated transport, was expected. However, turbulent flow associated with the high-amplitude tides (spring tides) characteristic of Glacier Bay might inhibit behaviorally mediated vertical migration, and cause early-stage larval vertical distribution to be evenly distributed. On the other hand, megalopae (capable of strong swimming) might be able to regulate their vertical position to facilitate transport. It is expected that these late-stage larvae would immigrate into the estuary as has been documented in other studies (Christy & Morgan 1998).

METHODS

Study Site

The majority of Glacier Bay is a recently (< 250 years ago) de-glaciated fjord (some is still glaciated). Glacial fjords are complex estuarine systems that are influenced by high rates of fresh water discharge, high sedimentation rates, and narrow constrictions (Hooge & Hooge 2001, Etherington et al. 2004). Glacier Bay is approximately 100 km long from the mouth to the northern reaches and varies in width from approximately 15 km to 4 km at its narrowest region, which is the location of the study site (Sitakaday Narrows) (Figure 1). Significant freshwater input, mainly from run-off and glacial meltwater in the upper bay, contributes to a net flow of water down-

bay. Mixed semi-diurnal tides reach an average tidal range of approximately 3.7 m at Bartlett Cove in the southern bay and 4.2 m in the northern locations. Based on average tidal current speeds, a parcel of water was hypothesized to travel a distance of 43 km from the outer waters of Cross Sound into Glacier Bay (Figure 1) during an average spring flood tide series (Hooge & Hooge 2001). Surface drifter deployments in 2002 suggested that during average spring tides, surface waters traveled 32 km during a single flood tide event, which generally supports this hypothesis (Fisher, unpublished data).

Plankton Sampling

Discrete depth (10 m and 30 m) and surface plankton samples were collected approximately weekly ($n = 22$ days sampled) from April 26-October 5, 2002 (see Chapter 1 for details). Within each tide cycle (ebb and flood), 3 sites were sampled in Sitakaday Narrows (West, Middle, and East) (Figure 1). These sites were located in approximately 50 m of water and were systematically chosen to represent a spatial distribution across the narrows. To reduce bias and small-scale temporal variability, the order in which sites (and depths within sites) were sampled was chosen randomly each day. Generally, each site was sampled during ebb and flood tide the same day. However, if all sites were not completed within a day, they were completed the following day or were not sampled.

During October 4-6 night tows were also conducted at each tide, depth, and site to assess the effect of light/dark regimes on megalopal abundance. Bartlett Cove was

also sampled during this time to target *Cancer magister* megalopae that were observed there in large numbers (Figure 1).

Sample Processing

Each sample was preserved in a buffered 4% formalin solution in seawater and all densities were standardized to a constant volume (# larvae/100m³). All brachyuran larvae were picked out by hand using a dissecting microscope (10X-40X) and identified to stage and species whenever possible using a variety of larval keys (Hart 1935, Knudsen 1959, Hart 1960, Kurata 1963, Poole 1966, Trask 1970, Lough 1974, Ally 1975, Haynes 1981, Iwata & Konishi 1981, Debrosse et al. 1990a, Debrosse et al. 1990b). If larvae could not be identified to species, they were identified to genus or lumped by family (see Chapter 1 for details).

Larval Flux

Concurrent with the plankton sampling, sub-surface current speed and direction were determined using a 250 kHz SonTek Acoustic Doppler Current Profiler (ADCP) with a maximum sampling depth 160 m. The ADCP was temporarily mounted on a 9.6 m vessel with an integrated differential global positioning receiver, and sampling was conducted continuously while underway. SonTek software was used to correct for vessel position and speed, and current speed and direction were calculated *in situ*. The ADCP data were not tide-corrected, therefore the velocity depth bins corresponded to the actual depth where plankton tows were collected. The data were averaged every

minute for each depth bin (2 m), reducing Doppler noise to ± 1 cm/s, and were displayed in three dimensions in a geographic information system (ArcView 3.2) to facilitate visualization (computer code written by B. Eichenlaub, National Park Service and JL Fisher).

Because ADCP data were not collected for every plankton tow (due to logistical or equipment constraints), a harmonic relationship was calculated between the observed velocity data from the ADCP and the modeled current data (hereafter “modeled velocity”) using current prediction software (Tide and Currents v2.0a, Nautical Software Inc.). For each site, velocity data were averaged within depth bins that corresponded to the depths of plankton tows. The surface, midwater, and bottom depths encompassed the 0-4 m, 5-16 m, and 17-38 m depth bins, respectively. For each site and depth bin sampled, the *in situ* current velocity (V_{obs}) was subtracted from the modeled velocity (V_{model}) for each minute sampled (eq. 1.1). Harmonic regression was used to fit curves to these differences (ΔV). Three parameter sinusoidal curves fit the calculated differences (Figure 2), which allowed the prediction of velocity difference ($\Delta V_{\text{predicted}}$) for each site, and depth bin for any date and time (Table 1). Predicted velocities ($V_{\text{predicted}}$) were calculated for all dates, times, sites, and depths sampled by adding the predicted difference value ($\Delta V_{\text{predicted}}$) from the non-linear regression to the modeled velocities (V_{model}) (eq. 1.2).

$$\Delta V = V_{\text{obs}} - V_{\text{model}} \quad (1.1)$$

$$V_{\text{predicted}} = V_{\text{model}} + \Delta V_{\text{predicted}} \quad (1.2)$$

To compare plankton samples collected at different times in the tidal cycles, a standard measure of water volume was used to calculate larval flux values. Water velocity was integrated over an entire tidal cycle (i.e. ebb or flood) to obtain a measure of volume transport (V_{flux}) for each depth bin and site in a 1m x 1m cube (eq. 1.3). Larval flux (F) then is the product of larval density and volume transport for each site, depth, and tide (eq. 1.4). Net larval flux (F_{net}) was calculated as the sum of the values of larval flux for each tide that was sampled within a day (i.e. only daytime ebb and flood) (eq. 1.5). Net larval fluxes into and out of the Bay are considered positive and negative, respectively.

$$V_{\text{flux}} = \int V_{\text{predicted}}(\text{site, depth, tide}) \quad (1.3)$$

$$F = \rho_{\text{larvae}} * V_{\text{flux}} \quad (1.4)$$

$$F_{\text{net}} = F_{\text{ebb}} + F_{\text{flood}} \quad (1.5)$$

To determine whether or not a relationship existed between larval abundance and water velocity, regression analyses were used for each species and stage.

Statistical Analysis

Plankton samples in time were serially correlated; therefore a mixed-model, repeated-measures analysis of variance (ANOVA) was used to determine whether there were differences in larval abundance among tides, sampling depths, and/or sites. The

mixed-model repeated-measures ANOVA was conducted for each species and stage combination ($n = 26$) using both larval density and larval flux as dependent variables, date as the “within factor”, and tide, sampling depth, and site as “between” factors. All interaction terms (up to fourth order terms) were initially tested in the model, and all statistically non-significant interactions were removed. Only significant interaction terms are reported. Sites were considered spatial replicates when the effects of site and the corresponding interactions were non-significant. For species and stage combinations where the effects of site or interactions were significant, the repeated-measures analysis was conducted without replication. The mixed-model ANOVA was used instead of the general linear model because it incorporated into the analysis a user-selected covariance matrix specific to the data, and it also allowed for missing data (Wolfinger & Chang 1995). Numerous variance-covariance matrixes are available in SAS (release 8.02), and Akaike's Information Criteria (AIC) was used to determine which algorithm best described the covariance structure for each species and stage (SAS online documentation, <http://www.ncsu.edu/it/sas/help/>). Additionally, modeling the autoregressive structure of the data allowed less restrictive adherence to assumptions of general linear model ANOVA. Specifically, the model does not assume homogeneous variability (Wolfinger & Chang 1995).

To test for differences in megalopal abundance verses light/dark regimes, tide, station, and sampling depth, a four-factor non-parametric ANOVA (Scheirer-Ray-Hare extension of the Kruskal-Wallis Test, (Sokal & Rolf 1995) was conducted for each species. Larvae were absent or in very low numbers in the bottom and midwater tows,

so only the surface tows were used for comparisons. Pairwise differences were calculated using the Tukey-Kramer procedure (SAS release 8.02). Only three species (*Cancer gracilis*, *Cancer magister*, and *Cancer oregonensis*) were abundant enough to warrant analysis.

RESULTS

Larval Density (zoeae stage I-V)

Twelve species of brachyuran crabs, representing five families were collected. Of these, seven species were collected in large enough numbers to warrant analysis. For all species except *Cancer magister*, all stages were observed in relatively high numbers initially, and subsequent stages declined over time (see Fisher, Chapter 1 for details).

The results for the repeated-measures analysis for each species and stage analyzed are summarized in Table 2. Significant interactions among factors precluded a direct interpretation of the main effects in most cases. There was no effect of tide for any stage of any species and there were no statistically significant differences in larval abundance for any stage of any species among sites.

Fourth order interactions of tide, sampling depth, site, and date were significant for stage I zoeae of *Cancer oregonensis* (Table 2), indicating that larvae of this stage were changing their vertical position in the water column at different tides and sites over time. Indeed, large pulses of larvae were observed at the surface and midwater depths (Figure 3), and those pulses mainly occurred at the middle and west sites during

ebb tides, and at the middle site during flood tides. Tide, sampling depth, and date interactions were significant for zoeae stage I larvae of *Telmessus cheiragonus*, the Majidae group, and *Pugettia* spp. (Table 2). While these significant interactions could have implications for import or export when larvae are first released, the patterns were not apparent.

With the exception of *Fabia subquadrata*, all species had significant sampling depth and date interactions, indicating that larvae changed their vertical position in the water column over time. Specifically, the interactions were caused by high larval abundance at the surface during specific dates for all zoeal stages of *Cancer oregonensis*, *Telmessus cheiragonus*, and *Pugettia* spp., and stage II zoeae of the Majidae group (Figures 3-6), and by high abundance of stage I zoeae of Majidae and *C. magister* in the midwater tows (Figure 5 and 7). With the exception of *C. magister*, the dates corresponding to the highest larval abundance at the surface for most species, and the midwater for Majidae stage I zoeae, were generally coincident with new and full moons (Figure 8). For *C. magister*, however, larval abundance was highest during quarter moons in the midwater depths (Figure 8). Although interactions of sampling depth and date were non-significant for *F. subquadrata*, the highest abundance for this species occurred at the surface during a full moon (Figure 8).

Statistical interactions of sampling depth and date prohibited direct interpretation of results for larval vertical distribution, however several patterns were apparent. First, the vertical distributions of *Cancer oregonensis*, *Telmessus cheiragonus*, and Majidae were stage-specific. Stage II-V (stage II for Majidae) zoeae

of these species were clearly more abundant in the surface waters, whereas stage I zoeae were more variable, but tended to be higher in both the surface and midwater tows (Figures 3-5). The vertical distribution of *C. magister* zoeae varied among stages, with stage I zoeae abundant in the midwater and little pattern evident for stage II zoeae (Figure 7). All stages of *Pugettia* spp. and *Fabia subquadrata* showed inconsistent patterns of vertical distribution (Figures 6 and 9).

Sampling date was highly significant, demonstrating that larval abundance followed a distinct seasonal pattern for all species and stages. Abundance throughout the larval stages was low at the beginning of the sampling period (with the exception of *Telmessus cheiragonus* which were abundant at the onset of sampling) followed by a peak, and subsequent decline (see Fisher, Chapter 1 for details).

Daytime Megalopal Density

Megalopae of *Cancer oregonensis*, *Telmessus cheiragonus*, and *Hyas lyratus*/*Oregonia gracilis* were more abundant on incoming tides, whereas there were no differences in abundance between tides for *Pugettia* spp. or *Fabia subquadrata* (Figure 10 and Table 2). Megalopal vertical distribution in the water was highly variable with *T. cheiragonus*, and *H. lyratus*/*O. gracilis* megalopae more abundant on the surface, *C. oregonensis* in the midwater and bottom depths, and *F. subquadrata* at the bottom. *Pugettia* spp. showed little pattern in vertical distribution. There were no statistically significant differences in megalopal abundance for any species among sites. Third order interactions of tide, sampling depth, and site were significant for *Telmessus*

cheiragonus megalopae (Table 2), which was the result of higher abundance at the surface during flood tides at some sites compared to the other sites and depths.

Night Tows

Megalopae of all species were significantly more abundant during nighttime flooding tides on the surface (Figure 11). There were no significant differences in abundance among regions for *C. oregonensis*, but *C. gracilis* and *C. magister* were more abundant in Bartlett Cove (Table 3). No larvae were collected in the bottom tows, and very few larvae were collected in the midwater tows.

Water Velocity Estimates

Raw and modeled ADCP measurements indicated that water velocity in the north-south direction (into and out of Glacier Bay) varied little among depth, but velocity was highly variable across the inlet both within and between tides. During incoming tides, the water flowing into Sitakaday Narrows reached the eastern station first and then reached the western station approximately 60 minutes later (Figure 12). The magnitude of the current speeds between the ebb and flood tides also varied among stations. During both spring and neap tides, current speeds were much greater during flood tide on the eastern side of Sitakaday Narrows, whereas current speeds were much greater during ebb tide on the western side, exemplifying horizontal current shear. At the center station, there was no difference in velocity between ebb and flood spring tides, but velocities were much greater on ebb tide during neap conditions (Figure 12).

In summary, water was observed to flow into Sitakaday Narrows on the eastern side and out in the center and on the western side (Figure 1).

Integrated water volume exchange at each site was highly asymmetrical between tides, with a non-tidal residual volume of $+18.5 \times 10^6 \text{ m}^3$ at the eastern station and $+8.4 \times 10^6 \text{ m}^3$ at the center station. The western station was the most symmetrical, with a non-tidal residual volume of $-2.3 \times 10^6 \text{ m}^3$. This is a direct result of the average duration of flood and ebb cycles (as measured by the velocity vector in the inward direction) and the relative magnitude of the current speeds at the different stations across the inlet. Water was flowing into Glacier Bay (positive velocity) at the eastern station for an average of 8.4 hours and flowing out of Glacier Bay (negative velocity) at that same station for 3.7 hours, while the center and western stations were more balanced (Table 4).

Larval Flux and Net Transport

Due to the gross difference of water balance between ebb and flood tides, larval flux was not used as a dependent variable and net transport was not calculated. There was no relationship between larval abundance and water velocity (Figure 13).

DISCUSSION

In the present study, there were no statistical differences in larval abundance between tides, but the persistence of all larval stages of all the species (with the exception of *Cancer magister*) throughout the study suggests that these species live out

their entire larval period within Glacier Bay. However, patterns of behaviorally regulated transport were not apparent. The central concept in the literature explaining larval retention or export in estuaries is that larvae exhibit either passive or active transport (see Epifanio 1988 for review). Most studies have been conducted in areas with relatively low flow and decapod larvae in these areas exhibit active transport by vertically migrating to regulate their horizontal position in the estuary (Cronin & Forward 1982, Dittel et al. 1991, Drake et al. 1998, Garrison 1999, DiBacco & Chadwick 2001). However, no previous work has been conducted in tidally driven fjords where the horizontal flow is great and slack tides are minimal. During this study, some species and species groups exhibited differential or variable vertical stratification, indicating that larvae might be actively regulating their vertical position. However, these patterns were not similar to those that have been documented in other studies to facilitate active transport (Cronin & Forward 1982, Dittel et al. 1991, Garrison 1999) Arias and Rodriguez 1998,. Sitakaday Narrows is a well-mixed area, and high turbulence, standing waves, and mesoscale eddies are often observed. Therefore, stratified density layers, a proximal cue for vertical migratory behavior, were likely not present. Even if cues were present, the strong current speeds observed at the sampling sites could have precluded active vertical migration except during short periods of slack tide (on the scale of tens of minutes). Instead, vertical migration to facilitate the retention of larvae could have occurred on either side of the study area where current speeds are less extreme, the water column more stratified, and density-dependent cues more likely present.

While the persistence of all larval stages indicated the retention of most species, stage III-V zoeae of *Cancer magister* were observed in very low abundance, indicating that larvae of this species were behaving differently, and were possibly exported from the study area. It has been well documented that in open coast systems, such as the outer coast of California, Oregon, and Washington, *C. magister* larvae are advected offshore and return to nearshore habitats to settle Reilly 1983, (Lough 1976, Jamieson & Phillips 1988). The congener *C. oregonensis* has also been documented to exhibit similar behavior (Lough 1974, Jamieson & Phillips 1988). In Glacier Bay however, all stages of *C. oregonensis* appear to be retained while late-stage *C. magister* zoeae are absent. Whether zoeae stage III-V move into the upper reaches of the estuary is not known. A recent study targeting *C. magister* megalopal distributions throughout Glacier Bay collected some stage V zoeae in the upper reaches of the fjord (Eckert unpub. data), but whether that was a localized population or a small sample of a larger population is unknown. Whether stage III-V *C. magister* larvae are exported from or move into Glacier Bay warrants further study. I can conclude, however, that the zoeal stages of this species are behaving differently from their congener, *C. oregonensis* (along with the other species studied). This finding has not been documented previously and it demonstrates the importance of understanding species-specific dispersal patterns when designing marine reserves and evaluating their effectiveness.

Alternative hypotheses explaining the low abundance of stage III-V zoeae of *Cancer magister* include net avoidance, migration into deep water, and patchy distribution. *C. magister* and *C. oregonensis* larvae are very similar morphologically

and vary only slightly in size, with *C. magister* being the largest of the cancrid larvae. While large larvae are known to be strong swimmers, all stages of *C. oregonensis* were collected in large numbers, and megalopae of *C. magister* and other species were collected (albeit in low numbers during the day). Furthermore, although large zooplankters (e.g., euphausiids) and larval fish are adept at net avoidance, they were collected regularly. Therefore, net avoidance cannot adequately explain the low abundance of stage III-V *C. magister* larvae. Larvae could have migrated into deeper water during the day and thus out of my sampling range. Dibacco et al. (2001) observed stage I zoeae of *Pachygrapsus crassipes* burrowing into the sediments in the laboratory. While I was unable to sample the sediment-water interface or the benthic boundary layer, relative larval abundance was lowest in the bottom tows. However, this study does not adequately address whether larvae are utilizing near-bottom frictional forces or the sediment-water interface to retard horizontal transport. Late-stage larvae of *C. magister* could have been entrapped in, or utilizing, ephemeral oceanographic features (e.g., fronts, current shear zones). It has been documented that oceanographic fronts can play an important role in concentrating and transporting meroplankton (Mann & Lazier 1996, Eggleston et al. 1998). Current lines and areas of surface shear are common occurrences in Glacier Bay, and while these ephemeral features were not avoided during sampling, nor were they targeted. Therefore, future studies should address the importance of these features in transporting larvae in Glacier Bay.

While patterns of dispersal are unclear for late-stage zoeae of *Cancer magister*, the patterns of high megalopal abundance in the surface waters during nighttime flood tides for this species and other cancrids (*C. oregonensis* and *C. gracilis*), and during daytime flood tides for *Telmessus cheiragonus* and *Hyas lyratus/Oregonia gracilis*, imply that Glacier Bay is a settling area for these species. These results agree with other studies comparing abundance of megalopae vs. light/dark regimes, tide, and depth (Christy & Morgan 1998, Gonzalez-Gordillo et al. 2003) and supports work conducted by Eckert (unpublished data), who has collected *C. magister* megalopae in high abundance using light traps in Bartlett Cove. The relatively high abundance of megalopae collected at night implies that either nets are not effective at collecting megalopae or that the larvae are not present at those sites or depths during the day, which might explain the low megalopal abundance observed for all species during this study.

Most larvae were more abundant on the surface during periods of high water velocity (new and full moons), which was unexpected if high-amplitude tides inhibit vertical migration. A possible explanation could be that during new and full moons, increased water velocity creates hydrostatic instabilities in Sitakaday Narrows that force zooplankton and small fishes to the surface. Indeed, during these periods of high flow, whirlpools and standing waves are present, and seabirds were often observed actively feeding on the surface.

The gross differences in water volume transport between tide cycles may be explained in part by a large-scale eddy that forms when water leaves the Beardslee

Entrance (Figure 1). Water exiting the narrow and relatively shallow (10 m) Beardslee Entrance cannot make the sharp 90° turn down the eastern side of Sitakaday Narrows and is instead pushed out toward the center of the channel. This results in a cyclonic (counter-clockwise) eddy that pushes water landward along the eastern boundary of Sitakaday Narrows as exemplified by the longer flood tide period at the eastern site. Water moving northward along the eastern shore likely becomes entrained in the outward flow of the Beardslee Entrance and eventually exits Glacier Bay or remains in the eddy. Therefore, the longer time for northward-moving water (8.4 hours in each tide cycle) at the eastern station is likely an overestimate, because the overall fate of that water is unknown. It could easily be ejected from Glacier Bay when it cycles back towards the center channel (upon reaching the outflow at the Beardslee Entrance) instead of moving northward, further into the Bay. This hypothesized eddy, and the difficulty in measuring the true current shear, would directly affect estimates of net larval transport and needs to be fully understood before accurate measurements of larval flux can be calculated.

In conclusion, this study is the first to quantify the number of larvae entering or leaving Glacier Bay, which is the first step towards measuring the “recruitment effect” of this marine reserve. Although larval flux calculations were not made, this study suggests that Glacier Bay retains developing larvae of all species studied, except *Cancer magister*, whose export or retention patterns remain uncertain. Nevertheless, it appears that Glacier Bay is a settling area for *C. magister* and other species (*C. oregonensis*, *C. gracilis*, *Telmessus cheiragonus*, and *Hyas lyratus/Oregonia gracilis*).

Furthermore, large tidal fluctuations potentially extend the “effective larval mixing pool” beyond Sitakaday Narrows (into Icy Strait and the lower half of Glacier Bay proper), creating substantial potential for leakage of larvae into adjacent areas, even within a single tidal cycle. This mixing of larvae with adjacent areas, the observed larval retention of most species, and the influx of megalopae suggest that Glacier Bay is an effective and self-sustaining marine reserve. However, an accurate measure of water volume transport, information on larval mortality rates (from first stage larvae to megalopae), and the connectivity of Glacier Bay to adjacent areas are needed in order to accurately quantify the “recruitment effect” of this newly designated marine reserve. Future studies on the inter-annual variability in larval abundance, the presence or absence of larvae in other areas of Glacier Bay (specifically in the upper reaches and the adjacent waters), the influence that ephemeral oceanographic features have on larval transport, the potential for oceanographic fronts to act as barriers to dispersal within and outside Glacier Bay, and the impact that source waters have on larval delivery and transport are needed to put this work into broader context. Finally, a hydrodynamic model of water flow is greatly needed for Glacier Bay. Understanding water movement, residence time, extent of the tidal prism, the source waters, and the location and extent of oceanographic fronts and current shear zones would greatly enhance past, present, and future marine research in this dynamic system.

LITERATURE CITED

- Alexander SE, Roughgarden J (1996) Larval transport and population dynamics of intertidal barnacles: A coupled benthic/oceanic model. *Ecological Monographs* 66:259-275
- Ally R (1975) A description of the laboratory-reared larvae of *Cancer gracilis* Dana, 1852 (Decapoda, Brachyura). *Crustaceana* 28
- Bjorkstedt E, Grantham B, Shkedy Y, Rosenfeld L, Roughgarden J (1997) Ichthyoplankton distributions at coastal upwelling fronts off central California: Implications for larval transport. *Ichthyoplankton Ecology*
- Botsford LW, Hastings A, Gaines SD (2001) Dependence of sustainability on the configuration of marine reserves and larval dispersal distance. *Ecology Letters* 4:144-150
- Botsford LW, Wing SR, Largier JL (1998) Population dynamics and management implications of larval dispersal. *S. Afr. J. mar. Sci.* 19:131-142
- Christy J (1982) Adaptive significance of semilunar cycles of larval release in fiddler crabs (genus *Uca*): test of an hypothesis. *Biol Bull* 163:251-263
- Christy J, Stancyk S (1982) Timing of larval production and flux of invertebrate larvae in a well-mixed estuary. In: Kennedy V (ed) *Estuarine comparisons*. Academic Press, New York, p 489-503
- Christy JH, Morgan SG (1998) Estuarine immigration by crab postlarvae: mechanisms, reliability and adaptive significance. *Marine Ecology Progress Series* 174:51-65
- Cronin T, Forward R (1982) Tidally timed behavior: effects on larval distributions in estuaries. In: Kennedy V (ed) *Estuarine comparisons*. Academic Press, New York, p 505-520
- Cronin TW, Forward RB (1979) Tidal vertical migration: an endogenous rhythm in estuarine crab larvae. *Science* 205:1020-1022
- Crowder LB, Lyman SJ, Figueira WF, Priddy J (2000) Source-sink population dynamics and the problem of siting marine reserves. *Bulletin of Marine Science* 66:799-820
- Davis G, Dodrill J (1980) Marine parks and sanctuaries for spiny lobster fisheries management *Proceedings of the Gulf of the Caribbean Fisheries Institute*, p 194-207
- de Wolf P (1973) Ecological observations on the mechanisms of dispersal of barnacle larvae during planktonic life and settling. *Neth J Sea Res* 6:1-129
- Debrosse G, Sulkin S, Jamieson G (1990a) Intraspecific morphological variability in megalopae of three sympatric species of the genus *Cancer* Brachyura Cancridae. *Journal of Crustacean Biology* 10:315-329
- Debrosse GA, Baldinger AJ, McLaughlin PA (1990b) A comparative-study of the megalopal stages of *Cancer oregonensis* Dana and *Cancer productus* Randall (Decapoda, Brachyura, Cancridae) from the Northeastern Pacific. *Fishery Bulletin* 88:39-49

- Demartini EE (1993) Modeling the potential of fishery reserves for managing Pacific coral reef fishes. U S National Marine Fisheries Service Fishery Bulletin 91:414-427
- DiBacco C, Chadwick DB (2001) Assessing the dispersal and exchange of brachyuran larvae between regions of San Diego Bay, California and nearshore coastal habitats using elemental fingerprinting. J. Mar. Res. 59:53-78
- DiBacco C, Sutton D, McConnico L (2001) Vertical migration behavior and horizontal distribution of brachyuran larvae in a low-inflow estuary: implications for bay-ocean exchange. Mar. Ecol. Prog. Ser. 217:191-206
- Dittel AI, Epifanio CE (1982) Seasonal abundance and vertical distribution of crab larvae in Delaware Bay USA. Estuaries 5:197-202
- Dittel AI, Epifanio CE, Lizano O (1991) Flux of crab larvae in a mangrove creek in the Gulf of Nicoya Costa Rica. Estuarine Coastal & Shelf Science 32:129-140
- Drake P, Arias A, Rodriguez A (1998) Seasonal and tidal abundance patterns of decapod crustacean larvae in a shallow inlet (SW Spain). Journal of Plankton Research 20:585-601
- Eggleston D, Armstrong D, Elis Ward E, WS P (1998) Estuarine fronts as conduits for larval transport: Hydrodynamics and spatial distribution of Dungeness crab postlarvae. Marine Ecology Progress Series 164:73-82
- Emmerson WD (1983) Tidal exchange of 2 decapod larvae *Palaemon pacificus* (Caridea) and *Upogebia africana* (Thalassinidae) between the Swartkops river estuary and adjacent coastal waters. South African Journal of Zoology 18:326-330
- Epifanio CE (1988) Transport of crab larvae between estuaries and the continental shelf. In: Jansson, B.-O. (Ed.). Lecture Notes On Coastal And Estuarine Studies, Vol. 22. Coastal-Offshore Ecosystem Interactions; Meeting, Tiburon, California, Usa, April 7-22, 1986. Xv+367p. Springer-Verlag New York, Inc.: Secaucus, New Jersey, Usa; Berlin, West Germany. Illus. Maps. Paper. 1988. 291-306.
- Epifanio CE, Valenti CC, Pembroke AE (1984) Dispersal and recruitment of blue crab larvae in Delaware Bay USA. Estuarine Coastal & Shelf Science 18:1-12
- Etherington L, Hooge P, Hooge E (2004) Factors affecting seasonal and regional patterns of surface water oceanographic properties within a fjord estuarine system: Glacier Bay, Alaska. USGS, Alaska Science Center, Anchorage, AK, p 79
- Gaines SD, Gaylord B, Largier JL (2003) Avoiding current oversights in marine reserve design. Ecological Applications 13:S32-S46
- Garrison LP (1999) Vertical migration behavior and larval transport in brachyuran crabs. Marine Ecology Progress Series 176:103-113
- Gerber LR, Botsford LW, Hastings A, Possingham HP, Gaines SD, Palumbi SR, Andelman S (2003) Population models for marine reserve design: A retrospective and prospective synthesis. Ecological Applications 13:S47-S64

- Gonzalez-Gordillo JL, Arias AM, Rodriguez A, Drake P (2003) Recruitment patterns of decapod crustacean megalopae in a shallow inlet (SW Spain) related to life history strategies. *Estuar. Coast. Shelf Sci.* 56:593-607
- Halpern BS (2003) The impact of marine reserves: Do reserves work and does reserve size matter? *Ecological Applications* 13:S117-S137
- Hart J (1935) The larval development of British Columbia Brachyura: I. Xanthidae, Pinnotheridae (in part) and Grapsidae. *Canadian Journal of Research* 12
- Hart J (1960) The larval development of British Columbia Brachyura: II. Majidae, Subfamily Oregonidae. *Canadian Journal of Research* 38
- Haynes E (1981) Description of stage-I zoeae of Snow Crab, *Chionoecetes bairdi*, (Oxyrhyncha, Majidae) from plankton of lower Cook Inlet, Alaska. *Fishery Bulletin* 79:177-182
- Hooge P, Hooge E (2001) Fjord Oceanographic Processes in Glacier Bay, Alaska. US Geological Survey, Alaska Science Center, Anchorage, AK, p 142
- Iwata F, Konishi K (1981) Larval development in laboratory of *Cancer amphioetus* Rathburn, in comparison with those of seven other species of Cancer (Decapoda, Brachyura). *Publ Seto Mar Biol Lab* 27:369-391
- Jamieson GS, Phillips AC (1988) Occurrence of Cancer crab (*Cancer magister* and *Cancer oregonensis*) megalopae off the west-coast of Vancouver Island, British-Columbia. *Fish Bul* 86:525-542
- Knudsen J (1959) Life cycle studies of the Brachyura of Western North America, II. The life cycle of *Lophopanopeus bellus* diegenesis Rathburn. *Bulletin, Southern California Academy of Sciences* 58
- Kurata H (1963) Larvae of Decapoda Crustacea of Hokkaido 1. Atelecyclidae (Atelecyclinae). *Bull Hokkaido Reg Fish Lab Board Can Trans Series* 1124
- Lago RP (1993) Tidal Exchange Of Larvae Of Sesarma-Catenata (Decapoda, Brachyura) In The Swartkops Estuary, South-Africa. *South African Journal of Zoology* 28:182-191
- Largier JL (2003) Considerations in estimating larval dispersal distances from oceanographic data. *Ecological Applications* 13:S71-S89
- Lockwood DR, Hastings A., Botsford L. W. (2002) The effects of dispersal patterns on marine reserves: Does the tail wag the dog? *Theoretical Population Biology* 61:297-309
- Lough RG (1974) Dynamics of crab larvae (Anomura, Brachyura) off the central Oregon coast. PhD, Oregon State University
- Lough RG (1976) Larval dynamics of Dungeness Crab, *Cancer magister*, off Central Oregon Coast, 1970-71. *Fish. Bull.* 74:353-376
- Mann K, Lazier J (1996) Dynamics of marine ecosystems, Vol. Blackwell Sciences, Cambridge, MA
- McConaughy JR (1988) Export and reinvasion of larvae as regulators of estuarine decapod populations. *Am. Fish. Soc. Symp* 3:90-103
- Murray SN, Ambrose RF, Bohnsack JA, Botsford LW, Carr MH, Davis GE, Dayton PK, Gotshall D, Gunderson DR, Hixon MA, Lubchenco J, Mangel M, MacCall A, McArdle DA, Ogden JC, Roughgarden J, Starr RM, Tegner MJ, Yoklavich

- MM (1999) No-take reserve networks: Sustaining fishery populations and marine ecosystems. *Fisheries* 24:11-25
- Palumbi SR (2003) Population genetics, demographic connectivity, and the design of marine reserves. *Ecological Applications* 13:S146-S158
- Poole R (1966) A description of laboratory-reared zoeae of *Cancer magister* Dana, and megalopae taken under natural conditions (Decapoda Brachyura). *Crustaceana* 11:83-97
- Quinn JF, Wing SR, Botsford LW (1993) Harvest refugia in marine invertebrate fisheries: Models and applications to the Red Sea Urchin, *Strongylocentrotus franciscanus*. *American Zoologist* 33:537-550
- Rogers-Bennett L, Bennett W, Fastenau H, Dewees C (1995) Spatial variation in red sea urchin reproduction and morphology: Implications for harvest refugia. *Ecol Appl* 5:1171-1180
- Rowe PM, Epifanio CE (1994) Tidal stream transport of larval weakfish in Delaware Bay, USA. *Marine Ecology Progress Series* 110:105-114
- Russ GR, Alcala AC, Maypa AP, Calumpong HP, White AT (2004) Marine reserve benefits local fisheries. *Ecological Applications* 14:597-606
- Shanks AL, Grantham BA, Carr MH (2003) Propagule dispersal distance and the size and spacing of marine reserves. *Ecological Applications* 13:S159-S169
- Sokal R, Rolf J (1995) *Biometry The Principles of Statistics in Biological Research*, Vol. W.H. Freeman and Company, New York
- Stockhausen WT, Lipcius RN, Hickey BM (2000) Joint effects of larval dispersal, population regulation, marine reserve design, and exploitation on production and recruitment in the Caribbean spiny lobster. *Bulletin of Marine Science* 66:957-990
- Trask T (1970) A description of laboratory-reared larvae of *Cancer productus* Randall (Decapoda, Brachyura) and a comparison to larvae of *Cancer magister* Dana. *Crustaceana* 18:133-146
- Wheeler DE (1978) Semilunar hatching periodicity in the mud Fiddler crab *Uca pubnax* (Smith). *Estuaries* 1:268-269
- Wing SR, Largier JL, Botsford LW, Quinn JF (1995) Settlement and transport of benthic invertebrates in an intermittent upwelling region. *Limnology and Oceanography* 40:316-329
- Wolfinger R, Chang M (1995) Comparing the SAS GLM and MIXED procedures repeated measures SAS Institute Inc. SAS Institute Inc., Cary, NC
- Young C (1995) Behavior and locomotion during the dispersal phase of larval life. In: L M (ed) *Ecology of Marine Invertebrate Larvae*. CRC Press, Boca Raton, FL, p 249-278

Table 1. Results of a harmonic equation, $f = y_0 + A \cdot \sin(2\pi x/T + L)$, that predicts the difference in water velocity (m/s) from Acoustic Doppler Current Profiler data for each minute from modeled (Tide and Currents v2.0a, Nautical Software Inc.) slack ebb tide (x) for each site and depth sampled. y_0 is the mean of the data (m/s), A is the wave amplitude (m/s), T is the period (hours), and L is the initial wave location (radians).

Depth	Site	R ²	y ₀ (m/s)	A (m/s)	T (hours)	L (radians)
Surface	West	0.51	-0.50	1.17	12.7	6.28
	Middle	0.53	-0.01	0.76	12.1	6.04
	East	0.73	0.50	1.40	12.9	-0.02
Midwater	West	0.59	-0.43	1.15	12.8	6.28
	Middle	0.67	0.04	0.78	12.5	6.12
	East	0.77	0.52	1.50	12.6	-0.08
Bottom	West	0.71	-0.35	1.19	14.6	0.55
	Middle	0.75	0.09	0.85	13.0	-0.10
	East	0.89	0.48	1.68	12.4	-0.09

Table 2. Repeated measures ANOVA for each species and stage observed comparing the effects of tide, sampling depth, and site on larval abundance (larvae/100m³). Interaction terms that were insignificant for any species and stage combination are not shown. PL=megalopae, “ns”=p>0.1, **=p-value<0.01, ****=p-value<0.001.

Species	Stage	Tide (T)	Sampling Depth (Z)	Site (S)	Date (D)	Z X D	T X Z	T X Z X D	T X Z X S	T X Z X S X D
<i>Cancer oregonensis</i>	1	ns	0.08	ns	****	****	ns	ns	****	****
	2	ns	0.03	ns	****	****	ns	ns	ns	ns
	3	ns	ns	ns	**	0.01	ns	ns	ns	ns
	4	ns	ns	ns	**	**	ns	ns	ns	ns
	5	ns	0.08	ns	**	**	ns	ns	ns	ns
	PL	**	ns	ns	ns	ns	ns	ns	ns	ns
<i>Cancer magister</i>	1	ns	****	ns	****	****	ns	ns	ns	ns
	2	ns	ns	ns	****	ns	ns	ns	ns	ns
<i>Fabia subquadrata</i>	1	ns	0.02	ns	****	ns	ns	ns	ns	ns
	2	ns	0.04	ns	****	0.04	ns	ns	ns	ns
	3	ns	0.07	ns	ns	ns	ns	ns	ns	ns
	4	ns	ns	ns	ns	ns	ns	ns	ns	ns
	5	ns	ns	ns	ns	0.09	ns	ns	ns	ns
	PL	ns	ns	ns	0.02	**	ns	ns	ns	ns
<i>Pugettia</i> spp.	1	0.04	0.08	ns	****	****	ns	0.03	ns	ns
	2	ns	ns	ns	****	0.02	ns	ns	ns	ns
	PL	ns	ns	ns	****	ns	ns	ns	ns	ns
<i>Majidae</i>	1	**	**	ns	****	****	0.01	****	ns	ns
	2	ns	0.02	ns	****	****	ns	ns	ns	ns
<i>Hyas lyratus/Oregonia gracilis</i>	PL	ns	ns	ns	0.07	ns	ns	ns	ns	ns
<i>Telmessus cheiragonus</i>	1	**	****	ns	****	****	0.04	****	ns	ns
	2	****	****	ns	****	****	****	****	ns	ns
	3	**	****	ns	****	****	****	****	ns	ns
	4	0.04	****	ns	****	****	0.02	****	ns	ns
	5	ns	**	ns	0.03	ns	ns	ns	ns	ns
	PL	ns	ns	0.05	****	ns	ns	ns	****	ns

Table 3. Non-parametric ANOVA results for the effects of tide cycle, day/night, sampling depth (surface, midwater, bottom), and region (BC, West, Middle, East) on megalopal abundance. “ns”=p>0.1, **=p-value <0.01, ****=p-value <0.001.

Source	<i>Cancer gracilis</i>			<i>Cancer magister</i>			<i>Cancer oregonensis</i>		
	df	F-ratio	p-value	df	F-ratio	p-value	df	F-ratio	p-value
Tide	1	4.31	0.04	1	9.32	**	1	6.27	0.02
Day vs. Night	1	9.93	**	1	11.02	**	1	12.63	****
Sampling Depth	2	4.08	0.02	2	6.45	**	2	3.46	0.04
Site	3	7.01	****	3	21.53	****	3	0.62	ns

Table 4. Average time between succeeding slack tides (hours) for each site sampled in Sitakaday Narrows ($\pm$ SD) from corrected modeled data.

	Flood	Ebb	Total
West	5.8 ($\pm$ 1.3)	6.0 ($\pm$ 0.9)	11.8
Middle	7.0 ($\pm$ 0.4)	5.2 ($\pm$ 0.5)	12.2
East	8.4 ($\pm$ 0.75)	3.7 ($\pm$ 0.7)	12.1

FIGURE LEGENDS

Figure 1. Study area depicting the sampling sites in Sitakaday Narrows (West, Middle, East). The entire Bay is closed to the commercial harvest of *Cancer magister* and *Paralithodes camtschaticus*. The shaded area depicts the area open to the commercial harvest of *Chionoecetes bairdi*. The arrows depict the flow into and out of the Bay from Acoustic Doppler Current Profiler data during flood and ebb tide, and the current shear present near the Beardslee Entrance during ebb tide.

Figure 2. Harmonic regression curves fit to the differences between modeled current velocity (Tide and Currents v 2.0a, Nautical Software Inc.) and measured velocity from an Acoustic Doppler Current Profiler for each site and depth sampled.

Figure 3. Vertical distribution of stage I and II-V zoeae of *Cancer oregonensis* between tides for each date sampled. Sites (West, Middle, and East) are averaged and density (larvae/100m³) is reported ± 1 SE. Density of stage II-V zoeae are averaged. Open circles represent full moon and darkened circles represent new moon. The width of the bars are for display purposes only.

Figure 4. Vertical distribution of stage I and II-V zoeae of *Telmessus cheiragonus* between tides for each date sampled. Sites (West, Middle, and East) are averaged and density (larvae/100m³) is reported ± 1 SE. Density of stage II-V zoeae are averaged. Open circles represent full moon and darkened circles represent new moon. The width of the bars are for display purposes only.

Figure 5. Vertical distribution of stage I and II zoeae of *Majidae* between tides for each date sampled. Sites (West, Middle, and East) are averaged and density (larvae/100m³) is reported ± 1 SE. Open circles represent full moon and darkened circles represent new moon. The width of the bars are for display purposes only.

Figure 6. Vertical distribution of stage I and II zoeae of *Pugettia* spp. between tides for each date sampled. Sites (West, Middle, and East) are averaged and density (larvae/100m³) is reported ± 1 SE. Open circles represent full moon and darkened circles represent new moon. The width of the bars are for display purposes only.

Figure 7. Vertical distribution of stage I and II zoeae of *Cancer magister* between tides for each date sampled. Sites (West, Middle, and East) are averaged and density (larvae/100m³) is reported ± 1 SE. Low densities of stage III-V zoeae precluded display of these data. Open circles represent full moon and darkened circles represent new moon. The width of the bars are for display purposes only.

Figure 8. Larval abundance (larvae/100m²) with relation to lunar phase (full moon, first quarter, new moon, third quarter). Data are displayed by depth and species regardless of tide, site, or sampling date. Sampling effort (n) is the number of sampling trips $\pm 45^\circ$ from each lunar phase.

Figure 9. Vertical distribution of stage I and II-V zoeae of *Fabia subquadrata* between tides for each date sampled. Sites (West, Middle, and East) are averaged and density (larvae/100m³) is reported ± 1 SE. Density of stage II-V zoeae are averaged. Open circles represent full moon and darkened circles represent new moon. The width of the bars are for display purposes only.

Figure 10. Vertical distribution of megalopae between tides. All dates and sites (West, Middle, and East) are averaged and density (larvae/100m³) is reported ± 1 SE.

Figure 11. Mean larval abundance (± 1 SE) of *Cancer oregonensis*, *C. magister*, and *C. gracilis* megalopae in surface tows conducted during the night and day during consecutive tidal cycles at 4 sites; 1 in Bartlett Cove (BC) and 3 in Sitakaday Narrows (Middle, East, West).

Figure 12. Predicted water velocity (m/s) in Sitakaday Narrows versus the predicted time (hours) from the beginning of ebb tide from Tides and Currents (Nautical Software, v 2.0a). Velocities are averaged among the dates sampled during spring and neap tides. Negative values indicated ebbing tide and positive values indicate flooding tide. Current speeds were averaged among depths (surface, midwater, bottom) for each site, and the standard errors were small and unnoticeable, so they are not displayed.

Figure 13. Larval density ($\log_{10}$ larvae/100m³+1) of all stages of *Cancer magister* and *Cancer oregonensis* versus depth averaged water velocity (m/s) for each tide, site, and depth sampled. Velocity measurements are from raw ADCP measurements averaged throughout the entire water column in the north direction. Positive velocity values indicate flooding tides, negative values indicate ebbing tides.

Figure 1.

Figure 2.

Figure 3.

Figure 4.

Figure 5.

Figure 6.

Figure 7.

Figure 8.

Figure 9.

Figure 10.

Figure 11.

Figure 12.

Figure 13.