AN ABSTRACT OF THE DISSERTATION OF

Dafne I. Eerkes-Medrano for the degree of Doctor of Philosophy in Zoology presented on December 1, 2011.

Title: The Role of Oxygen and Other Environmental Variables on Survivorship, Abundance, and Community Structure of Invertebrate Meroplankton of Oregon Nearshore Coastal Waters.

Abstract approved:

Bruce A. Menge

The high productivity of Eastern Boundary Upwelling Ecosystems (EBUE), some of the most productive ecosystems in the globe, is attributed to the nutrient rich waters brought up through upwelling. Climate change scenarios for coastal upwelling systems, predict an intensification of coastal upwelling winds. Associated with intensification in upwelling are biogeochemical changes such as ocean hypoxia and ocean acidification.

In recent years, the California Current System (CCS) has experienced the occurrence of nearshore hypoxia and the novel rise of anoxia. This has been attributed to changes in the intensity of upwelling wind stress. The effects of some of the more severe hypoxia and anoxia events in the CCS have been mass mortality of fish and benthic invertebrates. However, the impacts on zooplankton in this system are not known.

Meroplankton, those organisms which have a planktonic stage for only part of their life cycle, are an important component of zooplankton communities. The larval

stage of benthic invertebrates forms an important link between benthic adult communities and planktonic communities. Larvae serve to disperse individuals to new locations and to link populations. They are also food for fish and planktonic invertebrates. This important life stage can spend long periods in the plankton (from days to months) where environmental conditions can affect larval health, subsequent settlement and recruitment success, and juvenile health.

This research assesses the role of hypoxia and larval survivorship, and the relationship between individual abundance and community structure of larvae to environmental factors in the field. In laboratory experiments (Chapter 2), a suite of 10 rocky intertidal invertebrate species from four phyla were exposed to low oxygen conditions representative of the nearshore environment of the Oregon coast. Results revealed a wide range in tolerances from species with little tolerance (e.g. the shore crab *Hemigrapsus oregonensis*) to species with high tolerance (e.g. the California mussel *Mytilus californianus*). The differential responses across larvae to chronic hypoxia and anoxia potentially could affect their recruitment success and consequently, the structure and species composition of intertidal communities.

Field studies (Chapter 3 & 4) explore the relationship between environmental variables and larval abundance and community structure. Chapter 3 focuses on broad taxonomic groups, while Chapter 4 focuses on larval decapods in particular. Fine focus was devoted to decapod larvae, due to laboratory findings of heightened sensitivity to hypoxia of decapod crabs. A finding that is also supported in the literature. The goal of field studies was to identify the environmental parameters that

structure meroplankton and larval decapod communities and identify which of these parameters play a significant role in influencing larval abundance. A number of environmental variables contributed to meroplankton assemblage structure and larval decapod assemblage structure. These included distance from shore, depth, date, upwelling intensity, dissolved oxygen, and cumulative wind stress. Some of these factors occurred frequently in larval abundance models. In Chapter 3, individual abundance across broad taxonomic groups was most commonly explained by upwelling intensity while in Chapter 4, individual abundance of different decapod species was explained by cumulative wind stress, which is a proxy for upwelling intensity. The prominent role of upwelling related factors in explaining individual abundance is important considering climate change projections of an increased intensification of upwelling winds in EBUE.

The Role of Oxygen and Other Environmental Variables on Survivorship, Abundance, and Community Structure of Invertebrate Meroplankton of Oregon Nearshore Coastal Waters

by
Dafne I. Eerkes-Medrano

A DISSERTATION

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

Presented December 1, 2011
Commencement June 2012

Doctor of Philosophy dissertation of Dafne I. Eerkes-Medrano presented on December 1, 2011.

APPROVED:

Major Professor, representing Zoology

Chair of the Department of Zoology

Dean of the Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Dafne I. Eerkes-Medrano, Author

ACKNOWLEDGEMENTS

Early in my undergraduate degree I viewed scientists as people who worked fairly independently. They developed theories, tested them, and published their findings. I didn't revisit this view in the last two years of my undergraduate degree when I was fortunate enough to work as a research assistant for some amazing scientists. I was absorbed in the excitement of the research and the never-ending questions that arose. My undergraduate research experience got me hooked on research and I decided to pursue a PhD.

It wasn't until the first year of PhD coursework was over and I begun actively doing research, that I begun to get enlightened of what it really takes to do science. I realized that the steps between the ideas for research and successful science benefitted, and in some cases only became possible, from the contributions of the community around me. In the course of my thesis research, I was challenged with a multitude of questions each step of the way: "How do I refine this idea?"; "How do I fund this?"; "What space will I use to carry out this experiment?"; "How will I build it?"; "How will I collect the samples?"; "How will I sort all these samples?"; "What's the best analysis to use?"; "How do I learn this analysis technique"; "How do I improve this manuscript?"…. And as I got through each step, I realized how in every case the research benefitted from outside help. As you can imagine, as a graduate student working to get an idea off the ground, I was extremely grateful when something worked! And with this, let me acknowledge all of those people who have played a role in making this PhD possible.

I believe the best place to start is with my undergraduate role models: Sally Leys, Gitai Yahel, Francis Choy, Verena Tunnicliffe, and Patrick von Aderkas. These great role models taught me how to: ask questions; set up and run experiments; troubleshoot problems; be persistent; and be methodical. Anne Parkinson, the University of Victoria biology co-op program coordinator facilitated multiple research experience opportunities. Thank you for preparing me for graduate school. Once I was here at OSU doing my doctoral degree, my supervisors Bruce Menge and Jane Lubchenco (before taking her position at NOAA) did a great job of supporting me through the course of my degree. You were not only inspirational role models, but I also appreciated the freedom and support you gave me in pursuing the research questions of interest to me.

The people who helped me get the research of my second chapter off the ground are Chris Langdon, Richard Emlet, Richard Strathmann and Tracey Smart. Thank you for: providing conceptual support, helping me design my experiments, and teaching me how spawn and rear those delicate larvae. Thanks also to Chris Langdon, Clare Reimers, Scott Heppell, and to the Hatfield Marine Sciences Center for providing space and resources to carry out these experiments. Amanda Amstutz and Christine Sislak were instrumental in carrying out the actual research. Amanda Amstutz was involved in pilot studies and refinements during the first year of the research. In the following year, Christine Sislak over the course of nine months gave up most weekends and many nights to count larvae. Jennifer Olson, Asako Yamamuro, Satoshi Kimura, Jeremy Henderson, and Margot Hessing-Lewis volunteered in the field to

collect animals for experiments. Alex Gulick volunteered to measure image of larvae. Silvia Yamada taught me how to identify adult crabs and showed me field sites for collections. Ron Morphis with HMSC facilities was HUGE help in fixing the ever-breaking cooling system of the refrigeration rooms. You can imagine the hand-wringing worry of a cooling system threatening to break in the middle of an experiment using larvae that took a month of delicate daily rearing attention. Ron was always there for the rescue. Rod Kaufmann and Larry Silva from Airgas helped me figure out what kind of gas and regulator fittings were best suited for my research and delivered it at times on a weekly basis. Melody Pfister coordinated up housing for me and my research assistants and Candace Rogers, Hollis Lundeen, Rick Brown, and Patty George, ensured that we had all the necessary clearances to work in NOAA buildings. Satoshi Kimura prepared many meals for me and helped me laugh during intensive experiment pull out days when I needed to be at the lab from 6am till midnight. To all of you, Thank You for making this research happen.

As with the second chapter, the research presented in my third and fourth chapters also benefitted from multiple contributions. I had the opportunity to interact and collaborate with many remarkable scientists. Lorenzo Ciannelli and Bill Peterson provided opportunities for intellectual discussion, gave me guidance on my research, and were great role models. The world of zooplankton was new to me. Charlie Miller, Jesse Lamb, and Cheryl Morgan provided expert instruction on zooplankton sorting techniques and zooplankton identification. Jennie Yoder and Rachel Mahler made a significant contribution to the plankton sorting effort. Vathani Logendran, Ryan

Braaten, and Sean Canfield also assisted in sorting plankton samples. Lorenzo Ciannelli, Scott Heppell and Vince Politano provided space and resources to carry out sample processing. The stage of data analysis for these chapters was one of the largest challenges in my thesis but also one of the greatest learning opportunities. Tarik Gouhier, Elizabeth Daly, Jennifer Fisher, and Rick Brodeur engaged in thoughtful discussion of data analysis and taught me valuable analyses techniques. Bryan Black, Sarah Henkel, Amanda Gladics, and Caren Barcelo also engaged in discussions of data analysis. Bruce McCune's course on Community Structure and Analysis put the task of using multivariate methods for community analysis within intellectual grasp. Bruce McCune was also kind enough to read over the method section I wrote on the 'nonparametric multiplicative regression' technique to make sure I have represented the method accurately.

As a student in the Zoology Department I was lucky to have the opportunity to work as a Teaching Assistant. I am grateful to Joe Beatty and Bob Mason respective chairs in Zoology and Biology for facilitating these opportunities. As a graduate student I never felt I would slip through the cracks and this was in large part because of the wonderful administrative staff of our Department and our lab. A big Thank you goes to Tara Bevandich, Torri Givigliano, Traci Durrell-Khalife, Trudy Powell, Cindy Kent, and Kathleen Norris.

This PhD journey started with an experiment that had to be abandoned due to logistical challenges. However, I would still like to acknowledge those people that contributed to that project. Richard Emlet, Richard Strathmann and Tracey Smart

provided expertise on barnacle larval biology. Richard Emlet also provided laboratory space for sorting plankton samples. Lynda Ciuffetti provided access to an epifluorescence microscope and Image Pro Plus software to measure lipid stores in larvae. Joe Tyburczy and Sarah Dudas were great help in brainstorming for the research and they also donned wetsuits to tow plankton nets (by swimming!) in the very nearshore waters off the shores of Long Marine lab in Santa Cruz. Margot Hessing-Lewis and John Schafers helped me brainstorm ideas on collecting larvae from surge channels in the rocky intertidal, and John played a big hand in building my larval rearing facility. Lindsay Hunter volunteered for field sample collections. Through the course of this degree, along with my senior role models, I also admired my fellow peers. With such bright people around me, I learned something from each of you. I appreciated the scientific insights you had and the support network you provided both in science and outside of science. I would like to acknowledge the members of the Lubmenge lab and the members of the Ciannelli lab. Lubmenge lab members included: Allie Barner, Elizabeth Cerny-Chipman, Sarah Dudas, Elise Granek, Kirsten Grorud-Colvert, Tarik Gouhier, Anne Guerry, Kimberly Heiman, Margot Hessing-Lewis, Alison Iles, Kimberly Page-Albins, Laura Petes, Jessica Reimer, Jeremy Rose, Chenchen Shen, Joe Tyburczy, and Luis Vinueza. Ciannelli lab members included: Morgan Bancroft, Caren Barcelo, Mac Barr, Valerio Bartolino, Amanda Gladics, Mary Hunsicker, Bobby Ireland, Angela Johnson, Marisa Litz, Jason Phillips, Dough Reese, Dongwha Sohn, and Cathleen Vestfals.

Aside from direct research, there was a big network of family and friends (and friends who felt like they became family) that kept me afloat during the most demanding times, who enriched my daily life in Corvallis and Newport, who shared adventures, and who made me smile, laugh, and feel loved. This network includes housemates, dodgeball friends, the Lubmenge lab, the Ciannelli group, Zoo-grads, my parents (John and Laura Eerkes-Medrano), my boyfriend Satoshi Kimura, my grandmothers (Maria Isabel Castro-Medrano and Epke Eerkes), and family. During my time in Newport, I was greatful to have a network of supportive friends including: Bryan and Genoa Black, Cathey Briggs (and Darla), Xiuning Du, Sarah Henkel, Judy Mullen, Rhea Sanders, Tracy Shaw, and Wade Smith. In Corvallis, friends (in alphabetical order) who were there through periods of growth include: Jennifer Buys, Kate Boersma, Angela Brandt, Elizabeth Cassidy, Jules Cooper, Mark Christie, Shelly Dayton, Cate Dolan, Sarah Eddy, Amanda Gladics, Tarik Gouhier, Margot Hessing-Lewis, Levi Kilcher, Logan Mitchell, Catherine Searle, Joe Tyburczy, Asako Yamamuro, Phoebe Lehmann Zarnetske, and Jay Zarnetske.

To all of the above people, thank you for all of your individual contributions!

CONTRIBUTION OF AUTHORS

Chapter 2. Dr. Chris Langdon provided facilities and resources to conduct this research. He was also involved in the experimental design of this chapter and provided input on the analysis and writing. Christine Sislak provided critical assistance in the data collection stage of this chapter.

Chapter 3. Dr. Lorenzo Ciannelli and Angela Johnson were involved in the methodological design, plankton sample collection, and collection of physical data. They both provided inputs on the writing. Dr. Tarik Gouhier provided guidance on R coding and provided input on the analysis and writing.

Chapter 4. Dr. Lorenzo Ciannelli and Angela Johnson were involved in the methodological design, plankton sample collection, and collection of physical data. They both provided inputs on the writing. Dr. Tarik Gouhier provided guidance on R coding and provided input on the analysis and writing.

TABLE OF CONTENTS

TABLE OF CONTENTS (Continued)

Page

TABLE OF CONTENTS (Continued)

Page

LIST OF FIGURES

LIST OF TABLES

Table Page

LIST OF TABLES

Table Page

LIST OF APPENDICES

Page

LIST OF APPENDIX TABLES

DEDICATION

To my grandmothers Epke Eerkes and Maria Isabel Castro Medrano. You have taught me many great lessons directly and some indirectly through the things you taught my parents (the wonderful adults you raised).

The Role of Oxygen and Other Environmental Variables on Survivorship, Abundance, and Community Structure of Invertebrate Meroplankton of Oregon Nearshore Coastal Waters

1 – General Introduction

Eastern Boundary Upwelling Ecosystems (EBUE) are highly productive systems of the world's oceans. With a fish harvest rate that is 100 times greater than the global mean, they provide a sizeable portion of the global fish catch, despite only occupying less than 1% of the global ocean area. As their name implies, EBUE occupy the eastern ocean margins along continents to either side of the equator and span several thousand kilometers latitudinally. The high productivity of these systems is attributed to the process of upwelling, which is generated by powerful trade winds and the earth's rotation, that bring deep nutrient rich waters to the surface (Rykaczewski and Checkley 2008; Chavez and Messié 2009; Fréon et al. 2009). The types of winds generated by atmospheric conditions result in different forms of upwelling and the type of upwelling affects ecosystem properties. For example, coastal upwelling arises from alongshore wind stress while offshore upwelling results from wind stress curl (Rykaczewski and Checkley 2008). The two types of upwelling differ in the source of the waters brought up and in the levels of iron and other nutrients. As a result the different types of upwelling are also suggested to lead to different food webs. Coastal upwelling is thought to be beneficial for the ecosystem because it brings more iron and leads to food webs that support larger organisms (Chavez and Messié 2009).

The role of upwelling, not only affects the productivity of upwelling ecosystems, but as a result of transporting forces also plays a role in zooplankton life

cycles. At high wind speeds, offshore transport has been suggested to carry larvae and zooplankton out of more productive nearshore habitats and to create a mismatch between predators and prey (Chavez and Messié 2009). Therefore zooplankton need mechanisms to maintain their position in more productive nearshore waters and many meroplankton need a way to return to recruiting habitats. These topics have been the focus of a number of studies in upwelling ecosystems (Roughgarden et al. 1988; Peterson 1998; Keister and Peterson 2003; Shanks and Shearman 2009). Indeed different zooplankton taxa have developed mechanisms that allow a population to remain within upwelling zones (Peterson 1998). In the case of larvae there is a controversial history on the role of upwelling in transport and dispersal of larvae, with early studies suggesting that stronger upwelling conditions carried larvae offshore and resulted in reduced recruitment (Roughgarden et al. 1988), and more recent studies finding that most larvae are found closer to and in waters deep enough to avoid the offshore Ekman layer (Shanks and Shearman 2009; Morgan et al. 2009b).

Another way in which upwelling of eastern boundary upwelling regions affects an ecosystem is through the biochemical properties of the water that is brought up. Upwelled waters are rich in nutrients and lower in dissolved oxygen than surface waters (Helly and Levin 2004; Chan et al. 2008). In some regions, where the aragonite saturation horizon is shallow, upwelled waters can also be undersaturated with respect to aragonite and lower in pH levels (Feely et al. 2008). Due to the already low oxygen levels of upwelled waters and the high nutrients, persistently strong upwelling events

can lead to hypoxia in nearshore waters. This has already been observed in the California Current System (CCS) in recent years, where changes in the intensity of upwelling wind stress have led to the rise of nearshore hypoxia and anoxia (Grantham et al. 2004; Chan et al. 2008). As climate change projections predict an intensification of upwelling winds, EBUEs will have an increased susceptibility towards hypoxic events (Bakun et al. 2010).

The California Current System, one of the four main EBUE, has some of the most taxonomically rich rocky intertidal ecosystems among the EBUE (Blanchette et al. 2009). Many of the invertebrates that occupy these systems have a planktonic larval stage that may last days to months to years (Morgan 1995; Pechenik 1999). The dispersive larval stage is important for population connectivity and dynamics, and is important in shaping adult community structure (Reed et al. 2000; Kinlan and Gaines 2003; Cowen and Sponaugle 2009). For example, the different ranges of species' dispersal distance can affect the spatial patterns in species abundance after a disturbance event (Reed et al. 2000), and some models of population persistence show that a returning larval stage is necessary for persistence (Hastings and Botsford 2006). There are also species specific differences in population connectivity and self-seeding that are influenced by location of source populations and oceanographic factors. For example, by using tracers to study dispersal of mussel larvae of *Mytilus californianus* and *Mytilus galloprovincialis*, Becker et al. (2007) showed that *M. californianus*

dispersed unidirectionally along the coast while *M. galloprovincialis* had regional self-seeding.

The dispersive larval stage also plays an important role in planktonic communities. During this planktonic time larvae are grazers (Martin et al. 1996; Gentsch et al. 2007) and food for fish and other invertebrates. Larval sand dollars are food for crab zoea and megalopae and post larval fish (Rumrill et al. 1985; Allen 2008). Larval crabs, shrimp, and barnacles are an important component of juvenile Pacific salmon diet (Boldt and Haldorson 2002; Beamish et al. 2004; Armstrong et al. 2005; Brodeur et al. 2007). The larval stage may last from days to months in the plankton and dispersal distances can range from <1km to hundreds of kilometers (Shanks 2009). Such a dispersive stage has its advantages and disadvantages. Advantages include increased dispersal to new habitats and reduced competition between siblings and between parents and offspring. Disadvantages include dispersal away from parent habitats and exposure to varying stresses, such as insufficient food and stressful environmental conditions (e.g. thermal stress, salinity stress and low oxygen conditions) (Pechenik 1999). Food availability and environmental conditions such as temperature and oxygen levels can have immediate effects on larval condition, growth, and can have carry-over effects on adults by affecting post-settlement success and juvenile survivorship (Baker and Mann 1992; Phillips 2002; Desai et al. 2006; Emlet and Sadro 2006).

Within a context of changing ocean conditions it is important to understand how the larval stage of a life cycle is affected, given that larvae may spend a considerable amount of time in the plankton and that their environment can play a significant role in their health and settlement success. I have set out to explore how oceanographic conditions influence planktonic larval invertebrates, with a specific focus on hypoxia due to the recent rise of hypoxic events in the CCS. Within this context I have explored the effects of environmental variables at the individual level and at the community level and have used both laboratory experiments and field observations to explore these effects.

In Chapter 2, laboratory experiments were used to address survivorship across a suite of larval species exposed to low oxygen conditions. These species represented important community members (including prey, habitat engineers and predators) of rocky intertidal systems. The focus of Chapter two on invertebrates of Oregon rocky intertidal communities was because these communities have a long history of investigation. The rich biodiversity and complex species interactions of intertidal communities have fostered the development and testing of fundamental ecological concepts. In Oregon, rocky intertidal community surveys date back to 1981 (Menge et al. 2011b). Therefore, the rich network of existing contextual information regarding the ecology of rocky intertidal community processes provides a framework within which to relate findings. The focus on the basic question of survivorship is a necessary first step in species' responses to hypoxia since the impact of hypoxia has not been

previously studied on any of the species of the present study. Larvae were exposed to three low oxygen conditions including hypoxia (DO <1.4ml/L) and microxia (DO <0.5ml/L) for up to six days. The majority of species were tolerant of low oxygen conditions for the period of exposures tested. The exception was the crabs, which had low tolerance to low oxygen conditions and experienced significant mortality within 12 hours. Such differential responses to chronic hypoxia or anoxia have the potential to alter the structure and species composition of intertidal communities.

In Chapter 3 and 4, species abundance and community composition of planktonic larvae in the nearshore waters of the Oregon coast were related to environmental variables. This was done using depth-stratified plankton samples collected during the upwelling season along three cross-shore transects in the nearshore waters of the Oregon coast. These were compared to environmental parameters: distance from shore, depth, temperature, salinity, dissolved oxygen, tidal amplitude, upwelling intensity, and cumulative wind stress. Multivariate statistical techniques were used to analyse the data. Redundancy analysis (RDA) was used to look at community structure in relation to environmental parameters. Non-parameteric multiplicative regression (NPMR) was used to develop models of species abundance in relation to environmental factors. The focus of Chapter 3 was on broad taxonomic groups of larval invertebrates: cirripedes, decapods, echinoderms, polychaetes, gastropods, bivalves, cnidarians, amphipods, isopods, and chaetognaths. Community was structured by multiple environmental conditions. The top contributors were

upwelling intensity, distance from shore, depth and date. In larval abundance models, multiple environmental conditions were important for abundance, however, upwelling intensity and distance from shore were again the most commonly occurring predictors of larval abundance.

The objectives of Chapter 4 were similar to those of Chapter 3, and the same samples and analysis techniques were used to relate larval abundance and community composition to environmental variables. However, in Chapter 4 the focus was specifically on decapod larvae, which were identified to species and developmental stage. The rationale for this fine focus on decapod larvae was based on evidence in the literature of heightened sensitivity of crustaceans to oxygen levels in their environment (Vaquer-Sunyer and Duarte 2008). While oxygen levels in the waters that were sampled, did not reach the hypoxic levels (<1.4ml/L) of previous years, dissolved oxygen did contribute to community structure. Similar to Chapter 3, findings from redundancy analysis of larval decapod assemblage composition revealed that various environmental variables were important for community composition. Among these were dissolved oxygen, upwelling intensity, cumulative wind stress (CWS), and distance from shore. These same variables showed up in species abundance models, but some variables were more frequently associated with abundance. For example, CWS was the most frequently occurring factor in abundance models. The findings from Chapter 3 and 4 show that both broad taxonomic groups of larval invertebrates and specific species are sensitive to upwelling related factors. This

is highly relevant given that climate change is predicted to impact upwelling intensity in EBUE.

2 – Differential effects of hypoxic conditions on survivorship of planktonic larvae of rocky intertidal invertebrates

Dafne Eerkes-Medrano, Bruce A. Menge, Christopher J. Langdon, and Christine Sislak

In review

ABSTRACT

Ocean hypoxia is increasing worldwide with detrimental effects on adults of many estuarine or deep-water species, but questions remain regarding effects on pelagic communities, and open coastal habitats. Hypoxia thresholds are species specific; thus predicting impacts on communities depends on impacts felt by different community members. Numerous laboratory investigations have focused on deleterious effects of hypoxia on individual species, but few have investigated impacts on a suite of community players, or on pelagic larval life stages of open coast species. Attention to hypoxia in these systems should become of increasing importance as climate change projections suggest intensified hypoxia in open coast upwelling systems. The recent rise of inner-shelf hypoxia and anoxia in the northern California Current Upwelling System resulted in mass mortalities of fish and benthic invertebrates but effects on planktonic organisms remain unknown. This situation offered a unique opportunity to investigate hypoxia effects on larvae of key rocky intertidal community members.

We conducted an investigation on mortality of planktonic larval invertebrates exposed to low oxygen conditions in controlled laboratory experiments. Hypoxic conditions, representative of the near shore environment of the Oregon coast, were generated by bubbling seawater with nitrogen gas. Results revealed a wide range of tolerances, from species with little tolerance to hypoxia (e.g. the shore crab *Hemigrapsus oregonensis*) to species with high tolerance (e.g. the California mussel

Mytilus californianus). These differential responses amongst intertidal taxa suggest that chronic hypoxia or anoxia potentially could affect their recruitment success and consequently, the structure and species composition of intertidal communities.

2.1 INTRODUCTION

Hypoxia is increasing in frequency and severity worldwide, with over 400 reported cases occurring in coastal waters globally as of 2008 (Diaz and Rosenberg 2008), and an exponential increase in the number of reported coastal hypoxic sites since the 1960's (Vaquer-Sunyer and Duarte 2008). Reduction in dissolved oxygen in some coastal waters has been cited as one of the fastest and most drastically changing environmental variables of ecological importance (Diaz 2001). Hypoxic events can lead to mass mortality in fish and invertebrates, and can generate areas of ocean devoid of most life, termed "dead zones" (Diaz 2001). Ecosystems experiencing severe hypoxia suffer from losses of fisheries and biodiversity, and altered food webs, and many of these ecosystems may be near collapse (Diaz 2001; Diaz and Rosenberg 2008). Hypoxic zones thus pose a global threat to coastal ecosystems, and rank as a major global environmental problem along with overfishing and habitat loss (Diaz and Rosenberg 2008).

The best known dead zones are those caused by land-to-sea flows of excess nutrients (e.g. Diaz 2001). Less appreciated are those that are driven by "natural" ocean dynamics. For example, in the past decade hypoxia has become an annual

occurrence in the waters of the northern California Current large marine ecosystem (CCLME), an Eastern Boundary Current region characterized by high biological productivity. Evidence shows that this dead zone is fueled by nutrient-rich upwelled waters (Chan et al. 2008). Low oxygen waters in the range of 1-3 ml l−1 are normal on the outer and middle continental shelf where a deep layer of water known as the Oxygen Minimum Zone (OMZ) intersects the continental slope. Most organisms living in the OMZ are adapted to low oxygen levels (Childress and Seibel 1998; Chan et al. 2008). In contrast to the outer and middle continental shelf, observations during the last half of the 20th century indicate that severe hypoxia (<0.5 ml l−1) was rarely documented on the inner shelf (less than 50m of water) of the Oregon and Washington coast. However, since 2000, a novel rise of severe hypoxia and even anoxia has occurred on the inner shelf waters of central Oregon. A particularly intense hypoxic episode occurred in 2006, with a 3000 km^2 hypoxic zone that extended from the shelf break to the inner shelf and occupied 80% of the water column. These events have caused mass mortalities in fish and benthic invertebrates (Chan et al. 2008). Further events such as these in coastal upwelling systems, are predicted to potentially intensify with changing climate conditions that lead to increased upwelling winds (Bakun et al. 2010) and ocean deoxygenation (Keeling et al. 2010).

Coastal upwelling systems are known as some of the most biodiversity-rich and productive ocean ecosystems. An intensification of hypoxia in coastal upwelling systems has important ecological and economic consequences. The CCLME, itself one

of the most taxonomically rich coastal ecosystems in the world, is home to productive ecosystems and economically important fisheries (Blanchette et al. 2009). It is also a system that has been highly studied; the rich biodiversity and complex species interactions of intertidal communities on the rocky shores of the Pacific Northwest have fostered the development and testing of fundamental ecological concepts. For example, rocky intertidal habitats have provided numerous contributions to ecological theory: predator-prey dynamics and food web complexity (e.g. Paine 1966); competition (e.g. Connell 1961); disturbance (e.g. Sousa 1979); community dynamics (e.g. Menge and Sutherland 1987); and when sufficiently large datasets exist, studies on community dynamics associated with climate change (e.g. Menge et al. 2011b).

A number of rocky intertidal habitats in the CCLME have been studied for long time periods (decades). In Oregon, rocky intertidal community surveys date back to 1981 (Menge et al. 2011b) and, through greater understanding, have allowed us to pose questions about the impact of changing environmental conditions on communities of these systems. This system poses a perfect opportunity to investigate how the rise of hypoxia and the novel rise of anoxia in the nearshore waters of this region (Chan et al. 2008) may affect the larval stages of rocky intertidal communities. In this study we ask:

> *Do the oxygen changes of nearshore waters have the potential to influence rocky intertidal communities via direct effects on the larval phase of the life cycles of rocky intertidal invertebrates? More specifically, does exposure to*

low oxygen waters result in differential larval mortality among intertidal species?

Many rocky intertidal invertebrate species have a bi-phasic life cycle in which a planktonic larval dispersal phase can result in recruitment over extensive intertidal areas. This important developmental phase can often last weeks to months (e.g. larvae of *Pisaster ochraceus* can be in the plankton 228 days (Strathmann 1978)), and during this time larvae are exposed to environmental conditions that may vary in time and space. There have been many studies on the impacts of environmental variables, such as temperature and food availability, on larval physiology, settlement and recruitment success as well as carry-over effects on later life stages. These studies show that environmental variables have significant effects on larval development, settlement success, and subsequent juvenile survivorship (e.g. Phillips 2002; Desai et al. 2006; Emlet and Sadro 2006).

Although the impact of hypoxia on the adult stages of a variety of invertebrate species has been well documented (see reviews by Herreid II 1980; Diaz and Rosenberg 1995), the effects of hypoxia on the larval stages of marine invertebrates are less known. Most larval studies have focused on species that occur in habitats with a history of hypoxia, such as bivalves in estuaries (Wang and Widdows 1991), or decapods (shrimp, crabs) in bays and estuaries (Tankersley and Wieber 2000). To our knowledge, studies investigating the impact of hypoxia have not focused on the larval stages of open coast species nor on the rocky intertidal species, either of the CCLME

or of other large marine ecosystems. Further, while most studies focus on the impacts of hypoxia on one or a few species, to our knowledge, none have focused on a suite of species whose adults interact in a community context.

To gain insight into how nearshore hypoxic events may influence the supply of new recruits to rocky intertidal communities, we determined survivorship of rocky intertidal invertebrate larvae exposed to low oxygen conditions. We studied a suite of ten rocky intertidal invertebrate species from four phyla that represented the diversity in this habitat. The phyla and species examined (with phyla in parenthesis) were: *Anthopleura xanthogrammica* (cnidarian), *Balanus glandula*, *Pollicipes polymerus*, *Cancer antennarius*, *Hemigrapsus nudus*, *Hemigrapsus oregonensis* (all arthropods), *Mytilus californianus*, *Onchidoris bilamellata* (both mollusks), *Pisaster ochraceus*, *Strongylocentrotus purpuratus* (both echinoderms). Five of these species are key rocky intertidal invertebrates: *M. californianus* (the California mussel), *B. glandula* (the acorn barnacle), *P. ochraceus* (the ochre star), *C. antennarius* (the spotted rock crab), and *S. purpuratus* (the purple urchin). Two species (*M. californianus* and *B. glandula*) are important prey items, habitat engineers, components in succession, and studied as model organisms in competition studies in rocky intertidal communities (Menge 1992; Harley et al. 2006). *P. ochraceus* and *C. antennarius* are predators in rocky intertidal habitats, and *P. ochraceus* in particular has been an important player in ecosystem studies investigating predation and top down effects (Dayton 1971;

Menge et al. 2004). Similarly, *S. purpuratus* can be an important ecologically dominant species and herbivore (Dayton 1975).

2.2 METHODS

2.2.1. Collection of adults and egg masses

All specimens were collected from the Oregon coast during the spring, summer and fall of 2009. See Table S1 for collection locations and dates. Collected egg masses and gravid adults were transported to the Hatfield Marine Science Center (HMSC), Newport, Oregon. The method of obtaining larvae from each different species varied (see Table S2). All spawning, fertilization, larval collection, and culturing techniques followed the methods outlined in Strathmann (1987). Adults of the urchin, *Strongylocentrotus purpuratus*, mussel, *Mytilus californianus*, and brooding crabs (*Cancer antennarius*, *Hemigrapsus nudus*, *Hemigrapsus oregonensis*) were collected in the field and brought back to the lab where they were induced to spawn (urchin and mussel), held until larvae hatched (crabs), or conditioned for later spawning (mussel). For barnacles (*Balanus glandula*, *Pollicipes polymerus*), ripe egg lamellae collected from adults in the field were induced to hatch in the lab. Egg masses of the nudibranch, *Onchidoris bilamellata* were collected in the field, and held in aquaria with running seawater until hatching. Gametes of the anemone, *Anthopleura xanthogrammica*, and the sea star, *Pisaster ochraceus*, were obtained by spawning captive individuals from a public aquarium at HMSC.

2.2.2. Larval husbandry

With the exception of barnacles, all larval culture methods (including spawning and fertilization) were performed as per the methods outlined in Strathmann (1987) (Supplementary material, Table S2). Barnacle cultures followed procedures outlined in Emlet and Sadro (2006). Cultures were incubated at 8-10oC and kept on a 10:14 hour light:dark photoperiod. The water used for larval rearing was filtered to remove all particles larger than 1 micron and UV filtered. All cultures were reared in 3L glass jars and cleaning and feeding of cultures occurred every other day. (see Table S2 for species specific larval culturing information including diet types).

2.2.3. Experimental setup

The experimental setup consisted of a gravity-fed system where a 500L header tank delivered seawater to four 50L diffuser tanks (Nalgene polypropylene carboys). Each diffuser tank then delivered water to four 1L polycarbonate bottles where the larvae were held for treatments (Figure 2.1). Water flowed into each 1L bottle through a ¼" inflow tube that injected water at the base of the bottle. Water exited the bottle through a double-sided cylindrical filter, covered with Nitex mesh. The filter sizes used, selected based on larval sizes, were 80, 100, or 250 micrometers. For each treatment, one of the four 1L bottles used as replicates had an additional 1L bottle connected to it for measuring dissolved oxygen and temperature of outflow (not

shown in Figure 2.1). The rate of flow into the 1L bottles was ~ 70 ml/minute. It took approximately 3hrs for one turnover of water through each 50L diffuser tank.

2.2.4. Experiment

All experiments were run within a temperature range of 8-10ºC and kept on a 10:14 hour light:dark photoperiod. Low oxygen conditions were created by bubbling seawater in diffuser tanks with nitrogen gas through glass bonded silica diffusers (Sweetwater Air Diffuser, 9" L x 1.5" W, 1/2" NPT, PE, Aquatic Ecosystems Inc.). Treatments were chosen based on the hypoxic conditions observed on the Oregon coast. Treatments included an extreme low oxygen treatment, called "microxia" (<0.5 ml/L), a hypoxic treatment called "hypoxia" (>0.5 and <1.4 ml/L), and a treatment that would represent the oxygen levels of summer upwelled waters called "upwelled water" (1.8-3.6 ml/L). In addition, there was a control treatment ("control," 5-7 ml/L) with oxygen levels representative of dissolved oxygen in the upper 10m of the water column (Grantham et al. 2004; Chan et al. 2008). Oxygen levels were monitored with an YSI Professional Optical Dissolved Oxygen (ProODO) instrument which was calibrated daily, following user manual instructions, in water-saturated air. Larvae were not introduced into the system until oxygen levels reached required treatment levels. Once oxygen treatments were set, dissolved oxygen levels remained stable within 10% of the set value and were monitored twice daily. Because bubbling with nitrogen gas affected the pH of our experiments (raising the pH to 8.3 in the microxia

treatment versus 8.1 in the control treatment), an additional set of experiments was run to check for an effect of an altered pH (see supplementary material for details). In these experiments pH was adjusted between treatments by bubbling with carbon dioxide gas in addition to nitrogen gas. The pH effects from low oxygen treatments did not significantly affect larval survivorship (alpha=0.05, mixed effects model ANOVA) as determined from experiments using the most sensitive taxa, the crabs (see supplement).

Larvae of all species were initially exposed to a 24-hour pilot trial to determine their sensitivity. Based on the results of this trial, animals were exposed to longer treatments (3-day and 6-day) if they were not sensitive or to shorter treatments (12-hours) if they were very sensitive to a 24-hour exposure. Six-day experiments were chosen to approximate as closely as possible a field-based scenario, where larvae may be caught in a low oxygen water mass for a number of days. Six day experiments were run with species that could be fed algal diets or species or larval stages that were large enough to use 100 or 250 micrometer Nitex filters. Six-day exposures were not possible for species that had small larvae (< 80 micrometers) or larvae that required non-algal foods because of clogging of filters. In these cases, 3-day experiments were carried out.

In most cases, experiments were carried out with older larval stages (2 weeks or older), except for crabs, which we were unable to rear in sufficiently high numbers to stages later than stage II zoea. The density of larvae exposed to each treatment

varied, based primarily on larval size (Table S3). We estimated survivorship following low-oxygen exposures based on larval movement. If larvae were swimming or moving in any way (e.g. moving limbs, beating cilia, or showing internal ciliate movement in case of bivalves) they were considered alive. In experiments with 100 larvae or fewer, all larvae were counted but in experiments with 1,500 larvae we counted subsamples. Most experiments were repeated 2-3 times through time. Experiments ran from May 2009 until December 2009 (Table S3).

2.2.5. Statistical analysis

Each experimental trial had either four treatments (control, upwelled water, hypoxia, and microxia) with four replicates of each treatment, or two treatments (the most extreme treatments: control and microxia) with eight replicates of each treatment. Experiments were run on a total of 10 different species and on more than one larval stage for three of these species; therefore analyses of larval survivorship were conducted on each species/stage combination (e.g. bipinnaria and brachiolaria larvae of *Pisaster ochraceus*). Analysis of survivorship was done using a mixed effects model ANOVA with survivorship in each dissolved oxygen treatment (control, upwelled water, hypoxia, microxia) as a fixed factor and the date of the experimental trial as a random effect. In 13 of 14 species/stage combinations, treatment effects did not vary by trial date, so survivorship was averaged across dates for each treatment and species-stage. Multiple pairwise comparisons were carried out using Tukey's HSD

to determine differences among treatments (alpha=0.05). In order to adhere to the assumptions of the ANOVA, all analyses were carried out with logit-transformed data (percent survivorship of larvae from treatments was converted to proportions and logit transformed, i.e., log[p/(1-p)] where p=proportion). This transformation for the analysis of proportional data is preferable to the arcsine transformation (Warton and Hui 2011). While all analyses were done on logit-transformed data, for ease of interpretation, the figures of results are presented on untransformed percent survivorship data rather than the transformed proportion data. All analyses were performed using R version 2.12.2 (http://www.r-project.org/). We note that constraints of the system required a common water source, so the experiments were pseudoreplicated in that sense. However, we attempted to minimize the importance of this issue by random assignment of treatments among the diffuser tanks.

2.3 RESULTS

2.3.1. Larval survivorship

Three crab species were sensitive to low oxygen conditions: stage I zoea of *Hemigrapsus nudus* (the Purple Shore Crab), stage I zoea of *Hemigrapsus oregonensis* (the Green Shore Crab), and stage I zoea of *Cancer antennarius* (the Pacific Rock Crab). Survivorship patterns were similar across all three species, with all species exhibiting significant mortality in hypoxia (>0.5 and <1.4 ml/L) and microxia (<0.5 ml/L) treatments within a 12-hour period (p-values < 0.0001, see Table 2.1). All

species had high survivorship (>95%) in control and upwelled water (1.8-3.6 ml/L) treatments. For all three crab species, mean survivorship in hypoxia treatments was under 50% but above 25%, as it varied among species, and under 25% for microxia treatments.

In contrast, the rest of the species examined in this study were tolerant to low oxygen conditions for three or six day exposure periods (see Table 2.1, Figure 2.2). Following three day exposures, survivorship in control (DO 5-7 ml/L) and microxia (DO <0.5 ml/L) treatments did not differ for planula larvae of *Anthopleura xanthogrammica* (the Giant Green Anemone, p= 0.436), veliger larvae of *Onchidoris bilamellata* (the Rough-Mantled Doris, p= 0.543), bipinnaria larvae of *Pisaster ochraceus* (the Purple Ochre Sea Star, p= 0.299), or the 6 arm pluteus larvae of *Strongylocentrotus purpuratus* (the California Purple Sea Urchin, p= 0.708). Across treatments including the control, *A. xanthogrammica* and *P. ochraceus* larvae had the highest survivorship, with both being >70%. Survivorship was lower for *O. bilamellata* and 6 arm pluteus larvae of *S. purpuratus* at ~50% and ~60% across treatments, respectively.

In six day exposure experiments, survivorship did not differ among any of the experimental treatments – control (DO 5-7 ml/L), upwelled water (DO 1.8-3.6 ml/L), hypoxia (DO >0.5 and <1.4 ml/L) and microxia (DO <0.5 ml/L) – for pediveliger larvae of *Mytilus californianus* (the California mussel, p= 0.355) or the brachiolaria stage of *Pisaster ochraceus* (the Purple Ochre Sea Star, p= 0.749). Mean survivorship

across treatments for both these species was high, at ~70% for *M. californianus* and >95% for *P. ochraceus*. In contrast, survivorship of stage IV nauplii of *Balanus glandula* (the Acorn Barnacle, $p=0.004$) and the 8 arm pluteus larvae of *Strongylocentrotus purpuratus* (the California Purple Sea Urchin, $p<0.0001$) differed among treatments; however, survivorship in microxia and hypoxia treatments was not lower than in the control treatment. For *B. glandula* the difference was due to lower survivorship in the upwelled water treatment (mean survivorship 89%) in contrast to control (91%), hypoxia (95%), and anoxia (95%), differences that are not likely to be ecologically significant. In *S. purpuratus* the difference was due to higher survivorship in the upwelled water (98%), hypoxia (88%), and microxia (95%) treatments in contrast to the control (32%). This result occurred both times the experiment was run but we do not know the causal mechanism for low control survivorship.

Given the high tolerance of stage IV *Balanus glandula* nauplii to six day exposures, further experiments with larval stages V and VI of *B. glandula* and with stage IV nauplii of *Pollicipes polymerus* (the Goose Neck Barnacle), only tested the most extreme low oxygen treatment (microxia) along with the control. Survivorship did not differ between control and microxia treatments following six day exposures for stage V nauplii of *B. glandula* ($p= 0.669$), for stage VI nauplii of *B. glandula* ($p= 0.067$), and for stage IV nauplii of *P. polymerus* ($p= 0.141$). Survivorship for *B. glandula* was high (>90%), across control and microxia treatments for stage V nauplii but lower (30-37%), for stage VI nauplii. For stage IV *P. polymerus* nauplii, mean

survivorship values for the control and microxia treatments were 55% and 66%, respectively.

2.3.2. Survivorship trends hold across larval stages – sea star, urchin, and barnacle

Trends in survivorship held across larval stages for the sea star, urchin and barnacle. For each of these species, both younger and older larval stages showed high tolerance of hypoxia and microxia after three or six-day exposures. Specifically, mortality of *Pisaster ochraceus* bipinnaria did not differ between control and microxia treatments after three day exposures ($p=0.299$). Mortality of brachiolaria did not differ between control and low oxygen treatments after six day exposures ($p=0.749$). Mortality of the six-arm pluteus stage of *S. purpuratus* did not differ between control and microxia treatments following three-day exposures ($p=0.708$). The eight-arm pluteus stage of *Strongylocentrotus purpuratus* also exhibited tolerance to the low oxygen treatments. While there was a difference between treatments for this latter species ($p<0.0001$), this was because the control treatment had lower survivorship than hypoxic and microxic treatments. *Balanus glandula* nauplii stages also showed similar trends in their tolerance of low oxygen conditions. Stage IV nauplii was another case where hypoxic and microxic treatments had no negative effect on survivorship following six day exposures, but the control had lower survivorship ($p=0.004$). For stage V and VI nauplii, *B. glandula* nauplii survivorship controls did not differ from that in microxia treatments ($p=0.669$ and 0.067 respectively).

2.4 DISCUSSION

2.4.1. Tolerance of larvae to hypoxia

We expected to observe considerable variability in larval survivorship, but also expected most species in our system to exhibit poor survivorship under hypoxic conditions. This expectation was based on findings from Grantham et al. (2004), where remotely operated video surveys in the inner-shelf waters of the Oregon coast revealed high mortality of fish and invertebrates during a hypoxic event. However, these observations were of adult individuals, not larvae, and larvae may have different tolerances to these environmental conditions.

Most studies on larval sensitivity to hypoxia have focused on bivalve and decapod larvae of species living in bays and estuaries where oxygen depletion is common. Examples include oysters in Chesapeake Bay, blue crabs in estuaries along the Gulf of Mexico and the Atlantic coast, and mussels and scallops in estuaries and bays (see Table 2.3). These studies document relatively wide ranges in species tolerances. For example, under anoxic conditions (DO <0.5ml/L), the 50% mortality time ranges from 1.3 hours in blue crab megalopae to 84 hours in recently settled oyster spat. The high tolerance to anoxia of some of the bivalve larval species tested may be explained by adaptations to the habitat in which these animals are found. Indeed, there are many documented cases of extended periods of hypoxia and anoxia tolerance in adult bivalves (de Zwaan 1977; Rosenberg et al. 1991). Authors attribute this tolerance to adaptation by bivalves to hypoxic conditions during shell closure or in

their habitats (de Zwaan 1977). Eutrophication events in estuaries and bays are common as these are areas where high nutrient environments can occur and sluggish circulation can favor stratification (Diaz 2001).

Given these earlier results, the finding that the majority of larval species in our system were tolerant to six-day (144 h) low oxygen exposures was surprising. While we expected tolerance to vary among species and larval stages, we did not expect the majority of animals tested to tolerate microxic conditions for lengthy periods of time. Further, the wave-exposed, open coast waters along the Oregon coast are generally considered to be well oxygenated and it thus seemed likely that these organisms would be exposed to low oxygen infrequently. Indeed, nearshore hypoxia was not a frequent occurrence prior to 2000 (Chan et al. 2008). Even after the onset of hypoxia in 2002, there is no evidence that hypoxia actually reached the shore, and rocky intertidal habitats, with their persistent surf, should have remained well oxygenated. However, rocky intertidal adult invertebrates do experience emersion on a daily basis due to tidal fluctuations. During emersion, many intertidal organisms experience a drop in internal oxygen levels. In some organisms, such as the purple urchin, *Strongylocentrotus purpuratus*, this drop in internal oxygen levels is temporary as they have mechanisms to maintain aerobic respiration (e.g. Burnett et al. 2002). Other organisms such as the intertidal porcelain crab, *Petrolisthes eriomerus*, have an extended decrease in internal oxygen levels as they revert to anaerobic metabolism during emersion (Stillman and Somero 1996). In yet other organisms, such as intertidal acorn barnacles of the genus

Chthamalus and *Semibalanus*, the organisms experience reduced internal oxygen levels during both emersion and immersion (Davenport and Irwin 2003). Natural encounters with hypoxia, such as emersion of sessile organisms, may have led to adaptations that may be inherited by the offspring.

A survey of the literature for hypoxia tolerance in adults, belonging to the taxonomic groups tested in the present study, reveals hypoxia tolerance in some intertidal animals. While we did not find studies on the particular species we tested, there were studies on species within the same animal infraclass or class. Two studies investigated the impact of emersion and anoxic submersion on adult barnacles (infraclass cirripedia). Lopez et al. (2003) found time to 50% mortality of *Austromegabalanus psittacus* barnacles was ~8 and ~4 days during emersion and anoxia respectively. Castro et al. (2001) found *Jehlius cirratus* barnacles survive longer periods of low oxygen exposure than did *A. psittacus* in the Lopez et al. (2003) study. Fifty percent of *J. cirratus* individuals survived 25 days under emersion hypoxic conditions and ~8 days under anoxic submersion, and some individuals could last up to 80 days in anoxic conditions. Two other studies investigated the impact of low oxygen conditions on bivalves. Laboratory experiments exposing the intertidal mussel *Perna perna* to anoxia (<0.05 ml/L) documented mussels surviving up to 30 days of exposure (Hicks and McMahon 2005). In a different intertidal mussel, *Mytilus galloprovincialis*, median mortality time in anoxia (<0.1 ml/L) was 5 days (Babarro et al. 2007).

During their dispersal, larval stages may have natural encounters with seawater low in dissolved oxygen levels. Some species such as the bivalve *Mya arenaria* have high larval densities in deep nearshore waters (Shanks et al. 2003). Larvae of the barnacles *Balanus glandula*, *Balanus crenatus*, and *Semibalanus cariosus* can be found as deep as 30 to 40m in nearshore waters of the Oregon coast (Shanks and Shearman 2009). At such a depth, in nearshore Oregon coast waters, oxygen levels can drop to 2-3 ml/L (Grantham et al. 2004).

Crab larvae do not exhibit the tolerance to hypoxia that other invertebrates have. This sensitivity may be related to the higher mobility of adult and larval crabs. There are limited studies on swimming speeds of larvae but studies on species of the same genus (*Cancer*) as used in this study, reveal that *Cancer magister* crab megalopae have swimming speeds up to 8.5cm/s (Fernandez et al. 1994) while *Strongylocentrotus purpuratus* blastula swimming speeds are approximately 0.045cm/s (McDonald and Grünbaum 2010). As mobile animals, crab adaptations for dealing with hypoxia may be to move to a more suitable area.

2.4.2. Future directions: Sublethal effects and implications

A next step in studying the impact of hypoxia on these species would be investigation of sublethal effects. Physiological conditions and behaviors that could be monitored for detecting sublethal impacts of hypoxia include growth, development, metabolic rates, feeding, and movement. Sublethal impacts of hypoxia/anoxia on

larvae have been detected in several studies including: reduction in larval settlement of *Crassostrea virginica* oysters (Baker and Mann 1992); reduced ingestion rates in *Crassostrea virginica* larvae (Baker and Mann 1994); delayed metamorphosis in *Callinectes sapidus* (blue crab) megalopae (Tankersley and Wieber 2000); reduced feeding and growth rates of *Mytilus edulis* mussel larvae (Wang and Widdows 1991); inhibited embryonic development, and altered swimming behavior and disintegration of the larval velum of the bay scallop *Argopecten irradians irradians* (Wang and Zhang 1995).

Negative impacts on one aspect of larval biology (behavior or physiology) can have carry over effects on other aspects of larval physiology/condition and on post-larval parameters. In the present study, survivorship of most of the species tested was not affected by hypoxia and microxia, but we do not know how larval metabolism and behavior was affected. If low oxygen exposures depressed metabolism of larvae, various activities could have been affected (e.g. swimming and feeding). Reduced swimming and feeding could impact larval nutritional condition. Impacts on larval nutritional condition could eventually translate into impacts in larval development, settlement success, recruitment success, and juvenile growth (Phillips 2002; Emlet and Sadro 2006).

Delayed development may increase the time larvae spend in the plankton, and increase chances of mortality due to predation and environmental stress (Pechenik 1999). Another potential risk is the immediate effects of hypoxia on larval swimming

behavior. Bay scallop veligers cease swimming during hypoxia exposure (Wang and Zhang 1995), which could impact the larvae's ability to feed or escape predators.

2.4.3. Differential survivorship – Implications for community dynamics

Previous studies have found that marine benthic communities experiencing periodic hypoxic events exhibit lower community biomass and species richness (e.g. Dauer 1993; Nilsson and Rosenberg 1994). Like benthic communities, rocky intertidal communities may also be affected by hypoxic events. The link between nearshore hypoxic events and rocky intertidal communities lies in the potential impacts on larval stages. Mortality events in the plankton can impact supply of new individuals to adult communities (Roughgarden et al. 1988; Pechenik 1999). Although many marine animals have a bipartite life cycle with a planktonic larval stage, fewer studies have investigated the effects of hypoxia on larval stages than on adults. Understanding how larvae are impacted by the environment is important for understanding community changes due to altered recruitment (Roughgarden et al. 1988; Navarrete et al. 2005).

Here we found differential impacts of hypoxia and microxia on larval invertebrates, with the majority of species surviving low oxygen treatments for the duration of time tested, and only a few crab species exhibiting high sensitivity to low oxygen levels. We infer that crab larvae are less likely than other intertidal invertebrate species to survive prolonged anoxic events in nearshore waters. Hence, during hypoxic events, there may be fewer crab larval recruits to adult communities.

This may be of concern because of the role that crab species, such as *Cancer magister*, play in commercial fisheries (Armstrong et al. 2003), and in benthic and intertidal community interactions. Certain crab species can have important direct and indirect interactions with other crab species (Visser et al. 2004; Casariego et al. 2009). For example Visser et al. (2004) found that first-year individuals of *Hemigrapsus oregonensis* are a dominant competitor for refuge space with the commercially important *C. magister*. Crabs can also be important in regulating the abundance of prey items, such as mussels and snails (Shinen et al. 2009; Ingólfsson 2009). *Cancer antennarius,* one of the crab species investigated in this study, is a predator of the mussel in this study, *Mytilus californianus*, as well as a predator of the other common mussel species, *M. trossulus*, present on the Oregon coast (Shinen et al. 2009). Hypoxic events may have a differential top-down impact on intertidal communities by removing the larval stages of important predators, while not removing larvae of prey species.

2.4.4. Implications of climate change / applications of knowledge in future studies

The last 50 years have seen an exponential increase in coastal hypoxic zones, which are now ranked as a major global environmental problem, along with overfishing, harmful algal blooms, and habitat loss (Diaz 2001; Diaz and Rosenberg 2008). Global climate change has the potential to exacerbate the likelihood of hypoxic events by leading to increased ocean stratification and warming (Diaz and Rosenberg

2008). In eastern boundary current systems, such as the CCLME, global climate change has the potential to generate increased hypoxia via modulations in upwelling wind stress (Chan et al. 2008; Bakun et al. 2010). Global oceans are also predicted to experience deoxygenation, drops in dissolved oxygen (Keeling et al. 2010). Understanding how component species respond to hypoxic events will be important for predicting how coastal communities will change with global warming. This study contributes toward developing this understanding by providing novel insights into the impacts of hypoxia on a suite of intertidal invertebrate larvae playing key community roles in rocky intertidal communities from the Pacific Northwest. Several issues remain, however. An analysis of 872 studies on hypoxia thresholds spanning a range of benthic metazoans (Vaquer-Sunyer and Duarte 2008) highlighted the range of sensitivity of organisms to low oxygen conditions and cautioned against using a uniform threshold oxygen level for mortality across species. Much as existing field studies that focus on community impacts have done, there is a need when conducting laboratory investigations on the impacts of hypoxia, to take a multi-species approach to assess the extent of the effect on different community members. Vaquer-Sunyer and Duarte (2008) also highlight the importance of conducting field studies to determine how species are affected by hypoxia in the field. Laboratory studies are more numerous than field studies, but are limited in extrapolation of findings from the controlled laboratory conditions to the field (Vaquer-Sunyer and Duarte 2008). Field studies on the effects of hypoxia will be required to corroborate lab studies.

ACKNOWLEDGEMENTS

We thank Marileen Reavis for maintaining and providing algal cultures, Kiril Chang-Gilhooly for technical advice and assistance in larval husbandry, and Tarik Gouhier for advice on using the R programming language. This research was supported by the Natural Sciences and Engineering Research Council of Canada, Oregon State University Department of Zoology, a Mamie Markham Research Award from the Hatfield Marine Sciences Center, and in part by grants from the David and Lucile Packard Foundation, the Gordon and Betty Moore Foundation, the Wayne and Gladys Valley Foundation, the Andrew W. Mellon Foundation, the United States Department of Agriculture, and the national Institute of Food and Agriculture. This is publication number XXX from the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO), funded primarily by the Gordon and Betty Moore Foundation and the David and Lucile Packard Foundation.

Table 2.1 Summary of experimental results. The first column indicates the species used in experiments with species separated by phyla. The next three columns indicate the experimental trials duration, the number of experimental trials repeated through time, and the number of replicates included in each treatment. The four dissolved oxygen treatments are indicated as separate columns with smaller case letters indicating where significant differences ($p<0.05$) between treatments occur (Tukey's HSD results). Negative signs indicate where survivorship was significantly lower than other treatments. In cases where only the two most extreme treatments were tested, NA's are included in the upwelled water treatment and hypoxia treatment columns. The F-values and P-values are provided for results from the mixed model ANOVAs.

Table 2.1

Species	Duration	No. trials	No. reps	Control DO 5-7 ml/L	Upwelled water DO 1.8-3.6 ml/L	Hypoxia DO >0.5 and <1.4 ml/L	Microxia DO <0.5 ml/L	F-value	P-value
Cnidarian									
Anthopleura xanthogrammica	3 days	2	8	a	NA	NA	a	0.62	0.436
Arthropods									
Balanus glandula stage IV	6 days	2	4	ab	a -	b	b	5.55	0.004
Balanus glandula stage V	6 days	1	4	a	NA	NA	a	0.20	0.669
Balanus glandula stage VI	6 days	1	8	a	NA	NA	a	3.98	0.067
Pollicipes polymerus	6 days	1	4	a	NA	NA	a	2.46	0.141
Cancer antennarius	12 hours	2	4	a	a	b -	c -	242.24	<0.0001
Hemigrapsus nudus	12 hours	3	4	a	a	b -	c -	195.46	<0.0001
Hemigrapsus oregonensis	12 hours	3	4	a	a	b -	c -	149.33	<0.0001
Mollusks									
Mytilus californianus	6 days	2	4	a	a	a	a	1.13	0.355
Onchidoris bilamellata	3 days	2	8	a	NA	NA	a	0.38	0.543
Echinoderms									
Pisaster ochraceus bipinnaria	3 days	2	8	a	NA	NA	a	1.12	0.299
Pisaster ochraceus brachiolaria	6 days	2	4	a	a	a	a	0.41	0.749
Strongylocentrotus purpuratus 6 arm pluteus	3 days	2	4	a	NA	NA	a	0.15	0.708
Strongylocentrotus purpuratus 8 arm pluteus	6 days	2	4	b -	a	a	a	35.16	<0.0001

Table 2.2 Mean survivorship and standard errors for different species in low oxygen treatments. In cases where only the two most extreme treatments were tested, NA's are included in the upwelled water treatment and hypoxia treatment columns.

Species	Control DO 5-7 ml/L	Upwelled water DO 1.8-3.6 ml/L	Hypoxia DO >0.5 and <1.4 ml/L	Microxia DO <0.5 ml/L
Cnidarian				
Anthopleura xanthogrammica	80.44 (±3.41)	NA	NA	70.81 (±7.59)
Arthropods				
Balanus glandula stage IV	91.33 (±1.66)	88.81 (±2.28)	94.60 (±1.38)	94.77 (±1.14)
Balanus glandula stage V	95.0 (±1.29)	NA	NA	94.0 (±1.41)
Balanus glandula stage VI	37.25 (±2.64)	NA	NA	30.29 (±2.06)
Pollicipes polymerus	55.5 (±7.04)	NA	NA	66.25 (±3.36)
Cancer antennarius	98.75 (±0.82)	98.12 (±0.92)	48.75 (±5.41)	2.5 (±1.90)
Hemigrapsus nudus	99.17 (±0.56)	97.5 (±0.97)	26.25 (±4.49)	5.83 (±3.74)
Hemigrapsus oregonensis	99.58 (±0.42)	97.08 (±1.44)	43.75 (±3.75)	20.0 (±5.67)
Mollusks				
Mytilus californianus	72.5 (±6.99)	68.17 (±8.01)	71.67 (±9.99)	73.5 (±880)
Onchidoris bilamellata	50.55 (±2.64)	NA	NA	47.92 (±3.66)
Echinoderms				
Pisaster ochraceus bipinnaria	98.75 (±0.52)	NA	NA	97.5 (±0.94)
Pisaster ochraceus brachiolaria	99.58 (±0.42)	98.75 (±0.88)	99.58 (±0.42)	99.58 (±0.42)
Strongylocentrotus purpuratus 6 arm pluteus	62.0 (±4.44)	NA	NA	60.67 (±2.93)
Strongylocentrotus purpuratus 8 arm pluteus	32.38 (±6.47)	97.83 (±1.12)	88.08 (±5.20)	94.79 (±1.76)

Table 2.3 Literature findings of sensitivity of larvae to low oxygen conditions (Hx – hypoxia, Ax – anoxia).

Species	Stage	Habitat	Dissolved Oxygen exposure ml/L	Time to 50% mortality	Reference
oysters, *Crassostrea virginica*	Recently settled spat	Chesapeake Bay	1.05 (Hx), <0.05 (Ax)	131 hours (Hx), 84 hours (Ax)	Baker & Mann, 1992
blue crabs, *Callinectes sapidus*	Megalopae	estuaries along the Gulf of Mexico and the Atlantic coast	1.05 (Hx), 0.5 (Hx), <0.05 (Ax)	12.3 hours (Hx), 4 hours (Hx), 1.3 hours (Ax)	Tankersley & Wieber, 2000
mussels, *Mytilus edulis*	Early prodissochonch, later veliconch	in estuaries, bays, and shallow coastal waters	<0.05 (Ax)	15 hours (prodissoconch), 39 hours (veliconch)	Wang & Widdows, 1991
bay scallop, *Argopecten irradians irradians*	Larvae with mean shell length 108 and 140µm	bays and estuaries	<0.05 (Ax)	<15 hours	Wang & Zhang, 1995

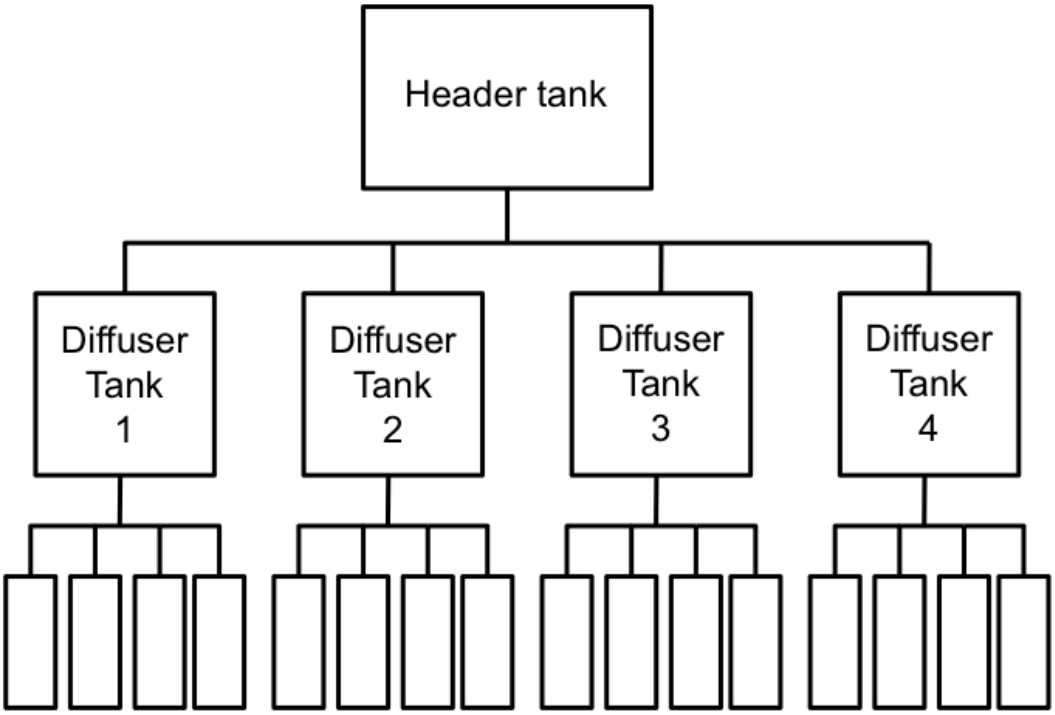

Figure 2.1 Diagram of experimental setup. The 500L header tank feeds seawater by gravity to four 50L diffuser tanks where seawater is bubbled with nitrogen gas. Each diffuser tank feeds by gravity into four 1L containers. Each 1L container serves as one replicate, resulting in a total of four replicates for each oxygen treatment.

Figure 2.2 Percent survivorship of different larval species and stages under different oxygen treatments: control (DO 5-7 ml/L), upwelled water (DO 1.8-3.6 ml/L), hypoxia (DO >0.5 and <1.4 ml/L) and microxia (DO <0.5 ml/L). The different species are: *Anthopleura xanthogrammica*, *Balanus glandula*, *Pollicipes polymerus*, *Cancer antennarius*, *Hemigrapsus nudus*, *Hemigrapsus oregonensis*, *Mytilus californianus*, *Onchidoris bilamellata*, *Pisaster ochraceus*, and *Strongylocentrotus purpuratus*. Significant differences ($p<0.05$) as indicated by a Tukey's HSD are indicated with letters above each bar. Error bars are standard errors.

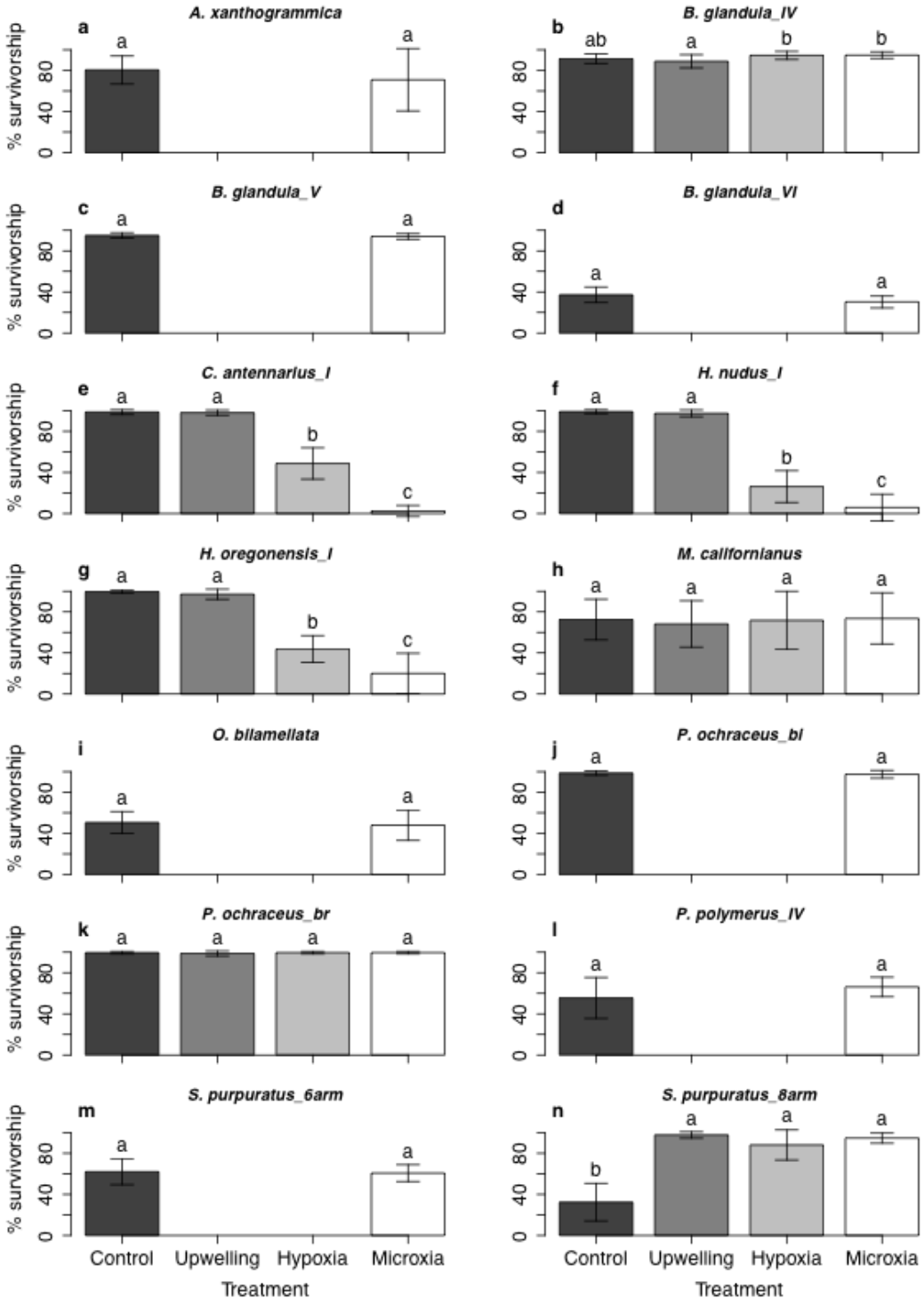
A. xanthogrammica
B. glandula_IV
B. glandula_V
B. glandula_VI
C. antennarius_I
H. nudus_I
H. oregonensis_I
M. californianus
O. bilamellata
P. ochraceus_bl
P. ochraceus_br
P. polymerus_IV
S. purpuratus_6arm
S. purpuratus_8arm
% survivorship
Control
Upwelling
Hypoxia
Microxia
Treatment

Figure 2.2

3– The role of local processes in structuring Meroplankton assemblages in the nearshore waters of the Oregon coast

Dafne Eerkes-Medrano, Bruce Menge, Lorenzo Ciannelli, Angela Johnson, and Tarik Gouhier

ABSTRACT

Eastern boundary upwelling ecosystems (EBUE) are among the most productive regions of the world's oceans and support economically important fisheries. Their high productivity is attributed to nutrient-rich waters brought up by upwelling. Therefore there is a concern about climate change effects on upwelling. Among predicted climate changes in upwelling systems are an intensification of upwelling winds and a potential increase in hypoxic events. Among the EBUEs, rocky intertidal habitats of the California EBUE are the most taxonomically rich. Many of the benthic invertebrates forming rocky intertidal communities have a planktonic larval stage that links benthic adult communities with the planktonic communities. We are interested in understanding what environmental conditions affect structure of Meroplankton assemblages and larval abundance. We found that multiple environmental conditions contributed to community structure with upwelling intensity, distance from shore, depth and date among the top contributors. Upwelling intensity and distance from shore were also commonly occurring predictors in larval abundance models. These findings are relevant given that climate change is predicted to impact upwelling intensity in EBUE.

3.1 INTRODUCTION

Globally, ocean ecosystems are experiencing physical and chemical changes associated with climate change. These include warming temperatures, increased storm events, changing ocean currents, and changing ocean chemistry such as ocean

acidification and ocean deoxygenation (Meehl et al. 2000; Hansen et al. 2006; Keeling et al. 2010; Tyrrell 2011). These changes can lead to alterations in marine biota. Some of the biological changes that have already been observed or are predicted to occur include: changes in the composition of plankton communities such as microbes (Sarmento et al. 2010) and phytoplankton (Hallegraeff 2010); range shifts in zooplankton (Richardson 2008) and fish (Perry et al. 2005); trophic mismatch in pelagic communities (Edwards and Richardson 2004); and changes in diversity and productivity of coastal communities (Harley et al. 2006).

Eastern boundary current systems are some of the most productive regions of the world's oceans and support economically important fisheries (Chavez and Messié 2009). Their high productivity is attributed to the nutrient rich waters that are brought up through upwelling (Aquarone and Adams 2008; Bakun et al. 2010). Due to these dynamics, potential impacts on productivity resulting from climate change or anthropogenic influences on upwelling patterns are of concern. For example, under a climate change scenario coastal upwelling is predicted to intensify as a result of increasing strength of upwelling winds (Bakun et al. 2010). Given that the productivity of these systems relies on upwelling in coastal waters, this change likely would have significant effects. Other alterations that may be associated with changes in the strength of upwelling are ocean hypoxia and ocean acidification (Chan et al. 2008; Feely et al. 2008). Some of these changes have already been observed in regions of the California Current System (CCS), the study area of the present investigation. Upwelling winds have intensified and sea surface temperatures have warmed in the

last half of the 20th century (Schwing and Mendelssohn 1997; Mendelssohn and Schwing 2002), and upwelling has intensified in two eastern boundary current upwelling systems, the Benguela Current and California Current Systems (Bakun and Weeks 2004; Iles et al. 2011). In the CCS, an associated event has been the rise (since 2000) of annual summer hypoxia in inner shelf water (Chan et al. 2008).

Rocky intertidal communities of the CCS may feel the impact of climate change events through changes in the adult communities, e.g., changes in biomass through increased growth rates from warmer temperatures (Menge et al. 2008); and through changes in the input of new individuals via propagule supply and recruitment, e.g., altered recruitment from changes in upwelling (Navarrete et al. 2005; Menge et al. 2009, 2011a). The input of new individuals into adult communities can be a key factor shaping communities (Menge and Sutherland 1987; Connolly and Roughgarden 1999; Navarrete et al. 2005), with recruitment rates and adult abundances often reflecting the input of new individuals (Minchinton and Scheibling 1991; Menge 2000).

Possession of a free-living larval stage is very common in the life cycle of many benthic marine invertebrates, and this stage can last from days to weeks to months (Pechenik 1999). In addition to the often assumed increase in dispersal distance conferred by long planktonic residence time, lengthy periods in the plankton can expose larval stages to greater variation in the physical and chemical processes in nearshore waters. For example, variation in temperature, water chemistry, and food availability can have direct effects on larval condition and performance (Phillips 2002;

Desai et al. 2006; Emlet and Sadro 2006; Vaquer-Sunyer and Duarte 2008; Crim et al. 2011). These exposures can in turn influence the survivorship success of the planktonic larval stage and even the performance of settled juveniles (Phillips 2002; Emlet and Sadro 2006; Allen and Marshall 2010). The physical conditions such as water currents and upwelling can impact larval dispersal, the composition of planktonic communities, and the input of new individuals to rocky intertidal communities (Minchinton and Scheibling 1991; Menge 2000; Yoshinaga et al. 2010; Kim and Barth 2011). Thus, studies focused on larval stages will be useful in predicting the ways in which climate-related changes in the CCS may impact larval supply to adult communities in both intertidal and subtidal habitats, as well as how pelagic food webs may be affected.

This paper explores the composition of Meroplankton assemblages and the abundance of meroplankton individuals in nearshore waters of the Oregon coast in relation to environmental parameters. The goal is to identify the environmental parameters that structure Meroplankton assemblages and identify which of these parameters play a significant role in influencing larval abundance. By exploring these relationships we will be able to address the questions:

I) What environmental conditions structure Meroplankton assemblages?

II) What environmental factors are important for the planktonic larval stage of rocky intertidal invertebrates?

3.2 METHODS

3.2.1. Zooplankton sampling

Plankton samples were collected along three transect lines (LB, or Lincoln Beach; NH, or Newport Hydroline; and SH, or Strawberry Hill) oriented roughly perpendicular to the Oregon coast (Figure 3.1). Research vessel-based transects were done during the months of May to September in 2008 and along the Newport Hydroline during the months of June to August in 2009 (Table 3.1). Samples were collected using a 300 micron multiple plankton sampler (MultiNet generation, Hydro-Bios) with a 0.5 m^2 aperture, and equipped with five 9 m net bags. An integrated pressure sensor allowed for the collection of five depth-stratified plankton samples. The MultiNet was equipped with two electronic flow meters and a CT set which contained one conductivity sensor, one temperature sensor, and one oxygen sensor. During each cast an additional CTD (SeaBird Model 19 CTD) equipped with an oxygen sensor was used to collect oxygen, salinity, and temperature data to cross-validate the data collected by the MultiNet.

Samples were collected between sunrise and sunset. Samples were taken as close as 2.3 km from shore to as far as 27.4 km from shore at depths spanning between 29.3 m and 88 m deep. Sampling with the MultiNet allowed collection of up to five consecutive depth stratified samples. As the instrument sampled the water column, opening of the next net automatically caused the closing of the previous net. Tows were taken within <10 m of the bottom and the MultiNet sampled in 10-20 m bins depending on sampling site depth. Nets sampled a greater vertical distance and

remained open longer at deeper sites. In order to capture variability in dissolved oxygen, trigger positions for opening/closing of nets were referenced from the bottom, because that is where sharper dissolved oxygen gradients occur. Oblique tows, at a 45°angle, were taken at a rate of 10 m/min while the ship travelled at 3-4 knots and lasted from 15 to 20 minutes. Electronic flowmeters mounted on the MultiNet calculated the volume of water filtered by the net for each sample (filtered volume ranged from 5 to 101 m^3).

The 300 micron mesh captured late larval stages but failed to capture early stages of some species (for example, the first naupliar stages of barnacles or early stages of echinoderms and bivalves). Following collection, plankton samples were preserved in 10% buffered formalin. In the laboratory, samples were subsampled following techniques of Lamb and Peterson (2005), and Shanks et al. (2002). Samples were rinsed in a 100 micron sieve with fresh water, transferred to graduated cylinder to determine settled volume, and diluted up to 10 times the settled volume. The sample was then randomly mixed with a stirring rod and subsampled with a 5ml Stempel pipette. For the more numerous taxa, subsamples were counted until at least 100 individuals were enumerated. This yielded a sample standard deviation of ~10% for the most abundant organisms (Venrick 1978; Shanks et al. 2002). In the case of the less common taxa the whole sample was counted.

The plankton samples were sorted under a dissecting microscope and 11 types of organisms were identified: cirripedes, decapods, echinoderms, polychaetes,

gastropods, bivalves, cnidarians, amphipods, isopods, and chaetognaths. Taxa were identified following the keys of (Shanks 2001) and (Smith and Johnson 1996).

3.2.2. Predictor variables

Predictor variables used in analyses included date of sampling, latitude, sampling depth, distance from shore, oxygen, bottom oxygen, temperature, salinity, upwelling intensity, upwelling intensity at a two day lag, tidal fluctuation, and cumulative wind stress for one week and two weeks prior to sampling. Oxygen (ml/L), temperature (°C), salinity (ppt), and depth (m) were recorded in situ at the time of sampling by the CT sensors on the MultiNet and by the additional CTD (SeaBird Model 19 CTD) sensor deployed at each cast, but for analysis only the CTD environmental measurements were used. The lowest recorded oxygen concentration, temperature, salinity, and the maximum depth recorded in each plankton sampling depth bin were used in analyses. Bottom oxygen, the lowest oxygen concentration recorded in the water column at each sampling station, was also included as an additional predictor variable. Distance from shore (km) was calculated from the GPS coordinates of sampling stations. Daily upwelling index (m^3/s/100m) values for 125°W 45°N were obtained from the Pacific Fisheries Environmental Laboratory (PFEL, http://www.pfeg.noaa.gov/). The PFEL derives upwelling indices from 6-hourly sea level pressure gridded fields. Cumulative wind stress data were obtained from a website managed by S. Pierce and J. Barth (http://damp.coas.oregonstate.edu/windstress/). Their data on cumulative wind stress

are derived from observed winds at Station NWPO3 - Newport, OR (National Data Buoy Center) using Large and Pond's (1981) method (see Barth et al. 2007). A proxy for the contribution of cumulative wind stress (Nm^{-2}days) was obtained by calculating the slope of cumulative wind stress for one week and two weeks prior to the sample collection date. A more negative slope indicates stronger upwelling conditions. Tidal range (m) was obtained by subtracting the highest high tide from lowest low tide for each sampling date and each sampling location. Tidal data came from the WWW Tide/Current Predictor (http://tbone.biol.sc.edu/tide). Tidal data used for the Lincoln Beach stations came from Depoe Bay, tidal data used for Newport Hydroline stations came from Newport, and the data used for Strawberry Hill stations came from Heceta Head.

3.2.3. Community Structure Analysis

Analysis of the meroplankton assemblage structure was conducted in R version 2.12.2 using redundancy analysis (RDA; (Legendre and Legendre 1998). Redundancy analysis is a constrained ordination that searches for linear combinations of explanatory variables that best explain the variation of the dependent variable matrix (Legendre and Legendre 1998). In this study, RDA was used to relate zooplankton assemblage structure to a suite of predictor variables. To properly assess the statistical relationship between species composition and the explanatory variables via RDA, the abundance data was Hellinger-transformed to reduce the weight accorded to rare species (Legendre and Gallagher 2001). The Hellinger transformation is most

appropriate for this community data-set because it deals well with the many zeros, and thus allows the use of the RDA Euclidean based ordination method. The formula for calculating Hellinger distance between sites x_1 and x_2 across p species is

$$D_{Hellinger}(x_1, x_2) = \sqrt{\sum_{j=1}^{p}\left[\sqrt{\frac{y_{1j}}{y_{1+}}} - \sqrt{\frac{y_{2j}}{y_{2+}}}\right]^2}$$ were the species abundance table $Y=[y_{ij}]$ has samples (rows) $i=\{1\ldots n\}$ and species (columns) $j=\{1...p\}$, and row sums are noted y_{i+} (Legendre and Gallagher 2001). An ANOVA-like permutation test was run on the RDA to determine the significance of each explanatory variable or constraint (Legendre and Legendre 1998). Specifically, to determine the significance of each focal explanatory variable, the residuals of the community data after partial RDA using the remaining non-focal explanatory variables are randomized and used to compute a pseudo-F statistic based on the ratio of constrained to unconstrained inertia. This procedure is repeated 1000 times to get a distribution of the pseudo-F statistic. The p-value is then calculated by determining the proportion of randomizations with a pseudo-F statistic that is greater than or equal to the pseudo-F statistic obtained with the original data.

3.2.4. Species response models

We used the method of Non-Parametric Multiplicative Regression (NPMR) to model species responses to the predictor variables. Alternative species response models such as least-squares multiple linear regression, generalized linear models, and

generalized additive models are often additive and accommodate interactions with terms that include more than one predictor. However, including the interaction terms in these models is a challenge because as the number of factors in the model increases the potential interactions also increase exponentially. NPMR overcomes this limitation by parsimoniously modeling complex interactions between predictors by applying a multiplicative kernel smoothing technique, which eliminates the need to specify interactions (see McCune 2006 for more details). This smoothing (averaging) technique weights observations through the use of kernel functions that are multiplied across predictors, thereby capturing potentially complex interactions between predictors. The software package Hyper Niche version 2.13 (McCune and Mefford 2009) performs an interactive step-wise search through possible models to create multiple best models. With the addition of each new predictor variable, the variables already in the model are evaluated for removal or adjustment in importance. To guard against overfitting, HyperNiche uses leave-one-out cross-validation (LOOCV), a form of jackknifing, in the process of variable selection (McCune 2006). The process of LOOCV uses many partitions of a dataset to evaluate a model. Each sample in a dataset of size n is left out sequentially and the model is fit to the partitioned (n-1) dataset, and then applied to estimate the omitted point. This is repeated for every data point, and the results accumulated in a measure of fit. In the process of variable selection, as each new variable is added to the model, a measure of fit is calculated through the process of LOOCV (McCune 2011). In addition to cross-validation, parsimony in the number of predictors is controlled by setting a minimum average

neighborhood size and by setting an improvement criterion (percent improvement of model fit with the addition of a new predictor, a criterion set by the analyst). Neighborhood size takes into account the amount of data used to estimate the model. It estimates how much data is brought to bear, on average, on making a point estimate. Setting a minimum neighborhood size protects the model from using predictor space with insufficient data (McCune and Mefford 2009; McCune 2011). Model quality is evaluated with a cross-validated R^2 value (xR^2). The cross-validated R^2 is calculated in the following way: $xR^2 = 1 - \frac{RSS}{TSS} = 1 - \frac{\sum_{i=1}^{n}(y_i - \hat{y}_i)^2}{\sum_{i=1}^{n}(y_i - \bar{y}_i)^2}$, where n is the number of sample units, i , $\hat{y}$ is the estimated response while excluding point i, $\bar{y}$ is the mean response, *RSS* is the residual sum of squares and, *TSS* is the total sum of squares. The xR^2 is different from traditional R^2 because through the process of cross-validation calculation, data point i is not included in the estimated response (McCune 2006).

In conducting nonparametric multiplicative regression (NPMR) there is a choice of how a model relates to sample space. Global models apply a relationship throughout the whole sample space. For example, in a simple linear regression, the whole dataset is fit at once by a global model as a straight-line relationship through sample space. In contrast, local models weight data points that are near the point of estimation more heavily than points that are distant from the point of estimation. This allows different relationships to emerge in different parts of the sample space. In the simple linear regression example, there is no local model as the global model fits the

whole dataset simultaneously. In NPMR, a global model is unspecified but a local model is specified. A weighing function applied to the local model specifies how data points are weighted according to their distance from the target point. A Gaussian weighing function gives observations that are further from the target lower weights (McCune 2011).

We chose NPMR models for analysis of meroplankton individual abundance in relation to environmental variables because: 1) more than one predictor was involved, 2) NPMR allowed us to look at non-linear relationships between the response variables and predictors, 3) NPMR models allowed for multiplicative interactions of predictors on the response variable, and 4) the dataset was large enough for this analysis (n>10 times the number of critical factors). We used NPMR with a local model based on a local mean estimator with a Gaussian weighting function. We modeled the relationships between twelve predictor variables and the abundance of individuals in each meroplankton group. The percentage improvement criterion for including new predictors in the model was 5% and the minimum average neighborhood size was set at 0.05(n). The importance of predictors in the 'best' NPMR models was evaluated with sensitivity analyses, and Monte Carlo randomization tests with 100 simulation runs were conducted to examine the statistical significance of models. The sensitivity analysis is a unit-less ratio represented by differences in the response and predictor variables that are scaled to their respective ranges. It is obtained by measuring the change in response variable when the predictors are nudged up and down from their observed values. A sensitivity value of

0 is produced when nudging a predictor has no measurable effect on the response and a value of 1 is produced when nudging a predictor results in a change in response of equal magnitude (McCune 2006; McCune and Mefford 2009). Contour plots, based on NPMR model outputs, of individual abundance for taxonomic groups were created using model predictor variables that had a sensitivity of 0.1 or higher. Contour plots are a two variable representation of larval abundance, and therefore provide the most accurate representation of larval abundance with respect to predictor variables for models with two variable solutions. In cases where models have more than two predicator variables the contour plots give a sense of the relationships of individual abundance to predictor variables but may not capture all possible interactions.

3.3 RESULTS

3.3.1. Explanatory variables

Across samples, dissolved oxygen (hereafter DO) levels dipped as low as 1.04 ml/L therefore reaching hypoxic (DO <1.43ml/L) levels (Figure 2). Bottom dissolved oxygen (hereafter BDO) levels ranged from 1.03 to 3.69ml/L with a mean of 1.30 and a median of 1.53ml/L. Temperature ranged from 6.7°C to 11.4°C, and salinity ranged from 27.6 to 34.0 ppm. The range in tidal fluctuation across samples was 1.8 m to 3.8 m. Upwelling intensity the day of sampling reached 81.0 m^3/s/100 m and two days prior to sampling reached 114.0 m3/s/100 m but the means were similar between upwelling intensity the day of sampling and two days prior at 28.4 m^3/s/100 m. The mean and median slope of the cumulative wind stress for one week (CWS1w) and two

weeks (CWS2w) prior to sampling were -0.022 and -0.019, and -0.014 and -0.022 respectively. The negative slope indicates the existence of upwelling conditions.

3.3.2. Community structure

The RDA explained 32.7% of the total variance in the distribution of taxa (Table 3.2) and the proportion of variance contributed by the constraining variables was 0.263 for the first three axes (Table 3.3). Permutation ANOVA results revealed that significant explanatory variables ($p<0.05$) for community composition were date, depth, distance, BDO, salinity, upwelling intensity the day of sampling, DO, latitude, tide, and CWS1w (Table 3.4). Date and upwelling were positively associated with each other and with RDA axis one (Figure 3.3 and Table 3.5). Species that had a strong association with upwelling and date (i.e., large positive loadings on axis one) were bivalves, cirripede cyprids, and decapod zoea (Table 3.6). Distance from shore, CWS1w and BDO were positively associated with each other and negatively associated with upwelling intensity and date (Figure 3.3 and Table 3.5). Species associated with distance, CWS1w and BDO (i.e., having large negative loadings with RDA1) were gastropods (Table 3.6). Depth, salinity, and tide (with positive loadings on RDA2) were positively associated with chaetognaths and isopods and negatively associated with polychaetes (Figure 3.1, Table 3.5, and Table 3.6).

3.3.3. Environmental factors associated with individual abundance

With the exception of echinoderms and bivalves, all taxa occurred in more than 50% of samples (Table 3.7). The five most commonly occurring taxa were gastropods (in 97% of samples), decapod zoea (92% of samples), amphipods (87% of samples), chaetognaths (86% of samples), and isopods (81% of samples). When present in samples, the taxonomic groups that had 1 or more individuals per cubic meter sampled, were cirripede napulii and cyprids, gastropods, chaetognaths, decapod zoea, and cnidarians (Table 3.7).

With the exception of echinoderms, non-parametric multiplicative regression (NPMR) models explained 27% to 64% of the variation in individual abundance across the different taxonomic groups. The final models for each taxa along with the sensitivities of predictor variables, and model xR^2 and p-value are indicated in Table 3.7. Selection of final models was decided when an additional 3% of the variation (xR^2) in a model was not explained by the addition of another predictor variable. Three models had a four variable solution, six models had a three variable solution, and three models had a two variable solution (Table 3.8). Monte Carlo randomizations for all final models indicated that models were statistically significant ($p<0.05$).

Among the most important predictor variables associated with the largest proportion of variance (as indicated by high sensitivity values) in individual abundance of zooplankton taxa were upwelling intensity, distance from shore, oxygen levels, bottom oxygen, temperature, salinity, and tidal amplitude (Table 3.8). The two variables that occurred most frequently were upwelling intensity and distance from

shore. The models for cirripede nauplii (xR^2=0.51) and cirripede cyprids (xR^2=0.64) had three and four variable solutions respectively. The two most important variables associated with variation in nauplii abundance were upwelling intensity and distance from shore while the two most important variables associated with variation in cyprid abundance were oxygen levels and distance from shore. Nauplii abundance peaked at moderately strong upwelling intensities, 50 m^3/s/100m, with the peak in abundance focused in shallower waters between 5 and 10km from shore (Figure 3.4a and b). Cyprid abundance also peaked between 5 to 10 km from shore and their peak was associated with oxygen levels around 2ml/L (Figure 3.5e).

Models for decapod zoea (xR^2=0.44), decapod megalopae (xR^2=0.27), and echinoderms (xR^2=0.09) had two variable solutions. The most important variables associated with individual abundance of decapods were upwelling intensity and distance from shore. Highest larval abundance occurred during stronger upwelling intensity (50 m^3/s/100m and higher) and at distances closer to shore (Figure 3.4 c and d). The peak in megalopae abundance occurred at even stronger upwelling intensities, ~80 m^3/s/100m, and closer to shore than the peak in zoea abundance at ~63 m^3/s/100m (Table 3.8).

Amphipods (xR^2=0.30), and isopods (xR^2=0.49) had four variable solutions in individual abundance models. The top three predictor variables for individual abundance of amphipods were tidal fluctuation, distance from shore, and upwelling intensity. Most amphipods occurred within 15km from shore, during tides of low amplitude, and during strong, 70-80 m^3/s/100m, upwelling periods (Figure 3.4 e and

f). For isopods the top three predictor variables were salinity, distance from shore, and bottom oxygen. Peaks in isopod abundance were found closer to shore, within 5km, and were associated with higher salinity and bottom oxygen values greater than 3.0ml/L (Figure 3.5 a and b).

Other than the cirripede nauplii, the other taxa with three variable model solutions were bivalves (xR^2=0.36), chaetognaths (xR^2=0.44), cnidarians (xR^2=0.53), gastropods (xR^2=0.31), and polychaetes (xR^2=0.50). The most important variables associated with individual abundance for bivalves and cnidarians were upwelling intensity and distance from shore. Bivalves peaked at upwelling intensities of 63 m^3/s/100m and their presence was diffuse through distance from shore (Figure 3.4 g). In contrast, cnidarian abundance peaked at upwelling intensities of 50 m^3/s/100m and their abundance was concentrated with distance from shore, focused around 10km from shore (Figure 3.4 i).

Chaetognaths and polychaetes both had oxygen as an important variable associated with individual abundance. Most polychaetes were found at higher oxygen levels (>6ml/L) and within 5km from shore (Figure 3.5 c), while most chaetognaths occurred at low oxygen levels, 2ml/L (Figure 3.5 f). Other important variables for chaetognaths were tidal amplitude (Figure 3.5 f) while for polychaetes they were bottom oxygen and distance from shore (Figure 3.5 d). For gastropods the most important variables associated with individual abundance were temperature, distance from shore, and cumulative wind stress for two weeks prior to sampling. Gastropods had two peaks in abundance with respect to temperature with one peak occurring

above 9ºC and one peak occurring around 7ºC, but both peaks occurred within 5km from shore (Figure 3.5 g). With respect to cumulative wind stress for two weeks prior to sampling, gastropods were most abundant when the slope of CWS2w was strongly negative indicating persistent upwelling conditions and abundance peaked at 5km from shore but also exhibited a second peak around 27km from shore (Figure 3.4 h).

3.4 DISCUSSION

3.4.1. Community structure

A variety of environmental conditions were important in structuring zooplankton communities in the present study. Date, depth, upwelling strength, and distance from shore explained a large and significant proportion of the meroplankton assemblage variation. These are all factors that have been found to be important in explaining zooplankton community structure in other studies. A recent study on micronekton communities (including fish, cephalopods and crustaceans of lengths from 2-10cm) of the Northern California Current System (CCS), found that micronekton community structure was best explained by sea-floor depth and distance from shore (Phillips et al. 2009). These cross-shelf gradients were associated with nearly all dominant taxa investigated. To a lesser extent, Ekman transport, representative of upwelling conditions, also influenced micronekton community structure (Phillips et al. 2009). In other studies along the Oregon coast (Keister and Peterson 2003), and in other coastal upwelling zones of the world such as the Central/South-central Chile (Manríquez et al. 2009), upwelling has also been found to

structure zooplankton community structure. The latter two studies focused on copepod community structure and noted that summer upwelling communities were composed of different species from those of non-upwelling communities found in winter. Ordination analyses by Keister and Peterson (2003) included date as an important predictor of community structure, suggesting that zooplankton community structure progressed over time and they found a distinction between offshore and nearshore zooplankton communities in summertime, and also between summertime and wintertime communities. The study by Manriquez et al. (2009) found zooplankton community structure was represented by variables that represent upwelling conditions: the ascent or descent of the upper boundary of the oxygen minimum zone, the value of Ekman transport, and salinity.

One of the advantages of the present study is that zooplankton sampling was not integrated through the whole water column but rather collected as depth stratified samples. This allowed us to match physical gradients with community composition or individual abundance. Salinity, oxygen, and bottom oxygen levels explained a lower proportion of the variation in the community structure than did depth, distance and upwelling, but were still significant explanatory variables of community structure ($p<0.05$, permutation ANOVA). While hypoxia in pelagic systems is an understudied topic (Ekau et al. 2009), existing studies do suggest that low dissolved oxygen waters play a role in structuring planktonic communities (Auel and Verheye 2007; Kimmel et al. 2010). For example, hypoxic events affect the vertical distribution of large sized mesozooplankton (Kimmel et al. 2010). Salinity has also been shown to be associated

with zooplankton community structure. The study of micronekton community structure in the waters of the Northern CCS mentioned above found that in addition to depth and distance from shore, salinity, and temperature also influenced micronekton community structure (Phillips et al. 2009). Manriquez et al. (2009) suggested that the link between salinity and community structure in mesozooplankton communities on the coast of Chile was another reflection of upwelling intensity.

3.4.2. Individual abundance and its association with environmental variables

Just as community structure was associated with a diversity of explanatory variables, so was the abundance of individual taxa. The most commonly occurring predictor variables in NPMR models were distance from shore and upwelling followed by oxygen or bottom oxygen levels. For the days sampled, the upwelling index ranged from -12 to 81 m^3/s/100m. All larvae whose abundance was associated with upwelling intensity had peaks in abundance at upwelling intensities above 50 m^3/s/100m. Cnidarians and cirripede nauplii both had peaks around 50 m^3/s/100m, decapod zoea and bivalves had peaks around 63 m^3/s/100m, and decapod megalopae and amphipods had peaks around 70 m^3/s/100m. Upwelling intensity as a model predictor had high sensitivities for decapod zoea and megalopae, cirripede nauplii, and cnidarians, with values of 0.696 or higher, suggesting that upwelling intensity provided strong contributions to individual abundance. Recall that a sensitivity of 1 is produced when nudging a predictor results in a change in response of equal magnitude and a sensitivity value of 0 is produced when nudging a predictor has no measurable effect

on the response (McCune 2006; McCune and Mefford 2009). Thus, the high sensitivity values of upwelling for decapod zoea and megalopae, cirripede nauplii, and cnidarians indicates that this predictor is an important driver of individual abundance. Gastropods were also associated with upwelling to some extent. Among the top predictors of their abundance was the cumulative wind stress (CWS) slope for two weeks prior to sampling. They were associated with more negative CWS slopes indicating an association with more persistent upwelling. As a trend, it appears that stronger upwelling periods are associated with increased concentrations of larvae in certain taxonomic groups.

Upwelling and its link to meroplankton distribution has a controversial history. Early studies suggested that offshore-flowing surface waters in upwelling events carried planktonic particles in the Ekman layer offshore (Roughgarden et al. 1988). Subsequent studies have investigated vertical water-column and cross-shore larval distributions to relate upwelling to larval distributions and potential mechanisms of larval transport (Shanks and Brink 2005; Morgan et al. 2009a; Shanks and Shearman 2009). Some of these studies have found that water column and cross-shore larval distributions differ by larval species and stage. For example in the CCS a study of crustacean larvae showed that larval distributions were associated with life stages (Morgan et al. 2009b). Early developmental stages occurring in surface waters were carried offshore in upwelling events, but found a return to shore by either migrating to deep waters where upwelled waters would return them to shore, or by remaining near the surface where relaxation events or internal waves brought them shoreward.

However, most species in the study (92%) remained close to shore, within 6km, by keeping their position below the offshore moving Ekman layer (Morgan et al. 2009b). Shanks and Shearman (2009) found similar cross-shore distributions of larvae, with the majority of larvae concentrated within 5km from shore. This position of larvae close to shore kept them landward from the upwelling front thus preventing offshore transport.

In our study, distance from shore was the next predictor, after upwelling intensity, picked up in NPMR models for cnidarians, cirripede nauplii, decapod zoea and megalopae, bivalves, amphipods, and gastropods. However, sensitivity values were not as high, ranging from 0.11 to 0.28. Peaks in larval abundance were focused at distances of 5 to10km from shore in all groups. Since each taxonomic group in the present study represents multiple species, the broad range in distributions with distance from shore may reflect the different life histories of different species. It has been shown that the parental source of larvae is reflected in water column distributions of larvae. Adults that live in nearshore or shallow subtidal zones have a larval stage that is found in nearshore waters, while adults that have broad distributions have a larval stage with a wider cross-shelf distribution (Shanks et al. 2002). The cross-shelf distributions of decapod larvae in the present study are within the range of distributions of crustacean larvae observed in a study conducted off the California coast (Morgan et al. 2009b). Morgan et al. (2009b) found that crustacean larvae when categorized by life stage fell within three cross-shelf categories: those found in the nearshore (1 and 3km from shore), midshelf (6 and 13km) and outer shelf (22 and

30km). This life-stage related pattern in cross-shelf distribution might also be reflected by the other taxa in the present study.

Because species were not identified in the present study, the nonparametric multiplicative regression model results showing strong upwelling and distance from shore as good predictors of larval abundance do not address mechanisms driving larval water column-distributions and transport in upwelling regimes as previous studies of meroplankton in the CCS have done (Morgan et al. 2009a; Shanks and Shearman 2009). However, our results do highlight the strong association of intense upwelling with high larval abundance. As noted in other studies, oceanographic conditions represent correlated variables and zooplankton individuals do not necessarily respond to a single variable but to the whole of oceanographic conditions (Manríquez et al. 2009; Phillips et al. 2009). The strong association between larval abundance and stronger upwelling intensities thus may be a reflection of the sum of oceanographic conditions during these temporal events. Strong upwelling events are associated with increased nutrients, cooler more saline waters, and acidic and less oxygenated waters (van Geen et al. 2000; Grantham et al. 2004; Feely et al. 2008). In our study, we've measured temperature, salinity and oxygen levels, but have not captured pH levels or nutrients. The association of high larval abundance of cirripede nauplii, amphipods, gastropods, bivalves, decapods, and cnidarians with stronger upwelling rather than other environmental variables might reflect larval aggregations due to a culmination of environmental factors associated with upwelling or underlying upwelling processes which were not measured, such as increased nutrients or phytoplankton.

After upwelling and distance from shore, the next most common predictors of larval abundance in NPMR models were dissolved oxygen levels and bottom oxygen levels. Of the larval groups whose abundance was associated with dissolved oxygen levels, the cirripede cyprids and chaetognaths were associated with lower oxygen levels (peaks in abundance at ~2ml/L) and the polychaetes were associated with higher oxygen levels (peaks in abundance at >6ml/L). Different species have different tolerances to low dissolved oxygen levels (Vaquer-Sunyer and Duarte 2008), and species living in systems frequently exposed to low oxygen levels such as oxygen minimum zones have adaptations to survive in these systems (Childress and Seibel 1998). For example, midwater crustaceans from low oxygen environments in the waters off southern California have lower critical partial pressures that allow them to maintain aerobic metabolic rates at low oxygen concentrations than midwater crustaceans in Hawaiian waters where oxygen levels are higher (Childress and Seibel 1998). A study conducted off the coast of Chile investigating chaetognath distributions in relation to oxygen minimum zones found that the two dominant species of chaetognath had contrasting distributions with relation to oxygen minimum zones (Giesecke and González 2004). One species, *Sagitta enflata*, was abundant above the OMZ while the second species was abundant within the OMZ. The latter species, *Sagitta bierii*, is also a common species of the CCS (Alvariño 1965; Rau et al. 2003) and may be one of the species contributing to high abundance at low oxygen levels in the present study. Literature on the tolerance of barnacle larvae for hypoxia is limited. However, existing studies do suggest some tolerance of nauplii to hypoxia. One study

found that mortality was less than 50% in hypoxic conditions (0.5ml/L and 1ml/L) for *Balanus amphitrite* feeding nauplii (Desai and Prakash 2009). Some of our own experiments show that nauplii of *B. glandula* and *P. polymerus* survive multiple day exposures to hypoxic (<1.4ml/l) and microxic (<0.5ml/L) conditions without significant mortality (Eerkes-Medrano et al. in review).

Some species of zooplankton are specifically adapted to hypoxic events and may use hypoxic waters as a way to escape predation (Auel and Verheye 2007; Kimmel et al. 2010). Thus, one possible explanation of higher cyprid abundance in lower oxygen waters may be that they were escaping predation. The greater abundance of polychaetes with higher oxygen levels in contrast to the higher abundance of cirripedes at lower oxygen levels was interesting given reports of low oxygen tolerance of polychaetes (Llanso and Diaz 1994; Diaz and Rosenberg 1995). The association of polychaetes with higher oxygen levels may reflect an underlying process not measured in the current study. For example, higher oxygen levels might be associated with areas of higher air-sea gas exchange such as tidal fronts and Langmuir cells (Baschek and Jenkins 2009; Chiba and Baschek 2010). Fronts are known to be areas of high productivity and are often associated with high abundance of phytoplankton and zooplankton (Fernández et al. 1993; Genin et al. 2005; Munk et al. 2009). Polychaetes may have been more abundant in more oxygenated waters which may have also been areas of higher food availability. Other than the association of larvae with dissolved oxygen levels, some larvae had increased abundances at certain bottom oxygen levels. This association might reflect an indirect effect as the larvae

were not necessarily found at depth where bottom oxygen levels were measured. However, as water column oxygen levels change, the distribution of certain species may change. This change may be in direct response to oxygen or it may be a response to changing distributions of predators or prey. For example, hypoxic events in Lake Eerie compress walleye habitat, but also result in greater prey availability as prey become concentrated in waters of favorable dissolved oxygen and temperature (Brandt et al. 2011). Species interactions can be shifted into upper parts of the water column when oxygen levels are depleted at the bottom of the water column (Breitburg et al. 1999). Another alternative for high larval abundance being associated with low bottom oxygen levels may be that low bottom oxygen represents other underlying factors such as stronger upwelling conditions. Manriquez et al. (2009) noted the ascent and descent of the OMZ was a representation of upwelling conditions. In the present study lower bottom oxygen values may be representative of stronger upwelling conditions that bring in low oxygen waters.

Less commonly occurring predictors of individual abundance were temperature for gastropods, salinity for isopods, and tidal amplitude for chaetognaths and amphipods. Higher larval abundance of gastropods was associated with temperatures above 9ºC. Isopod abundance peaked at salinities above 33ppm. Chaetognath abundance peaked when the tidal amplitude in 24 hours was 3m and amphipod abundance peaked when tidal amplitude was 2m. Temperature in other studies has been strongly associated with gastropod taxa. In observations of meroplankton abundance off Duck, North Carolina, USA, Shanks et al. (2003) found

gastropod larvae were categorized within an ordination cluster that was strongly associated with temperature. Studies of zooplankton association with characteristics of tides have also been documented in the literature but most studies have focused on estuarine systems. In the Southern Bight of the North Sea, meroplankton density has been found to be influenced by tidal cycle, with highest densities occurring after high water and before low water (Belgrano et al. 1990). In different estuarine studies barnacle nauplii abundance (Marques et al. 2009) and polychaete abundance (Hsieh et al. 2010) have been found to be associated with tidal fluctuations. In these studies the physical properties of tides such as tidally induced advective transport have been suggested to affect larval abundance, but so have the characteristics of water masses (e.g. salinity) associated with tides.

3.4.3. Conclusions

Based on our field observations, upwelling and upwelling-associated water features such as dissolved oxygen levels are clearly important for meroplankton assemblage composition and individual abundance. It seems reasonable that close associations exist between these physical characteristics of the water and Meroplankton assemblages given that many adult invertebrates have a larval meroplanktonic stage during the spring-summer when seasonal upwelling is in place (Huyer 1983; Strathmann 1987). Upwelling is one of the main features that defines the CCS and its ecosystems (Huyer 1983; Blanchette et al. 2009; Checkley Jr. and Barth 2009). Under climate change scenarios of enhanced greenhouse gases an

intensification of upwelling favorable winds in Eastern Boundary Current Systems such as the CCS is predicted (Bakun et al. 2010). Potentially associated with intensified upwelling is an increased occurrence of hypoxic events (Chan et al. 2008). Both of these predicted changes in the CCS likely will have important consequences for the meroplanktonic communities present. In the present study we have highlighted which factors are important for meroplanktonic community composition and individual abundance for broad taxonomic groups. A next step would be to conduct in-depth studies of the mechanisms driving the associations between environmental variables and community composition or individual species abundance. Further investigation would benefit from a species-specific focus as different meroplanktonic species exhibit different responses to their environment.

ACKNOWLEDGEMENTS

We are grateful for the assistance, guidance, and instruction various people provided. Charlie Miller, Jesse Lamb, and Cheryl Morgan provided instruction on plankton sorting techniques and zooplankton identification guidance. Rachel Mahler, Vathani Logendran, Ryan Braaten, and Sean Canfield assisted in sorting plankton samples. Elizabeth Daly and Ric Brodeur provided useful suggestions for data analysis. Scott Heppell and Vince Politano provided laboratory space to carry out sample processing. This research was supported by the Natural Sciences and Engineering Research Council of Canada, Oregon State University Department of Zoology, a Mamie Markham Research Award from the Hatfield Marine Sciences

Center, and in part by grants from the David and Lucile Packard Foundation, the Gordon and Betty Moore Foundation, the Wayne and Gladys Valley Foundation, the Andrew W. Mellon Foundation, and Oregon Sea Grant. This is publication number XXX from the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO), funded primarily by the Gordon and Betty Moore Foundation and the David and Lucile Packard Foundation.

Table 3.1 Sampling schedule and locations. Column heads indicate cross-shore station locations. E.g. NH-5 corresponds with Newport Hydroline station 5.

	-3	-5	-7	-10	-15
27 May 2008				NH	
29 May 2008		NH		NH	
30 May 2008		SH	SH	SH	
21 June 2008		NH	NH	NH	
26 June 2008		SH		SH	
27 June 2008		NH		NH	
2 July 2008		SH		SH	
3 July 2008		NH		NH, LB	
16 July 2008		SH			
25 July 2008		NH			NH
30 July 2008	SH	SH		SH	
25 Aug. 2008		NH			
27 Aug. 2008		NH			
28 Aug. 2008		NH		NH	
31 Aug. 2008				LB	
1 Sept. 2008		LB	LB		
12 June 2009		NH	NH	NH	
3 July 2009		NH		NH	
2 Aug. 2009		NH			
22 Aug. 2009		NH		NH	

Table 3.2 Redundancy analysis (RDA) proportion of the variance explained by constraining variables.

	Inertia	Proportion
Total	12.000	1.000
Constrained	3.927	0.327
Unconstrained	8.073	0.673

Table 3.3 Redundancy analysis (RDA) proportion of the variance explained by constraining variables for the first six axes.

	RDA1	RDA2	RDA3	RDA4	RDA5	RDA6
Eigenvalue	1.727	0.989	0.443	0.233	0.171	0.133
Proportion Explained	0.144	0.082	0.037	0.019	0.014	0.011
Cumulative Proportion	0.144	0.226	0.263	0.283	0.297	0.308

Table 3.4 Permutation ANOVA results exploring the contribution of explanatory variables to zooplankton community structure. Explanatory variables are ranked by F statistic and p-values.

Explanatory variable	F statistic	P value
Date	24.391	0.001
Depth	11.518	0.001
Distance	8.935	0.001
Bottom Oxygen	6.135	0.001
Salinity	3.320	0.002
Upwelling	3.237	0.002
Oxygen	2.890	0.003
Latitude	2.436	0.017
Tide	2.457	0.016
Cumulative wind stress slope (1 week)	2.056	0.033
Upwelling 2 days prior	1.408	0.173
Cumulative wind stress slope (2 week)	0.973	0.470
Temperature	0.788	0.611

Table 3.5 Zooplankton loadings for the first six redundancy analysis axes.

	RDA1	RDA2	RDA3	RDA4	RDA5	RDA6
Date	0.849	-0.174	-0.411	-0.134	-0.105	-0.134
Depth	-0.165	0.630	-0.559	-0.416	-0.060	-0.147
Distance	-0.513	-0.190	-0.347	-0.323	0.106	-0.511
Latitude	-0.284	-0.344	0.367	-0.250	-0.043	-0.362
Oxygen	-0.034	-0.075	0.381	0.345	-0.354	0.308
Bottom Oxygen	-0.193	-0.126	-0.162	0.422	-0.563	0.442
Salinity	0.194	0.468	0.123	-0.404	-0.098	-0.234
Temperature	0.046	-0.338	0.062	0.380	-0.217	0.236
Tide	0.019	0.212	-0.074	0.309	-0.503	-0.254
Upwelling	0.554	0.287	-0.214	0.223	0.556	-0.041
Upwelling 2 days prior	0.198	0.245	-0.224	0.230	0.485	-0.094
CWS1w	-0.236	-0.079	0.041	0.164	-0.462	0.009
CWS2w	0.001	-0.003	-0.328	0.349	-0.323	0.049

Table 3.6 RDA larval taxa/stage associations with axes. Taxa with strong associations with either RDA axis 1 (RDA1) or RDA axis 2 (RDA2) are boldface.

	RDA1	RDA2	RDA3	RDA4	RDA5	RDA6
Amphipods	-0.025	-0.276	0.368	-0.560	0.084	-0.121
Bivalves	0.919	-0.019	-0.266	0.229	-0.271	-0.008
Chaetognaths	0.325	1.231	-0.400	-0.106	0.288	-0.106
Cirripede cyprids	1.313	-0.138	-0.477	-0.176	-0.341	0.062
Cirripede nauplii	0.810	-0.620	0.481	0.326	0.081	-0.088
Cnidarians	0.797	-0.131	0.285	-0.428	0.059	0.122
Decapod megalopae	0.189	0.062	0.390	-0.082	-0.267	-0.258
Decapod zoea	0.748	0.127	0.344	0.326	0.278	0.033
Echinoderms	0.309	-0.220	-0.155	-0.118	0.054	-0.351
Gastropods	-1.199	-0.611	-0.234	0.024	-0.146	0.032
Isopods	-0.202	0.939	0.573	-0.014	-0.336	0.248
Polychaetes	0.362	-0.504	-0.150	-0.134	0.210	0.420

Table 3.7 Mean abundance of individuals in each taxonomic group when present and percent of samples in which each taxonomic group was present.

Taxonomic group	Mean abundance when present (±SD)	Percent of samples in which group was present
Cirripede nauplii	3.68 (8.99)	74
Gastropods	3.65 (5.47)	97
Chaetognaths	2.21 (5.61)	86
Decapod zoea	1.84 (5.80)	92
Cnidarians	1.20 (2.70)	74
Cirripede cyprids	1.07 (2.98)	63
Polychaetes	0.47 (0.94)	59
Isopopods	0.35 (0.49)	81
Amphipods	0.35 (0.52)	87
Bivalves	0.30 (0.78)	31
Decapod megalopae	0.09 (0.09)	62
Echinoderms	0.06 (0.06)	18

Table 3.8 NPMR model results. The first column contains the taxonomic group and in case of cirripedes and decapods the larval stage. The second and third column contain the cross-validated R^2 value and p-value. Each subsequent pair of columns contain an explanatory variable in the model and the corresponding sensitivity of the explanatory variable. Explanatory variables and sensitivities are ordered by decreasing sensitivity values. Explanatory variables in models include: dissolved oxygen (DO) in ml/L, bottom dissolved oxygen (BDO) in ml/L, distance from shore (Distance) in km, depth to seafloor (Depth) in m, upwelling intensity and upwelling intensity two days prior to sampling in $m^3/s/100m$, the slope of cumulative wind stress one week (CWS1w) and two weeks (CWS2w) prior to sampling, temperature (Temp) in °C, salinity (Sal) in ppm, tidal fluctuation in m, and date.

Table 3.8

Taxonomic group	xR^2	P-value	Explanatory Variable 1	Sensitivity	Explanatory Variable 2	Sensitivity	Explanatory Variable 3	Sensitivity	Explanatory Variable 4	Sensitivity
Cirripede Cyprid	0.645	0.0099	DO	0.255	Distance	0.241	Date	0.109	Upwelling 2 days prior	0.046
Cirripede Nauplii	0.511	0.0099	Upwelling	1.348	Distance	0.186	Depth	0.109		
Decapod Megalopae	0.274	0.0099	Upwelling	0.696	Distance	0.213				
Decapod Zoea	0.439	0.0099	Upwelling	0.883	Distance	0.261				
Amphipod	0.300	0.0099	Tidal fluctuation	0.358	Distance	0.280	Upwelling	0.144	Date	0.040
Bivalve	0.355	0.0099	Upwelling	0.217	Distance	0.110	Upwelling 2 days prior	0.084		
Chaetognath	0.440	0.0099	DO	0.623	Tidal fluctuation	0.599	Date	0.049		
Cnidarian	0.526	0.0099	Upwelling	0.700	Distance	0.118	Date	0.032		
Echinoderm	0.092	0.0396	BDO	0.461	Date	0.074				
Gastropod	0.314	0.0099	Temperature	0.494	Distance	0.324	CWS2w	0.320		
Isopod	0.488	0.0099	Salinity	0.692	Distance	0.265	BDO	0.122	CWS2w	0.048
Polychaete	0.495	0.0099	BDO	0.528	Distance	0.277	DO	0.147		

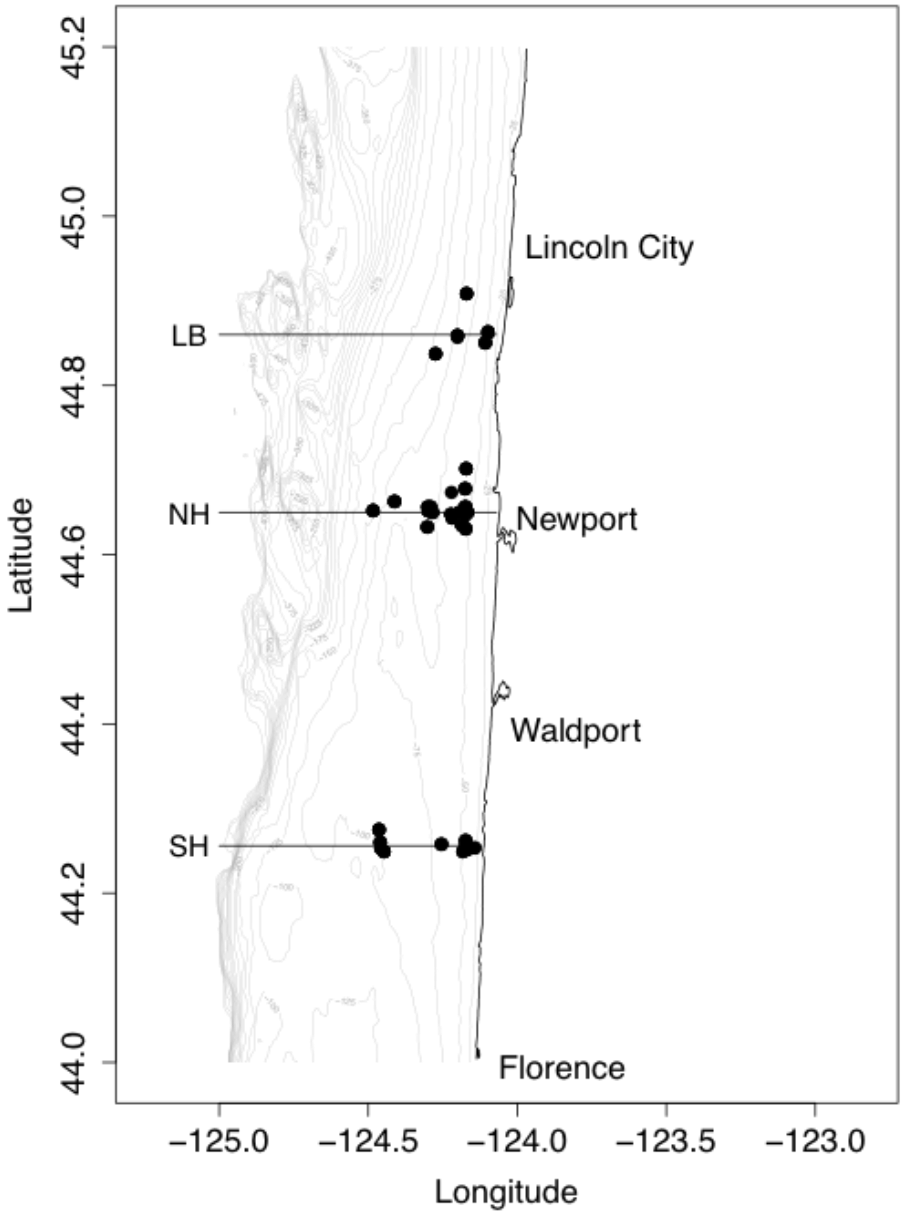

Figure 3.1 Sampling on the Oregon coast occurred along three transect lines: SH (Strawberry Hill), NH (Newport Hydroline), and LB (Lincoln Beach) with the highest frequency of sampling occurring along the NH line.

Figure 3.2 Boxplots of explanatory variables for total environmental data set with means (triangles), medians (solid lines), 25% and 75% quantiles, and outliers outside of the interquartile range.

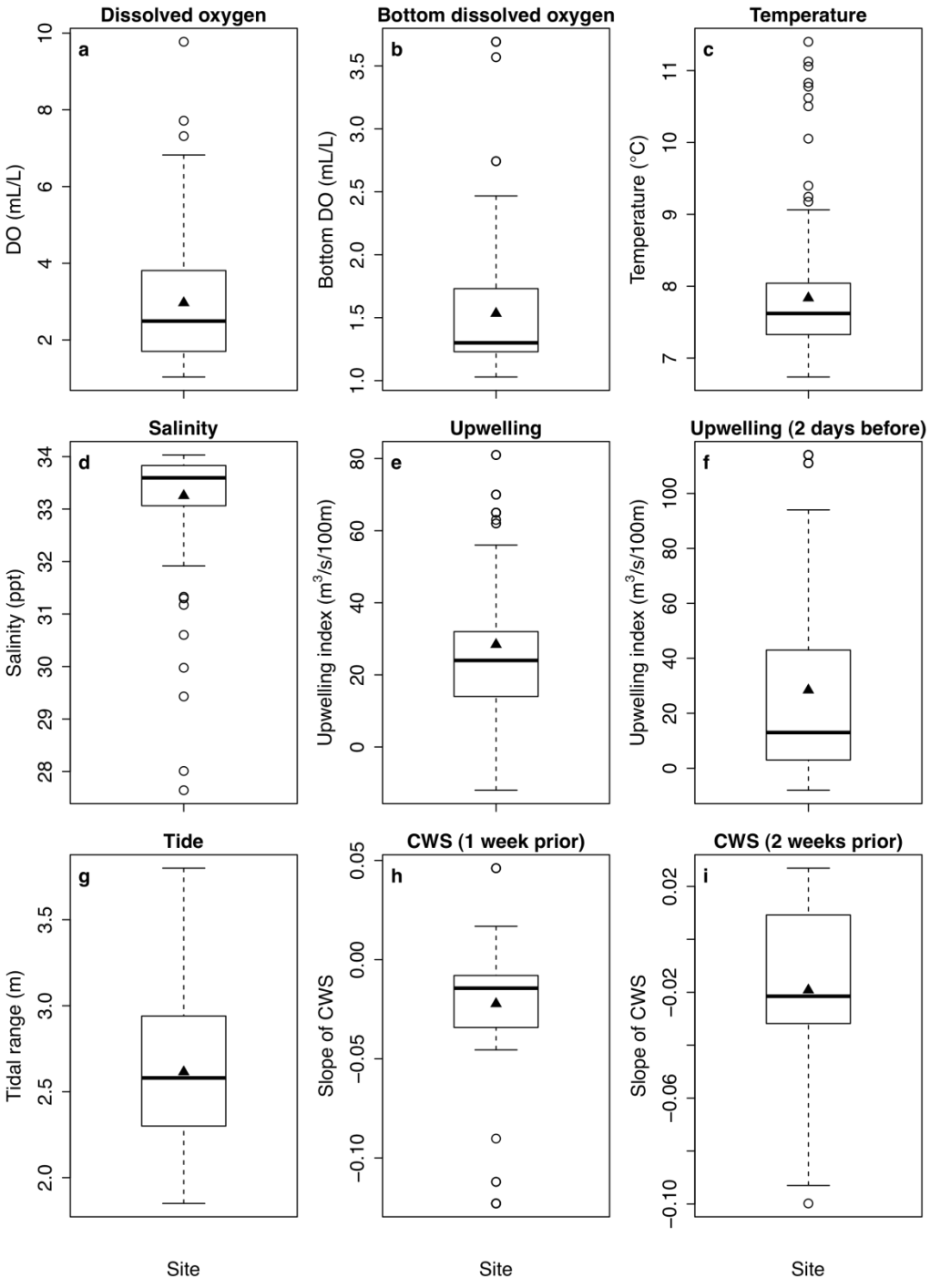
Dissolved oxygen
a
DO (mL/L)
Bottom dissolved oxygen
b
Bottom DO (mL/L)
Temperature
c
Temperature (°C)
Salinity
d
Salinity (ppt)
Upwelling
e
Upwelling index (m3/s/100m)
Upwelling (2 days before)
f
Upwelling index (m3/s/100m)
Tide
g
Tidal range (m)
CWS (1 week prior)
h
Slope of CWS
CWS (2 weeks prior)
i
Slope of CWS
Site
Site
Site

Figure 3.2

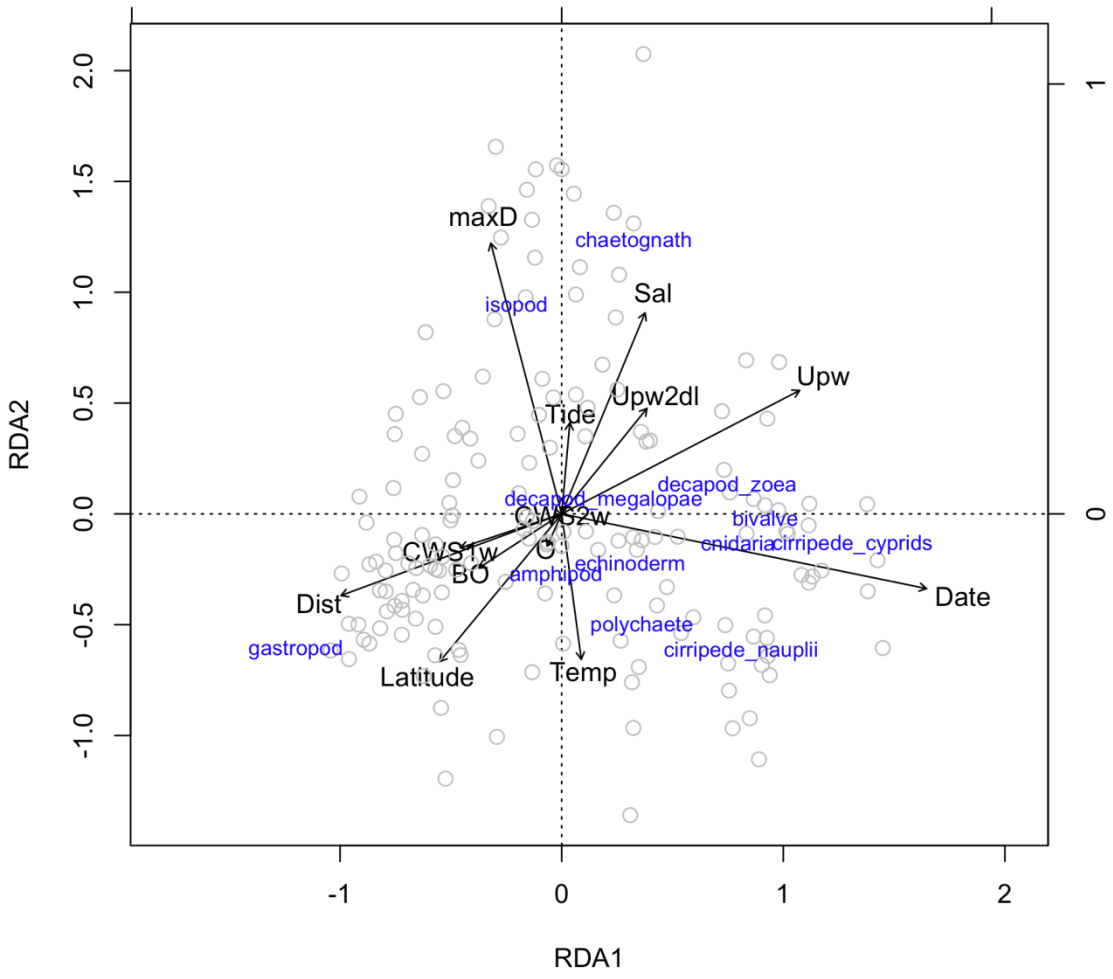

Figure 3.3 Redundancy analysis biplot. Axis 1 and 2 showing the distribution of zooplankton taxa (blue words) as a function of the environmental factors (black arrows). Environmental factors are: Latitude, dissolved oxygen (O) and bottom oxygen (BO), temperature (Temp), salinity (Sal), date of sampling (Date), distance from shore (Dist), depth to seafloor (maxD), tidal amplitude (Tide) in m, upwelling intensity the day of sampling (Upw) and two days prior to sampling (Upw2dl), and the slope of cumulative wind stress for one week (CWS1w) and two weeks (CWS2w) prior to sampling. The gray dots represent individual samples.

Figure 3.4 Two-predictor contour plots for larval abundance of different zooplankton taxonomic groups. Darker shades of gray indicate increasing abundance. White spaces are no data. Predictors appearing in plots are distance from shore (Dist) in km, depth to seafloor (Depth) in m, tidal amplitude (Tide) in m, upwelling intensity the day of sampling (Upw) in $m^3/s/100m$, and the slope of cumulative wind stress two weeks (CWS2w) prior to sampling. Contour plots are presented for the following taxonomic groups a) and b) Cirripede nauplii, c) Decapod zoea, d) Decapod megalopae, e) and f) Amphipods, g) Bivalves, h) Gastropods, i) Cnidarians.

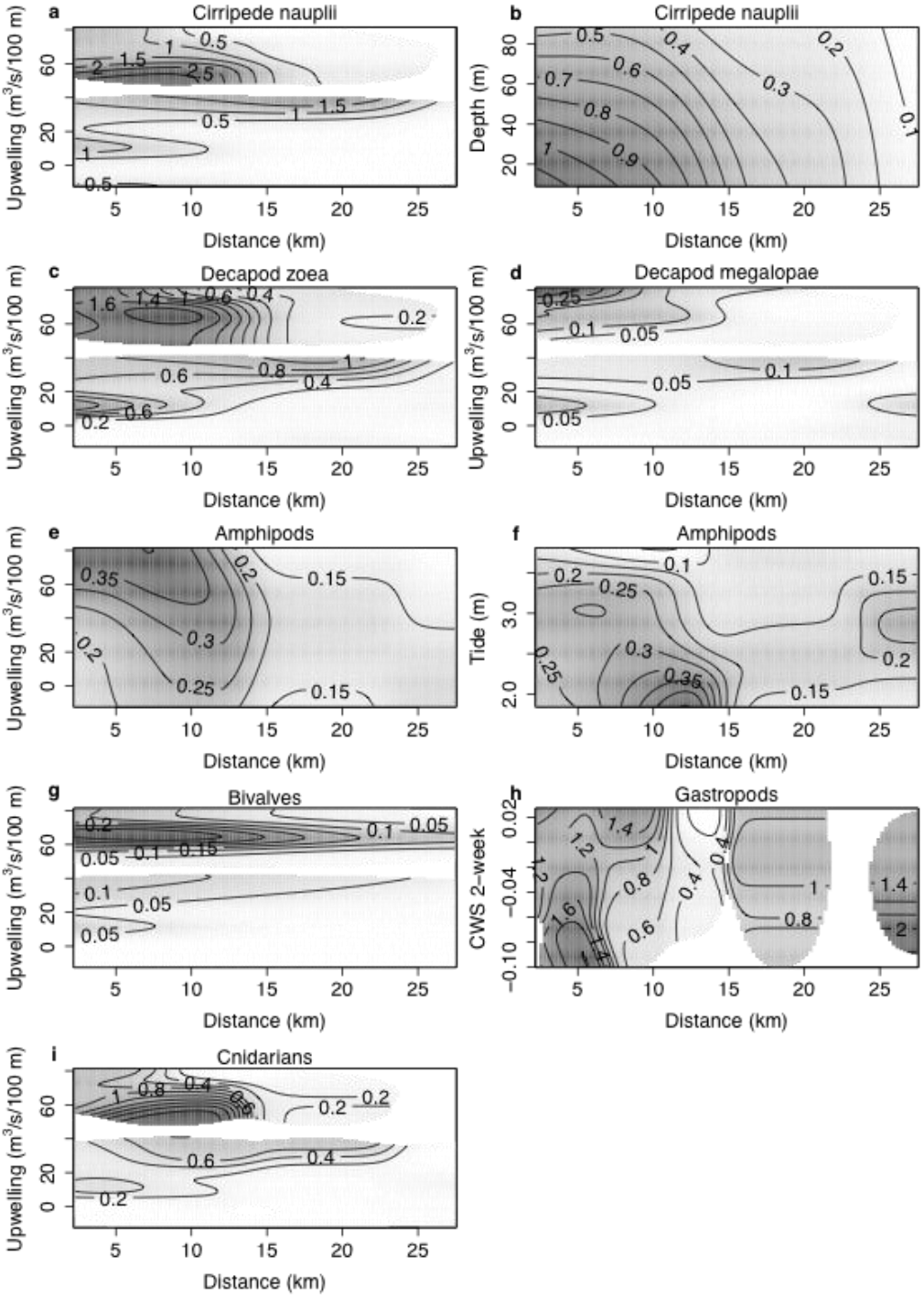
a
Cirripede nauplii
b
Cirripede nauplii
c
Decapod zoea
d
Decapod megalopae
e
Amphipods
f
Amphipods
g
Bivalves
h
Gastropods
i
Cnidarians
Upwelling (m3/s/100 m)
Depth (m)
Tide (m)
CWS 2−week
Distance (km)

Figure 3.4

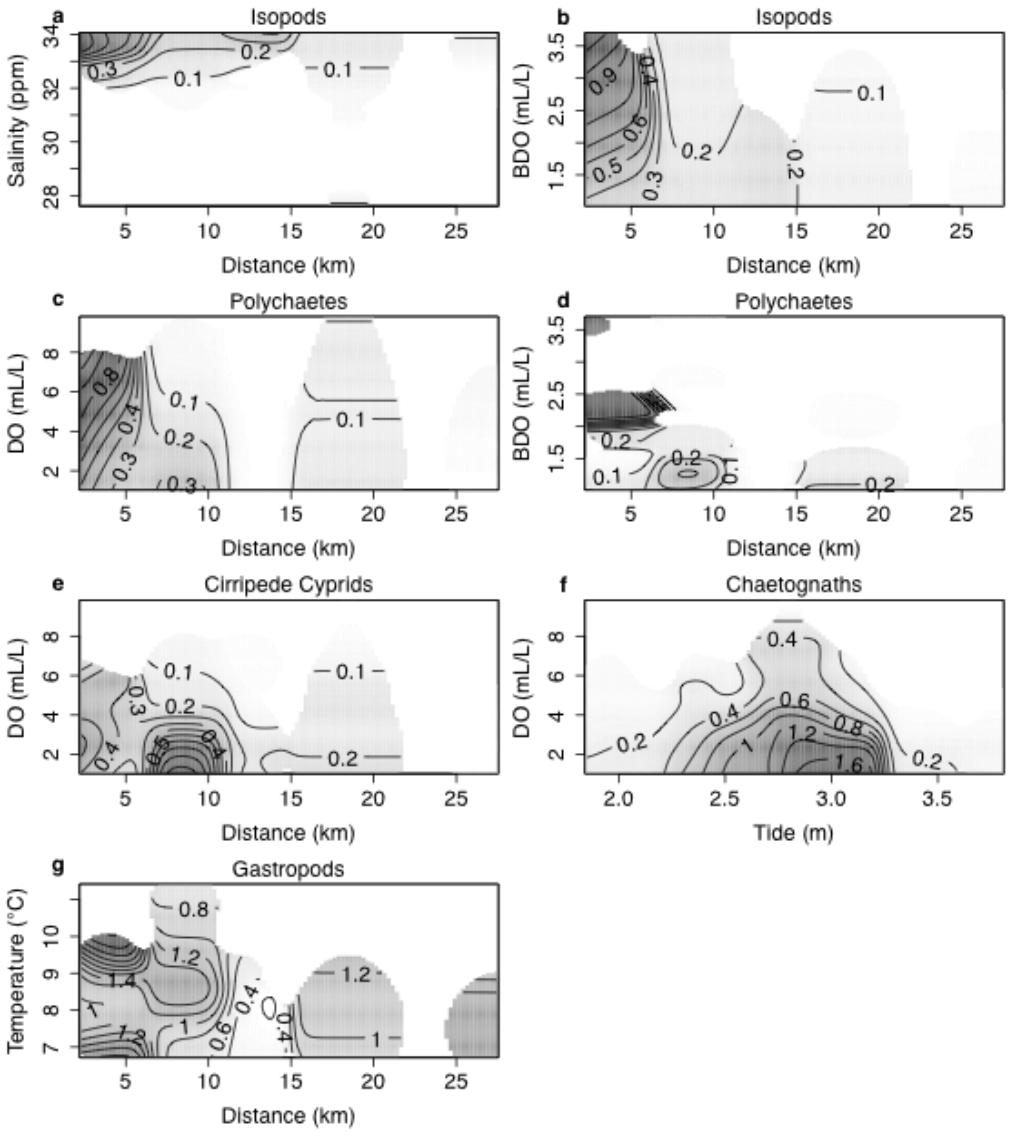

Figure 3.5 Two-predictor contour plots for larval abundance of different zooplankton taxonomic groups. Darker shades of gray indicate increasing abundance. White spaces are no data. Predictors appearing in plots are distance from shore (Dist) in km, date of sampling (Date) in Julian day preceded be the last digit of the sampling year, tidal amplitude (Tide) in m, oxygen (DO) and bottom oxygen (BDO) in ml/L, temperature (Temp) in ºC, and salinity (Sal) in ppm. Contour plots are presented for the following taxonomic groups: a) and b) Isopods, c) and d) Polychaetes, e) Cirripede Cyprids f) Chaetognaths, g) Gastropods.

4 – Differential effects of oxygen and nearshore environmental conditions on decapod meroplankton

Dafne Eerkes-Medrano, Bruce Menge, Lorenzo Ciannelli, Angela Johnson, and Tarik Gouhier

ABSTRACT

One predicted effect of climate change in Eastern Boundary Upwelling Ecosystems is the intensification of coastal upwelling, which may lead to intensified ocean hypoxia and ocean acidification. The California Current System has already experienced coastal hypoxia and nearshore anoxia, with documented cases of mass mortalities in fish and benthic invertebrates. The impacts on zooplankton communities are unknown. One group of zooplankton, meroplanktonic invertebrates, link the biology of benthic and intertidal communities and planktonic communities. Most benthic invertebrates have a dispersive planktonic larval stage that connects adult populations and influences population dynamics. While in the plankton, larvae may serve as grazers and food for fish. During this dispersive stage, larvae are exposed to oceanographic conditions that can have immediate effects on larval condition, growth, and carry-over effects on adults. We explored community structure and individual abundance of larval decapods in nearshore waters of the Oregon coast and related this to oxygen and other environmental variables. We documented the importance of various environmental variables on community composition. Among these were dissolved oxygen, upwelling intensity, cumulative wind stress (CWS), and distance from shore. These same variables contributed to species abundance, but certain variables had stronger associations with abundance. CWS was the most frequently occurring factor in abundance models. These findings are of importance given climate change predictions.

4.1 INTRODUCTION

The number of coastal sites reporting hypoxia has increased exponentially within the past forty to fifty years (Vaquer-Sunyer and Duarte 2008) and now has a global distribution with many of the 400-plus reported hypoxic sites occurring around well developed watersheds and major population centers (Diaz and Rosenberg 2008; Rabalais et al. 2010). In addition to hypoxic events occurring in coastal regions associated with human activity, evidence also suggests increased hypoxic events in coastal upwelling shelf systems (Chan et al. 2008; Monteiro et al. 2008; Hernández- Miranda et al. 2010) and a less oxygenated state and shoaling of oxygen minimum zones (OMZ) in these systems (Bograd et al. 2008; Díaz-Ochoa et al. 2011). Both types of hypoxic events, those caused by human inputs and those occurring in upwelling systems, are projected to increase in the future. The former is likely to increase as a result of increased human activity in coastal areas (Rabalais et al. 2010) and may be exacerbated by climate related changes such as increased stratification and ocean warming (Keeling et al. 2010). Climate projections also predict increased intensity of upwelling favorable winds in coastal regions, which may contribute to more coastal hypoxia (Bakun et al. 2010); recent evidence is consistent with this prediction (Iles et al. 2011).

In the California current system there has been an increased incidence of ocean hypoxia in nearshore waters and a novel rise of ocean anoxia in the last decade (Chan et al. 2008). The most intense episode of hypoxia occurred in 2006 following changes in upwelling favorable winds. This event affected a total area of 3000 km^2. Mass

mortalities of benthic invertebrates and the complete absence of all fish from rocky reefs were observed during this event (Chan et al. 2008). However, whether or not these hypoxic events affect the zooplankton community is unknown.

One particular group of the zooplankton community, the larval stage of benthic invertebrates, forms an important link between the biology of benthic and intertidal communities and that of the planktonic community. Food availability and environmental conditions such as temperature and oxygen levels can have immediate effects on larval condition, growth, and carry-over effects on adults by affecting post-settlement success and juvenile survivorship (Baker and Mann 1992; Phillips 2002; Desai et al. 2006; Emlet and Sadro 2006). Therefore it is important to understand how the rise of hypoxic events within the past decade on the Oregon coast may be affecting larvae. A recent review of the literature revealed that different taxonomic groups exhibit different sensitivities to hypoxia with crustaceans appearing among the most sensitive organisms to hypoxic conditions (Vaquer-Sunyer and Duarte 2008). Our own studies on intertidal species of the CCS found that crab larvae were among the more sensitive species to hypoxia (Eerkes-Medrano et al. in review). Studies on the impact of hypoxia on larval invertebrates suggest stage specific sensitivities to hypoxia. For example, early and late larvae of the mussel *Mytilus edulis* have different median mortality times when exposed to anoxia and different feeding and growth rates when exposed to hypoxia (Wang and Widdows 1991). In the oyster *Crassostrea virginica* hypoxia exposure affects the feeding activity of the youngest stages of post-settlement oysters more than the older stages (Baker and Mann 1994). In the blue crab

Callinectes sapidus megalopae were more tolerant of hypoxic conditions than newly metamorphosed juveniles (Tankersley and Wieber 2000). Given the taxon- and stage-specific sensitivities to hypoxia, and in light of the recent rise of nearshore hypoxia on the Oregon coast, we were interested in relating decapod assemblage composition and stage specific abundances for different species to dissolved oxygen levels and other environmental variables. The objective of this investigation was to determine if larval decapod assemblage composition and if species abundance are influenced by oxygen levels.

4.2 METHODS

4.2.1. Zooplankton Sampling

Plankton samples were collected along three transect lines perpendicular to the Oregon coast (Figure 4.1) during the months of May to September in 2008 and along one transect line from June to August in 2009. Transect lines sampled on each date are listed in Table 1. Samples were collected between the hours of sunrise and sunset. Sampling stations ranged in their distance from shore from 2.3 km to 27.4 km from shore. Depths sampled spanned 29.3 m to 88 m deep.

Samples were collected using a 300micron multiple plankton sampler (MultiNet generation, Hydro-Bios) with a 0.5 m^2 aperture, and equipped with five 9 m net bags. An integrated pressure sensor allowed for the collection of five depth stratified plankton samples. To capture variability in dissolved oxygen, trigger positions for opening/closing of nets were referenced from the bottom, where sharper

dissolved oxygen gradients occur. Sampling began within <10 m of the bottom and subsequent samples were collected in 10-20 m bins depending on sampling site depth. At deeper sites, nets sampled a greater vertical distance and remained open longer. The MultiNet was equipped with two electronic flow meters and a CT set which contained one conductivity sensor, one temperature sensor, and one oxygen sensor. During each cast an additional CTD (SeaBird Model 19 CTD) equipped with an oxygen sensor was used to collect environmental data to cross validate the data collected by the MultiNet. For analysis purposes only the CTD environmental measurements were used due to greater reliability of the CTD sensor package. Oblique tows, at a 45° angle, were taken at a rate of 10 m/s while the ship travelled at 3-4 knots and lasted from 15 to 20 minutes. Electronic flowmeters mounted on the MultiNet calculated the volume of water filtered by the net for each sample (filtered volume ranged from 5 to 101 m^3).

Based on Shank and Shearman's (2009) study the 300 micron mesh should capture all larval stages of decapods. Following collection, plankton samples were preserved in 10% buffered formalin. In the laboratory, samples were rinsed in a 100 micron sieve with fresh water, and all individual decapods in the sample were identified and counted. In cases where an individual species was extremely abundant (>300 individuals) the sample was subsampled for that species while the whole sample was sorted for the less abundant species. This subsampling for one particular species was only done in 5 samples out of 192 samples. Subsampling was done following the protocol in Shanks et al. (Venrick 1978; 2002). Samples were transferred to a 500 ml

graduated beaker and diluted to 300ml. The sample was then randomly mixed with a stirring rod and subsampled with a 5ml Stempel pipette. Subsamples were counted until at least 100 individuals of the abundant species were enumerated. This yielded a sample standard deviation of ~10% for the most abundant organisms (Venrick 1978; Shanks et al. 2002). For the less abundant species in the sample, the whole sample was sorted. Decapod species and stages were identified following the keys of Shanks (2001), Lough (1985), and Haynes (1985). Individuals from Infraorder Caridea were only identified to the family level (Haynes 1985) while members from the Thalassinidae, Anomura, and Brachyura were identified to the species level. All decapods were staged.

4.2.2. Explanatory variables

The explanatory variables used in analyses were: date of sampling, latitude, sampling depth, distance from shore, oxygen, bottom oxygen, temperature, salinity, upwelling intensity, upwelling intensity at a two day lag, tidal fluctuation, and cumulative wind stress (hereafter CWS) for one week and two weeks prior to sampling. From each depth bin sampled by the plankton net, the lowest oxygen (ml/L), temperature (°C), salinity (ppt), and the maximum depth (m) were used for analyses. Bottom oxygen, the lowest oxygen recorded in the water column at each sampling station, was also included as an additional predictor variable. Distance from shore (km) was obtained from sampling station GPS coordinates. Daily upwelling index (m^3/s/100m) values for 125°W 45°N were obtained from the Pacific Fisheries

Environmental Laboratory (PFEL, http://www.pfeg.noaa.gov/). Upwelling index data are derived from 6-hourly sea level pressure gridded fields on a 1° grid. As a proxy of CWS (Nm^{-2}days), slopes for wind stress were calculated for one week and two weeks prior to sampling. CWS data (http://damp.coas.oregonstate.edu/windstress/) were originally derived from observed winds at Station NWPO3, 124.067W 44.613N Newport, OR (National Data Buoy Center) using Large and Pond's (1981) method (see Barth et al. 2007). Station NWPO3 is a land based station, so provides coastal wind stress data. A proxy for the contribution of CWS was obtained by calculating the slope of CWS for one week and two weeks prior to the sample collection date. Tidal range (m) was obtained by subtracting highest high tide from lowest low tide for each sampling date and each sampling location. Tidal data came from the WWW Tide/Current Predictor (http://tbone.biol.sc.edu/tide). Tidal data used for the LB stations came from Depoe Bay, tidal data used for NH stations came from Newport, and the data used for SH stations came from Heceta Head.

4.2.3. Zooplankton analysis

For analysis, larval decapods were split into two groups, the Natantia decapods and the Reptantia decapods. The Natantia decapods are shrimp-like decapods and contained the Infraorder Caridea. The Reptantia decapods are the crabs, hermit crabs, Thalassinids, and other non-shrimp like decapods. Species belonging to this group fell within the Infraorder Thalassinidae, Anomura, and Brachyura. For each family/species, the larvae were categorized as early (zoea I & II), mid (zoea III & IV),

late (zoea V & VI), or post (megalopae) larvae. Analyses were conducted using the species-stage combination of each individual. For community structure analysis only species-stage individuals that occurred more than once were included in analyses. In modeling individual responses to models, only species-stage individuals that occurred in twenty ore more samples were used in analyses.

4.2.4. Community Structure Analysis

Community structure analysis was conducted in R version 2.12.2 using redundancy analysis (RDA; Legendre and Legendre 1998). RDA is a constrained ordination that searches for linear combinations of explanatory variables that best explain the variation of the dependent variable matrix (Legendre and Legendre 1998). RDA was used to relate decapod meroplankton assemblage structure to a suite of predictor variables. To properly assess the statistical relationship between species composition and the explanatory variables via RDA, the abundance data was Hellinger-transformed to reduce the weight accorded to rare species (Legendre and Gallagher 2001). Significance of explanatory variables was determined with permutation ANOVA with 1000 random runs.

4.2.5. Species response models

Hyper Niche version 2.13 was used to model the relationship between abundance of each meroplankton group and multiple predictor variables. We used the method of Non-Parametric Multiplicative Regression (NPMR) to model species

responses to the predictor variables. Species response models such as least-squares multiple linear regression, generalized linear models, and generalized additive models are often additive and accommodate interactions with terms that include more than one predictor. However, including the interaction terms in these models is a challenge. NMPR parsimoniously models complex interactions between predictors through the use of a multiplicative kernel smoothing technique, thus eliminating the need to specify interactions (McCune 2006). The software package HyperNiche (McCune and Mefford 2009) performs an iterative step-wise search through possible models to create multiple best models. With the addition of each new predictor variable, the variables already in the model are evaluated for removal or adjustment in importance. To guard against overfitting, HyperNiche uses leave-one-out cross-validation in the process of variable selection (McCune 2006). In addition to cross-validation, parsimony in the number of predictors is controlled by setting a minimum average neighborhood size and by setting an improvement criterion. Model quality is evaluated with a cross-validated R^2 value (xR^2).

We used NPMR with a local model based on a local mean estimator with a Gaussian weighting function. We modeled the relationships between twelve predictor variables and the abundance of individuals in each meroplankton group. The percentage improvement criterion for including new predictors in the model was 5% and the minimum average neighborhood size was set at 0.05(n). The importance of predictors in the 'best' NPMR models was evaluated with sensitivity analyses, and Monte Carlo randomization tests with 100 simulation runs were conducted to examine

the statistical significance of models. The sensitivity analysis is a unit-less ratio represented by differences in the response and predictor variables that are scaled to their respective ranges. It is obtained by measuring the change in response variable when the predictors are nudged up and down from their observed values. A sensitivity value of 0 is produced when nudging a predictor has no measurable effect on the response and a value of 1 is produced when nudging a predictor results in a change in response of equal magnitude (McCune 2006; McCune and Mefford 2009). Based on NPMR model outputs, contour plots of individual abundance for each species-stage were created using model predictor variables that had a sensitivity of 0.1 or higher. Since contour plots are a two variable representation of larval abundance, it is important to note that contour plots give the most accurate representation of larval abundance with respect to predictor variables for models with two variable solutions. In cases where models have more than two predicator variables the contour plots give a sense of the relationships of individual abundance to predictor variables but may not capture all possible interactions.

4.3 RESULTS

4.3.1. Environmental variables

Across all sampling locations and dates, the closest station sampled was 2.3 km from shore and the furthest station sampled was 27.4 km from shore. Across all samples, the deepest part of the water column that the net opened for sampling was 88m and the shallowest part was 9.8 m. Dissolved oxygen (hereafter DO) levels

ranged from 1.07 to 9.78 ml/L across all samples (Figure 4.2). Bottom dissolved oxygen (hereafter BDO) ranged from 1.03 to 3.69 ml/L. Salinity and temperature ranged from 27.6 to 34.0 ppm and 6.74 and 11.40ºC respectively with the mean and median at 33.3 and 33.6 ppm, and 7.8 and 7.6ºC respectively. Over the sampling period, the greatest tidal range was 3.8 m and the smallest tidal range was 1.8 m. Mean and median upwelling intensity on the day of sampling and two days prior to sampling was 29.3 and 25 m^3/s/100m, and 29.5 and 14 m^3/s/100m respectively. The slope of CWS for one week prior to sampling was negative in nearly all samples indicating upwelling conditions, while the slope of CWS for two weeks prior to sampling had more positive occurrences indicating relaxation events.

4.3.2. Community structure of Reptantia decapod larvae

The RDA of the Reptantia decapod larvae explained 18.7% of the total variance in the taxon distribution (Table 4.2) and the first three RDA axes contributed 9.7% of the variance (Table 4.3). Permutation ANOVA results reveal that latitude, date, distance, depth, DO, BDO, temperature, tide, upwelling intensity two days prior to sampling, and cumulative wind stress for one week prior to sampling (hereafter CWS1w) were significant contributors (p-value <0.05) to Reptantia decapod larval community structure (Table 4.4).

The variables associated with RDA axis one (i.e. having larger magnitude loadings with RDA1) were date, upwelling intensity, distance from shore, DO and CWS1w (Figure 4.3 and Table 4.5). Date and upwelling were negatively associated

with axis one, while distance from shore and CWS1w were positively associated with axis one (Figure 4.3 and Table 4.5). The variables associated with RDA axis two were BDO, temperature, depth and DO. Temperature, depth, and BDO had a negative association with RDA2 while DO had a positive association.

Temperature, depth, and BDO were positively correlated with each other and negatively associated with DO (Figure 4.3 and Table 4.5). The species that were positively associated with temperature, depth, BDO (i.e., RDA2) were *Cancer gracilis/antennarius* post larvae, and *Emerita* analoga early larvae (i.e., negative loadings ~0.3 on RDA2). The species positively associated with DO (i.e., having positive loadings on RDA1 and RDA2) were *Fabia subquadrata* early, late, and post larvae, and late larvae of *Cancer magister* and *Cancer productus* (Table 4.6).

Upwelling intensity was negatively associated with distance from shore and CWS1w (Figure 4.3 and Table 4.3). The species positively associated with upwelling (i.e., having negative loadings on RDA1) were *C. magister* mid stage larvae, *Lophopanopeus bellus* mid stage larvae, *Neotrypaea californiensis* mid and late stage larvae, and *Pagurus* spp. early, mid, and late larvae. *Cancer magister* post larvae, *Pugettia* spp. early and mid larvae had weakly negative associations with upwelling and weakly positively associations with distance from shore and CWS1w (i.e., having positive loadings on RDA1) (Table 4.6).

4.3.3. Community structure of Natantia decapod larvae

The RDA of the Natantia decapod larvae explained 20.4% of the total variance in the taxa distribution (Table 4.7) and the first three axes contribute 15.6% of the variance (Table 4.8).

The permutation ANOVA results for Natantia decapod larvae revealed latitude, sampling date, distance from shore, sampling depth, BDO, upwelling intensity two days prior to sampling, and CWS1w to be significant (p-value <0.05) explanatory variables (Table 4.4). Upwelling intensity the day of sampling was marginally significant (p=0.056). The variables associated with RDA axis one (i.e., having higher magnitude loadings on RDA1) were date of sampling, and BDO (Figure 4.4 and Table 4.9). Upwelling intensity, which was only marginally significant, also had a positive association with axis 1 (Table 4.9). The variables with the largest magnitude loadings on RDA axis two were upwelling strength two days prior to sampling, latitude, CWS1w, and distance from shore (Figure 4.4 and Table 4.9).

Distance from shore, latitude, BDO, and CWS1w were positively associated with RDA2 (Figure 4.4) and had larger positive loadings on RDA2 (Table 4.9). Upwelling intensity two days prior to sampling and depth were negatively associated with RDA2 (Figure 4.4 and Table 4.9). The larvae positively associated with distance and CWS1w (i.e., having positive loadings on RDA2) were Hippolytidae early larvae (Table 4.10). The larvae negatively associated with these variables (i.e., having negative loadings on RDA2), and positively associated with upwelling intensity and depth were Crangonidae mid and post larvae (Table 4.10).

4.3.4. Reptantia decapod larvae - Individual associations with environmental variables

Thirty two different species-stage combinations of larvae were identified belonging to 8 different genera: *Cancer*, *Emerita*, *Fabia*, *Lophopanopeus*, *Neotrypaea*, *Pachycheles*, *Pugettia*, and *Pagurus*, and the family Galatheidae (Table 4.11). When present in samples, the five most abundant species-stage individuals were *Neotrypaea californiensis* early, mid and late stage larvae, *Fabia subquadrata* late stages and *Cancer magister* mid stage larvae. With respect to their occurrence in samples, the five species-stages that occurred in most samples were *N. californiensis* early and mid stage larvae (52% and 28% of samples), *Cancer productus/oregonensis* post larvae (32% of samples), *Cancer gracilis/antennarius* post larvae (25% of samples), and *Pagurus* spp. mid stage larvae (25% of samples).

NPMR models were run on only 15 species-stage combinations as these were the individuals that occurred in a minimum of 20 samples (Table 4.12). With the exception of *Pugettia* spp., non-parametric multiplicative regression models explained 17% to 46% of the variation in individual abundance and Monte Carlo randomizations for all final models indicated that models were statistically significant ($p<0.05$). The final models for each taxon along with the sensitivities of predictor variables, and model xR^2 and p-value are indicated in Table 4.12. Selection of final models was decided when an additional 3% of the variation (xR^2) in a model was not explained by the addition of another predictor variable.

Predictor variables that appeared among the top two predictor variables in models across species and larval stages were CWS1w and cumulative wind stress for two weeks prior to sampling (CWS2w), depth, distance from shore, DO and BDO, temperature, and upwelling intensity (Table 4.12). Of the 15 species-stage larval combinations, two had four variable model solutions and three had two variable models while the remaining ten had three variable model solutions.

Among the top two explanatory variables for individual abundance of *Cancer* species were CWS1w, CWS2w, upwelling, depth, BDO, and temperature (Table 4.12). *Cancer gracilis* post larvae and *Cancer magister* early larvae had depth and CWS explaining individual abundance. Both larvae had a peak in larval abundance at shallower depths, 40m, when CWS was strongly negative indicating persistent upwelling conditions (Figure 4.5 a and b). For *C. magister* mid stage larvae upwelling intensity and CWS explained individual abundance, but highest larval abundance occurred at weaker upwelling (Figure 4.5 c). *C. magister* post larvae and *C. productus* post larvae both had BDO among the two most important predictor variables (Figure 4.6 a and c). Contour plots of larval abundance of both *Cancer* species show two peaks in abundance, one at BDO of 2 ml/L and one at BDO of 3.5 ml/L. *C. magister* had higher larval abundance when the bottom of the water column was more oxygenated (BDO >3ml/L) while the two peaks for *C. productus* at different BDO values seemed to have similar abundance. At BDO of 3.5 ml/L *C. magister* post larvae were found at depths ranging from 10 to 60 m, while at BDO of 2 ml/L highest larval abundance occurred above 40 m. *C. productus* post larvae were found at similar

depths, stretching from 10 m to 60 m with a peak at approximately 30 m, at both BDO levels. The next most important predictor for *C. magister* post larvae abundance was temperature (Figure 4.6 b). There were two peaks in *C. magister* abundance at approximately 8.5 and 11ºC.

Fabia subquadrata late larval abundance was explained by upwelling intensity, distance from shore, and tide (Table 4.12). Larval abundance for *F. subquadrata* late larvae was greatest at higher upwelling intensities and closer to shore (Figure 4.5 e). For early larvae of both *Lophopanopeus bellus* and *Neotrypaea californiensis* DO was an important predictor variable. Both larvae had highest larval abundance in more oxygenated waters (Figure 4.6 e and f). *L. bellus* had highest abundance when DO levels were above 8 ml/L and *N. californiensis* had highest abundance when DO levels were above 4 ml/L. Other important predictor variables for *L. bellus* larvae were BDO and depth (Figure 4.6 d). Like *C. productus* post larvae, *L. bellus* early larvae had two peaks in the BDO contour plot. However, unlike *C. productus*, the second peak at lower DO values was restricted to shallower waters. When BDO values were around 2.5 ml/L, *L. bellus* larvae were found in shallower waters (<25 m) while when BDO values were around 3.5 ml/L larvae were found as deep as 50 m. For *N. californiensis* early larvae, important predictors other than DO were distance from shore and the slope of CWS1w. Highest larval abundance occurred at strongly negative CWS (persistent upwelling conditions) and close to shore (<10 km) (Figure 4.5 g). Mid and late stage *N. californiensis* larvae both had CWS1w and distance as important predictor variables. While peaks in larval abundance still

occurred at negative CWS values, indicating upwelling conditions, the CWS was not as negative (not as persistent upwelling) as for early stage *N. californiensis* larvae and peaks in abundance stretched further offshore than early larvae (Figure 4.5 h and i). *N. californiensis* mid stage larval abundance was also influenced by temperature, having a peak in abundance at temperatures around 10ºC (Figure 4.6 g).

Pagurus spp. early larval abundance was explained by a two variable model solution with distance and upwelling as predictor variables (Table 4.12). Larval abundance was highest at stronger upwelling intensities and the peak in abundance occurred closer to shore with a focus around 5 km from shore (Figure 4.5 j). Mid, late, and post larvae of *Pagurus* spp. had three variable model solutions with CWS1w as the main predictor for all three stages and BDO and distance from shore as the next most important predictors for mid and late stage larvae. Highest abundance of *Pagurus* spp. mid stage larvae occurred when BDO concentrations were around 2.3 ml/L and late stage larvae had a peak when BDO concentrations were less than 2 ml/L (Figure 4.6 h and i). *Pagurus* spp. mid stage larval abundance had two peaks in abundance with respect to CWS1w. One peak occurred at strongly negative CWS1w slope and the other peak at a slightly less negative CWS1w slope (Figure 4.7 a). Late stage and post larvae of *Pagurus* spp. also had two peak in abundance with respect to CWS1w but the peaks for both later stages occurred at less negative CWS1w slopes than the mid stage larvae (Figure 4.6 i, Figure 4.7 b). Like *N. californiensis* mid and late stage larvae, abundance peaks for *Pagurus* spp. mid stage larvae stretched from the nearshore to ~15km offshore. *Pagurus* spp. post larvae had temperature and tide as the

second and third model predictors, and abundance peaked at temperatures around 10ºC (Figure 4.6 j). Like *Pagurus* spp. early larvae, *Pugettia* spp. early larvae also had a two variable model solution. However *Pugettia* had depth and BDO as the model predictor variables and the model was not significant (p=0.089).

4.3.5. Natantia decapod larvae - Individual responses to environmental variables

The Natantia decapod larvae in samples belonged to two families, Crangonidae and Hippolytidae (Table 4.13). The most abundant individuals were mid stage larvae of both the Crangonid and Hippolytid carideans and both groups were also among the most common individuals across samples. Crangonidae mid stage larvae occurred in 69% of samples and Hippolytidae mid stage larvae occurred in 57% of samples. The third common group was the Hippolytidae early larvae.

The NPMR models explained 10 to 45% of the variation in Natantia decapods larval abundance (Table 4.14) and all models were significant ($p<0.05$). Abundance of early, mid and late stage Crangonidae larvae was captured by three variable solution models. For Hippolytidae larvae early and late stage larval abundance was captured by two variable solution models and mid stage larval abundance was captured by a three variable solution model. Crangonidae larval abundance was influenced by DO levels. The most important variables explaining individual abundance of early larvae were salinity, BDO, and upwelling intensity two days prior to sampling. Larval abundance peaked when BDO levels were around 2.5 ml/L and salinities were close to 33 ppm (Figure 4.7 h). Both mid stage and late stage larvae had DO explaining individual

abundance. Mid stage larvae peaked at higher DO levels than late stage larvae (Figure 4.7 i and j). Mid stage larvae also had distance from shore and upwelling intensity as important predictors while late stage larvae had upwelling intensity two days prior to sampling and depth as predictor variables. A peak in mid stage larval abundance occurred at strong upwelling intensities and within 15km from shore (Figure 4.7 c). Late stage larvae peaked when upwelling intensity two days prior was weak and larval abundance was stretched down the water column to 60 m (Figure 4.7 d). In contrast to Crangonidae NPMR models, Hippolytidae models did not include DO as an important predictor of individual abundance. Hippolytidae early larvae had depth and distance from shore as predictor variables. Highest numbers of Hippolytidae early larvae were found closer to shore, around 5 km, and concentrated around a 40 m depth (Figure 4.7 e). Mid stage larvae had distance from shore and upwelling intensity as important predictors and late stage larvae had temperature and depth as important predictors. The peak in mid stage larval abundance was focused around 8 km from shore and occurred when upwelling intensity was high (Figure 4.7 f). Late stage Hippolytidae larvae occurred deeper in the water column than early stage larvae with peaks occurring near the surface and at depth around 60 m (Figure 4.7 g). Late stage Hippolytidae larvae were found in waters between 8-10ºC.

4.4 DISCUSSION

4.4.1. Factors structuring larval decapod assemblage

Dissolved oxygen levels did not reach the severe hypoxia (<0.5 ml/L) levels of 2006 and were not as persistently hypoxic as recorded in 2000-2005 (Chan et al. 2008). The lowest DO levels recorded were 1.07 ml/L but the mean and median levels were above the 1.4 ml/L mark for DO levels commonly defined as hypoxic in the literature (Diaz and Rosenberg 1995; Grantham et al. 2004). Despite the lack of severe low oxygen values, the RDA results revealed that both DO and BDO were significant explanatory variables for Reptantia decapod assemblage composition. There were more species-stages positively associated with DO than for any other explanatory variable, as revealed by the positive loadings of species-stages on both RDA axis one and two (Table 4.6) which match the orientation of DO loading on RDA1 and RDA2 (Figure 4.3 and Table 4.5). To some degree, eleven species-stages were positively associated with DO including: *Lophopanopeus bellus* early larvae, Galatheidae early larvae, *Fabia subquadrata* larvae of all stages, *Cancer gracilis* early and mid larvae, *Cancer magister* early and late larvae, and *Cancer productus* late larvae. The role of DO as an explanatory variable for community composition in Reptantia decapods may reflect the suggested heightened sensitivity of crustaceans to DO seen in the literature, in contrast to other taxonomic groups (Vaquer-Sunyer and Duarte 2008; Levin et al. 2009).

The contribution of DO as an explanatory variable of community composition for Reptantia larvae is in contrast to the Caridean decapod assemblage composition

where DO was not a significant explanatory variable (p=0.086). The lack of influence of DO on the Caridean decapods may have something to do with the ecological diversity of this group. Carideans can inhabit both benthic habitats, as infauna or epifauna, and pelagic habitats (Bauer 2004). The Infraorder Caridea also contains many benthic species and pelagic species that are found in deep ocean waters (e.g. King and Butler 1985; Hendrickx and Estrada-Navarrete 1989). Many larval decapods including Carideans undergo migration within the water column and are thus exposed to varying water properties (Queiroga and Blanton 2004; Schwamborn et al. 2008; dos Santos et al. 2008). With such a wide variety of habitats, Carideans may encounter a range of oxygen levels and may thus be adapted to function within a broad range of environmental conditions. Carideans found in deep water benthic habitats or in deep water pelagic habitats likely encounter low oxygen levels. Benthic marine habitats experience naturally low oxygen levels as a result of undercurrents that carry low oxygen waters from deeper water masses (Levin et al. 2009). In the California Current System upwelling brings low oxygen waters into the nearshore region (Chan et al. 2008). Indeed, species that inhabit low oxygen habitats have adaptations for living in those habitats (Levin et al. 2009). For example, in oxygen minimum zones, midwater organisms do not produce reduced biomass as a result of low oxygen levels (Childress and Seibel 1998). Some benthic fauna have been shown to tolerate oxygen levels in the range of 0.5 to 1.0 ml/L for days to weeks (Baden et al. 1990; Rosenberg et al. 1991). A study of continental slope decapod crustaceans in the Gulf of California found high species occurrence, particularly of Carideans, in the hypoxic depth range

and concluded that low oxygen levels are not an impediment for rich fauna (Hendrickx 2001).

Oxygen, however, was not the only explanatory variable contributing to larval Reptantia decapod assemblage composition. Community composition of both Reptantia decapods and Caridean decapods was influenced by a multitude of environmental variables. Reptantia decapods were influenced by more environmental variables than the Carideans. All measured environmental variables except salinity ($p=0.216$) and the CWS2w ($p=0.214$) were strongly associated with Reptantia decapods. BDO, temperature, depth, and CWS1w were associated with each other and the larval group most strongly associated with these variables was *Cancer antennarius*/gracilis post larvae. As these variables increased so did the abundance of *C. antennarius*/gracilis post larvae. Date and upwelling were positively associated with each other and the larvae associated with these variables were mid stage larvae of *C. magister* and *Lophopanopeus bellus*, mid and late stage larvae of *N. californiensis*, and all *Pagurus* spp. larval stages. Distance from shore and CWS1w were positively associated and the larvae most closely associated with these variables were *Pugettia* spp. early and mid larvae. As with the Reptantia community, the Caridean larval community was also influenced by date of sampling, distance from shore, depth, BDO, upwelling intensity two days prior to sampling and CWS1w. Similarly to the Reptantia community, the Caridean community was not influenced by salinity ($p=0.087$) or CWS2w ($p=0.999$). However, unlike the Reptantia decapods, Caridean community composition was not influenced by temperature ($p=0.291$), tide ($p=0.232$),

DO (p=0.086), and it was marginally influenced by upwelling intensity (p=0.056) the day of sampling. The pattern of fewer environmental variables influencing the Caridean community may have to do with larvae representing species that occupy a diversity of habitats and are therefore adapted to a range of conditions whereas the Reptantia community has many individuals that are intertidal or subtidal but in shallower subtidal depths than the Carideans (Table 4.15).

4.4.2. Generality of Results

How do these results compare to other published studies? There are some studies in upwelling systems that have found a multitude of environmental variables to be important to community composition of zooplankton and micronekton (Phillips et al. 2009; Manríquez et al. 2011). A study off the coast of Chile found significant correlations between temperature, oxygen, chl-a, and OMZ depth, and zooplankton community descriptors (Manríquez et al. 2011). In the CCS, a study of micronekton community structure found that distance from shore, seafloor depth, temperature, and salinity all influenced community structure (Phillips et al. 2009). As far as meroplankton and larval decapod communities are concerned, there have been studies in the CCS, but these studies focus on mechanisms of transport and address specific questions, such as the role of upwelling in larval dispersal (Morgan et al. 2009a, 2009b; Shanks and Shearman 2009). A result of this body of literature is an emerging understanding of larval cross-shore and water column distributions. These studies show that larvae are generally found closer to shore in the inner shelf with few larvae

found in surface waters, and these patterns hold regardless of upwelling or downwelling conditions. In other coastal systems, studies on communities of larval decapods and other meroplankton have taken a similar approach to those studies of the CCS by focusing on larval distributions in relation to upwelling. For example, a study of larval decapods on the Portuguese coast found inshore species were retained near the shelf despite upwelling conditions, and attributed this retention to diel vertical migration behavior of larvae (dos Santos et al. 2008). A study on the coast of Brazil also found larval decapods to be most abundant nearshore, but this study suggested an association with upwelling due to a positive correlation between larval abundance and chl-a variables (Yoshinaga et al. 2010). Few field studies in the CCS have taken a descriptive approach on the association of meroplankton to a multitude of environmental variables. Given that meroplankton species play a role in planktonic food webs, understanding how various oceanographic conditions are associated with community structure and individual abundance is important.

4.4.3. Factors contributing to individual abundance

The community structure analysis (RDA) revealed which environmental variables are predictors of community structure. It highlighted associations between environmental factors and provided a broad picture of how species respond to environmental factors. To gain a specific picture of what environmental factors are most important for species, we used non-parametric multiplicative regressions (NPMR). This habitat model analysis revealed which environmental variables were

most important in explaining individual abundance. Many of the same environmental variables that were associated with community structure were also associated with species abundance, however some environmental variables occurred more commonly in species abundance models. One noteworthy pattern was the role of upwelling either as upwelling intensity or the slope of cumulative wind stress for one week (CWS1w) or two weeks (CWS2w) prior to sampling appearing as the most commonly occurring explanatory variables for Reptantia and Natantia decapods. At least one of these three variables showed up in 13 of the 15 species-stage reptantia decapod models, with CWS1w occurring most frequently. In most species-stage models, higher larval abundance was associated with a more negative CWS1w (indicative of stronger more persistently upwelling winds) or with greater upwelling intensity values (Figure 4.6). In some species there was a trend towards earlier larval stages being associated with stronger upwelling conditions (more negative CWS1w values) than later life stages. This was the case for *C. magister* (Figure 4.6 b and c) and *N. californiensis* (Figure 4.6 g to i) where early larvae are associated with more negative CWS values than mid or late larvae. *Pagurus* spp. mid larvae were associated with more negative CWS1w values than *Pagurus* spp. post larvae (Figure 4.7 a and b). In species abundance models for Natantia decapods, upwelling intensity was a frequently occurring predictor found in four of six species-stage models. There was also a trend of earlier larval stages associated with stronger upwelling. Abundance of mid stage Crangonidae larvae peaked at stronger upwelling conditions (70 m^3/s/100m) while late stage larvae peaked at less strong upwelling conditions (20 m^3/s/100m) two days prior to sampling.

Previous studies on larval distributions on the Oregon or California coast have noted the occurrence of decapod larvae and other meroplankton in nearshore waters regardless of upwelling or downwelling conditions (Morgan et al. 2009a; Shanks and Shearman 2009), and have noted increased recruitment in Paguroidea and Grapsidae decapods in stronger upwelling years (Morgan et al. 2009a). These studies were conducted during stronger upwelling conditions than those recorded in the present study. The upwelling conditions noted in the present study peaked at 100 m^3/s/100m. These are strong upwelling conditions but not as strong as those recorded in other studies. The Shanks and Shearman (2009) study conducted during 2007 in southern Oregon recorded upwelling intensity values of 200 m^3/s/100m or more in the upwelling season. Studies conducted during 1996 to 2002 in central California and in 2006 in northern California recorded values that ranged from 100 to 200 m^3/s/100m (Morgan et al. 2009a, 2009b). The focus of these studies was to test the recruitment-limitation hypothesis and they thus focused on cross-shore larval distributions in relation to upwelling currents. However, detailed investigations of patterns in abundance with relation to gradients in upwelling intensity are lacking. Upwelling conditions are generally associated with a multitude of other oceanographic parameters, such as increased nutrients, colder temperatures, and higher chlorophyll-a levels (Chase et al. 2002). The patterns observed in the present study of larvae being associated with stronger upwelling conditions may reflect associations with the multitude of ocean conditions that upwelling or stronger/more persistent upwelling winds represent.

In other parameters, the observations from this study agree with literature observations on decapod and meroplankton distributions in the CCS. Among other explanatory variables that had frequent occurrence in species abundance models were distance from shore, depth, and BDO. Across models, peaks in larval abundance were within 15 km from shore, which is within the inner shelf region (Figure 4.1). There also appeared to be a trend of early larval stages having peaks that were more focused and occurred closer to shore (within 10 km) while later stages had abundance that was less focused and stretched a further distance (to 15 km). For example, *N. californiensis* and *Pagurus* early larvae had peaks occurring at 10 km from shore while mid and late stages of the same species spread out to 15 km (Figure 4.6 g-j and Figure 4.7a). Observations of abundance peaks in the nearshore region with earlier larval stages in particular occurring closer to shore, agree with findings of decapod cross-shore distributions in other published studies (Morgan et al. 2009a, 2009b). In models where depth was an explanatory factor, larval abundance peaks were spread out over a range of depths. Peaks of early larval stages seemed to occur at shallower depths, ~20 m, than later stages (peaks at 30-40 m). For example, *Cancer magister* early stages had a peak around 20 m (Figure 4.6 b) while *Cancer gracilis* and *Cancer productus* post larvae had peaks at 40 m (Figure 4.6 a and d). In nearshore occurring decapod larvae, Morgan et al (2009b) also observed larvae in deep waters throughout their development. They also observed later stages occurring in deeper waters than earlier stages. They also recorded onshore and alongshore flows during their study and suggested that the deep distributions of larvae allow for nearshore retention (Morgan

et al. 2009b). Models of copepods in upwelling systems suggest that nearshore retention is achieved by ontogenetic and diel migrations (Peterson 1998). Ontogenetic migrations allow retention through development of early life stages in deep onshore moving waters. Through diel migrations individuals maintain position by alternating time in onshore moving deep waters and offshore moving surface waters (Peterson 1998). For decapod larvae, the time that later stages spend in deep waters can offset the offshore transport of early stages that are in shallower waters (Morgan et al. 2009b).

Bottom dissolved oxygen was as common an explanatory variable in species abundance models as was distance from shore. *Cancer magister* post larvae had a peak at bottom oxygen values of ~3.5 ml/L, *Cancer productus* post larvae and *Lophopanopeus bellus* early larvae had peaks at BDO values of ~2 and 3.5 ml/L, and *Pagurus* mid and late stage larvae had peaks at BDO values of 2.5 ml/L or less (Figure 4.5). This is striking as lab experiments with *Cancer antennarius* in the first chapter showed very high sensitivity of larvae to hypoxia. This may be attributed to a difference in larval stages. The *Cancer antennarius* larvae exposed to hypoxia in experiments were early larvae while field results show an association of *Cancer productus* and *Cancer magister* post larvae with lower BDO values. Also, lab experiments represent direct exposure of larvae to hypoxia, while field findings of an association of larvae with BDO do not necessarily reflect a direct association of BDO with larval abundance. A hint of this can be seen in *L. bellus* early larvae which had a peak in abundance when BDO values were at ~2.5 and 3.5 ml/L but also had a peak in

abundance when ambient dissolved oxygen values were at ~8 ml/L. Thus, peaks in abundance do not necessarily indicate a direct exposure between the larvae and bottom oxygen values, but they may represent an indirect effect of BDO playing a role on water column distribution and/or community structure. For example, hypoxic or anoxic waters below the pycnocline can affect the vertical distribution, diel migration, and abundance of zooplankton and copepods. During hypoxic events in Chesapeake Bay and the Louisiana shelf, daytime samples from the lower water column had few organisms whereas during oxygenated conditions zooplankton and copepods were present or in high abundance (Roman et al. 1993; Qureshi and Rabalais 2001).

There may be various possible explanations for peaks in larval abundance at low BDO values. Abundance peaks may not reflect a direct association of larvae with low BDO, but a response of larval water column distributions to BDO. Larvae may aggregate in other parts of the water column in response to low BDO levels. Another explanation is that lower BDO values may reflect stronger upwelling conditions and the association of larval abundance with BDO may reflect associations with factors related to upwelling conditions such as high nutrients or chlorophyll-a levels. Other studies have noted larval abundance associations with chl-a and productivity. High larval abundance of invertebrate larvae can occur where upwelling events are associated with high chl-a levels (Yoshinaga et al. 2010). Reduced productivity may lead to reduced densities of fish larvae (Brodeur et al. 2006, 2008). Another possibility along the lines of correlated upwelling conditions and lower BDO values, is that peaks in larval abundance when there are low BDO levels may reflect a response of larvae to

physical water properties such as upwelling fronts. Upwelling favorable conditions can create fronts where larval barnacle cyprids get concentrated (dos Santos et al. 2007).

Dissolved oxygen, unlike BDO, was not a common explanatory variable in abundance models of Reptantia decapods. Many of the species positively associated with oxygen in the community structure analyses did not have large enough samples to be used in analyses of individual abundance. For the 15 species-stages that were included in analysis of individual abundance, there were two cases where oxygen was an important predictor for larval abundance. These larvae were both early stages, but there were species-specific differences in the oxygen levels where abundance peaks occurred. *N. californiensis* had a peak around oxygen concentrations of 4 ml/L while *L. bellus* had an abundance peak at 8 ml/L (Figure 4.5 e and f). The association of early larval stages with oxygen levels may reflect the suggestions in the literature of different larval stages being differentially influenced by environmental factors (Pechenik 1999). In hypoxia studies, early stages are often more susceptible to low oxygen conditions. In the mussel *Mytilus edulis*, the median mortality time more than doubles in going from the early prodissoconch larvae to the later veliconch larvae (Wang and Widdows 1991), and in the scallop Agropecten irradians irradians tolerance to hypoxia increased with larval size (Wang and Zhang 1995). The larval stage-specific differences in association with oxygen are also reflected in the Natantia decapods, where oxygen was an important predictor in Crangonidae mid and late stage larvae, but the younger larvae were more sensitive to oxygen levels. Mid stage larvae

had a peak in abundance at oxygen levels around 5 ml/L and late stage larvae had a peak in their abundance when oxygen concentrations were below 2 ml/L. Species-specific differences in tolerance to oxygen levels have been documented for adult crabs and copepods. A study on three species of calanoid copepods found that the species *Labidocera aestiva* and *Centropages hamatus* were more sensitive to low oxygen levels than the copepod *Acartia tonsa*. Survivorship of both *L. aestiva* and *C. hamatus* decreased at oxygen levels of 1 ml/L while survivorship *A. tonsa* did not change (Stalder and Marcus 1997). In intertidal crabs, different species respond differently to emersion. *Pachygrapsus crassipes* and *Hemigrapsus nudus* compensate for emersion induced respiratory acidosis while *Eurytium albidigitum* does not (Burnett and McMahon 1987). The role of oxygen as an important predictor of individual abundance of Crangonidae decapods and not for Hippolytidae decapods may explain the marginally significant role of oxygen in Natantia community structure analyses, as these were the two families composing the Natantia community.

4.4.4. Conclusions

Much more research on the impact of oxygen on organisms has been done in laboratory studies than in field studies (Vaquer-Sunyer and Duarte 2008). Most lab studies focus on individual species responses more than on community impacts, and field studies mostly focus on benthic species or communities. Few studies have investigated the role of oxygen on the ecology of pelagic species or on community impacts in pelagic systems (Ekau et al. 2010). In general, the structure and interactions

of benthic communities, and the abundance of their individuals are generally better studied than the planktonic larval stages. In the CCS, studies have explored the physiological and biological responses of some meroplankton members to environmental conditions. Examples include studies on the nutritional condition of barnacle and mussel larvae (Phillips 2002; Emlet and Sadro 2006), on the role of temperature on larvae (Zippay and Hofmann 2009), and on the influence of ocean acidification on various larvae (O'Donnell et al. 2008; Zippay and Hofmann 2010). Fewer studies have focused on the community ecology of Meroplankton assemblages. In the CCS, the majority of field studies on meroplankton have focused on questions of transport and dispersal (Miller and Emlet 1997; Shanks and Shearman 2009; Morgan et al. 2009b). In contrast, our study attempted to explore the relationship between larval decapod assemblage composition and environmental variables with a focus on oxygen levels in a system that experiences seasonal hypoxia. We found that oxygen along with a number of environmental variables was associated with patterns of distribution and abundance in pelagic communities. In addition to including the Reptantia decapods in this study, which have been the subjects of studies on larval distributions within the context of larval dispersal, we also included Natantia decapods. The larval stage of Natantia decapods, in this case comprised of Family Crangonidae and Family Hippolytidae, has not been well studied (Haynes 1985), and in particular very little is known about the Hippolytidae family overall (Baldwin 2011). Therefore in addition to the new knowledge on Reptantia decapods, this study also provides novel knowledge of Natantia decapods.

Since the inputs of larvae to marine ecosystems can have strong effects on community structure and diversity, understanding what environmental conditions impact the planktonic larval stage of such organisms is important. Meroplankton can be important components of planktonic food webs and also serve as the dispersive stage of species in adult communities. Poor ocean conditions that affect the larval stage can affect recruitment. For example depressed recruitment of mussels along the Oregon coast in 2005 was attributed to low chlorophyll levels in nearshore waters that year (Barth et al. 2007). Climate change projections for marine systems predict various potential changes to oceanographic conditions including reduced oxygen levels (Keeling and Garcia 2002; Keeling et al. 2010), increased stratification (Manabe and Stouffer 1993; Sarmiento et al. 1998), and ocean temperatures (Solomon et al. 2007). Further, coastal upwelling systems are predicted to experience intensified upwelling (Bakun et al. 2010) and shoaling hypoxic boundaries (Bograd et al. 2008). While only touching the tip of the iceberg, this study has shown that multiple ocean conditions are important for both community structure and species abundance. We have also seen differential effects of the environment on different species and larval stages. There were trends for some factors to be dominant forces. For example, CWS was an important determinant of species abundance for the majority of individuals. Thus predicted changes in ocean conditions, such as an intensification of upwelling, may impact the planktonic life stage of organisms. In our analyses, the measured environmental variables explained 20% of the variation in community structure and between 10% and 47% of variation in individual abundance. Clearly, there are other

factors that we have not accounted for explaining community composition and individual abundance, therefore continuing to gain a better understanding of the mechanics behind the relationships between Meroplankton assemblages and the environment and between individual abundance and environmental factors remains an important area of research.

ACKNOWLEDGEMENTS

We are grateful for the assistance, guidance, and instruction various people provided. Charlie Miller, Jesse Lamb, and Cheryl Morgan provided instruction on plankton sorting techniques and zooplankton identification guidance. Jennie Yoder, Rachel Mahler, and Vathani Logendran assisted in sorting plankton samples. Elizabeth Daly, Jennifer Fisher, Ric Brodeur, and Bill Peterson provided useful discussion and suggestions for data analysis. Scott Heppell and Vince Politano provided laboratory space to carry out sample processing. This research was supported by the Natural Sciences and Engineering Research Council of Canada, Oregon State University Department of Zoology, and in part by grants from the David and Lucile Packard Foundation, the Gordon and Betty Moore Foundation, the Wayne and Gladys Valley Foundation, the Andrew W. Mellon Foundation, and Oregon Sea Grant. This is publication number XXX from the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO), funded primarily by the Gordon and Betty Moore Foundation and the David and Lucile Packard Foundation.

Table 4.1 Sampling schedule and locations. Column heads indicate cross-shore station locations. E.g. NH-5 corresponds with Newport Hydrogline station 5. E.g. NH-5 corresponds with Newport Hydroline station 5.

	-3	-5	-7	-10	-15
27 May 2008				NH	
29 May 2008		NH		NH	
30 May 2008		SH	SH	SH	
21 June 2008		NH	NH	NH	
26 June 2008		SH		SH	
27 June 2008		NH		NH	
2 July 2008		SH		SH	
3 July 2008		NH		NH, LB	
16 July 2008		SH			
25 July 2008		NH			NH
30 July 2008	SH	SH		SH	
25 Aug. 2008		NH			
27 Aug. 2008		NH			
28 Aug. 2008		NH		NH	
31 Aug. 2008				LB	
1 Sept. 2008		LB	LB		
12 June 2009		NH	NH	NH	
3 July 2009		NH		NH	
2 Aug. 2009		NH			
22 Aug. 2009		NH		NH	

Table 4.2 Redundancy analysis (RDA) proportion of the variance explained by constraining variables for Reptantia decapod assemblage.

	Inertia	Proportion
Total	32.000	1.000
Constrained	5.990	0.187
Unconstrained	26.010	0.813

Table 4.3 RDA results for Reptantia decapod larvae. Proportion of the variance explained by constraining variables for the first six redundancy analysis axes.

	RDA1	RDA2	RDA3	RDA4	RDA5	RDA6
Eigenvalue	1.699	0.789	0.632	0.618	0.466	0.374
Proportion Explained	0.053	0.025	0.020	0.019	0.015	0.012
Cumulative Proportion	0.053	0.078	0.097	0.117	0.131	0.143

Table 4.4 Permutation ANOVA results for Reptantia decapod larvae (Brachyura, Anomura, Thalassinidea) and Natantia decapod larvae (Caridea). F statistic and p-values are provided. Non-significant values ($p<0.05$) are bolded.

	Reptantia decapod larvae		Natantia decapod larvae	
Explanatory variable	F statistic	P value	F statistic	P value
Latitude	2.131	0.001	3.136	0.002
Date	6.080	0.001	3.094	0.004
Distance	3.399	0.001	3.389	0.002
Depth	2.282	0.001	2.595	0.006
Oxygen	2.447	0.001	1.757	**0.086**
Bottom Oxygen	2.568	0.002	3.502	0.002
Temperature	2.309	0.003	1.192	**0.291**
Salinity	1.240	**0.216**	1.789	**0.087**
Tide	1.906	0.001	1.273	**0.232**
Upwelling	1.442	0.049	1.979	**0.056**
Upwelling (2 day prior)	1.696	0.011	2.937	0.003
Cumulative wind stress slope (1 week)	1.695	0.015	2.730	0.004
Cumulative wind stress slope (2 week)	1.199	**0.214**	0.168	**0.999**

Table 4.5 Loadings for the first six redundancy analysis axes in Reptantia decapod larval community composition.

	RDA1	RDA2	RDA3	RDA4	RDA5	RDA6
Date	-0.882	0.040	0.066	0.134	0.184	-0.249
Depth	0.103	-0.407	-0.008	-0.351	0.271	-0.344
Distance	0.366	-0.129	0.015	0.628	0.118	-0.357
Latitude	0.044	0.285	-0.358	0.363	-0.345	-0.108
Oxygen	0.336	0.331	0.136	-0.014	0.074	-0.109
Bottom Oxygen	0.047	-0.509	0.152	-0.295	-0.213	-0.088
Salinity	-0.169	-0.020	0.127	-0.328	0.142	-0.216
Temperature	-0.077	-0.410	-0.251	0.109	-0.065	0.222
Tide	0.066	-0.274	0.443	0.129	0.417	0.113
Upwelling	-0.450	0.159	0.161	-0.421	0.055	-0.050
Upwelling 2 days prior	-0.285	-0.193	0.319	-0.265	-0.166	0.503
CWS1w	0.315	-0.274	-0.392	-0.001	-0.365	-0.449
CWS2w	0.029	-0.428	-0.363	-0.138	-0.295	-0.214

Table 4.6 Reptantia decapod larval species/stage associations with axes.

	RDA1	RDA2	RDA3	RDA4	RDA5	RDA6
Cancer antennarius late	-0.102	0.156	-0.029	-0.102	-0.023	0.209
Cancer gracilis early	0.169	0.170	0.172	-0.043	-0.162	-0.158
Cancer gracilis mid	0.023	0.051	0.005	0.046	0.192	0.082
Cancer gracilis/antennarius post	0.129	-0.408	-0.040	-0.135	0.320	-0.045
Cancer magister early	0.171	0.179	-0.139	0.312	0.036	0.359
Cancer magister mid	-0.475	0.104	0.032	0.323	-0.238	-0.110
Cancer magister late	0.073	0.281	-0.548	0.028	-0.176	0.114
Cancer magister post	0.159	-0.145	-0.038	0.213	0.085	-0.019
Cancer productus mid	-0.147	0.150	-0.181	0.018	-0.168	0.026
Cancer productus late	0.039	0.134	-0.296	-0.086	-0.130	0.085
Cancer productus/oregonensis post	-0.093	0.035	0.321	0.459	0.055	-0.004
Cancer spp. mid	0.062	-0.028	0.020	0.129	0.130	0.050
Emerita analoga early	-0.061	-0.272	-0.286	0.024	0.126	0.210
Fabia subquadrata early	0.330	0.391	0.120	-0.086	0.225	-0.075
Fabia subquadrata mid	0.240	0.186	0.097	-0.058	0.231	-0.154
*Fabia subquadrata*_late	0.504	0.600	0.218	-0.152	0.038	-0.092
Fabia subquadrata post	0.241	0.482	0.004	-0.208	-0.029	-0.038
Galatheidae early	0.227	0.012	-0.044	0.414	-0.344	-0.114
Lophopanopeus bellus early	0.059	0.215	0.301	0.268	-0.189	0.047
Lophopanopeus bellus mid	-0.455	0.049	0.112	0.182	0.031	-0.010
Neotrypaea californiensis early	-0.238	-0.193	0.354	-0.405	-0.286	0.173
Neotrypaea californiensis mid	-0.905	0.113	0.268	-0.074	0.049	0.056
Neotrypaea californiensis late	-0.888	0.203	-0.054	0.010	0.342	-0.213
Pachycheles pubescens early	-0.025	0.320	0.057	0.050	0.165	0.197
Pagurus spp. early	-0.269	0.046	0.155	-0.255	-0.150	0.386
Pagurus spp. mid	-0.440	0.107	-0.088	0.060	-0.030	-0.003
Pagurus spp. late	-0.679	0.259	-0.136	0.082	-0.010	-0.003
Pagurus spp. post	-0.226	0.131	-0.452	-0.239	-0.159	-0.272
Pugettia gracilis post	-0.004	-0.229	0.188	-0.134	-0.325	-0.256
Pugettia spp. early	0.132	-0.073	-0.051	0.314	0.008	-0.079
Pugettia spp. mid	0.069	-0.134	-0.014	0.130	0.044	-0.019
Pugettia spp. post	-0.173	-0.046	-0.115	-0.089	0.059	-0.207

Table 4.7 Redundancy analysis (RDA) proportion of the variance explained by constraining variables for Natantia decapod assemblage.

	Inertia	Proportion
Total	9.000	1.000
Constrained	1.839	0.204
Unconstrained	7.161	0.796

Table 4.8 Proportion of the variance explained by constraining variables for Natantia decapods.

	RDA1	RDA2	RDA3	RDA4	RDA5	RDA6
Eigenvalue	0.660	0.502	0.240	0.172	0.113	0.079
Proportion Explained	0.073	0.056	0.027	0.019	0.013	0.009
Cumulative Proportion	0.073	0.129	0.156	0.175	0.187	0.196

Table 4.9 Loadings for the first six redundancy analysis axes in Natantia decapod larval community composition.

	RDA1	RDA2	RDA3	RDA4	RDA5	RDA6
Date	0.512	-0.017	-0.101	-0.165	-0.202	0.162
Depth	0.232	-0.149	0.650	0.033	0.142	-0.052
Distance	-0.232	0.412	0.184	0.189	0.580	0.161
Latitude	0.038	0.599	-0.307	-0.249	0.234	0.336
Oxygen	-0.472	-0.099	0.039	0.026	-0.214	0.161
Bottom Oxygen	-0.290	0.245	0.215	-0.401	-0.369	-0.469
Salinity	0.183	-0.308	-0.111	0.031	-0.352	-0.079
Temperature	-0.208	0.347	0.189	-0.028	-0.269	-0.369
Tide	-0.023	-0.076	0.134	-0.321	-0.158	-0.201
Upwelling	0.578	-0.272	0.094	0.207	-0.124	0.094
Upwelling 2 days prior	0.241	-0.620	0.008	-0.111	0.285	-0.344
CWS1w	-0.056	0.525	0.206	0.294	0.071	-0.272
CWS2w	0.155	0.319	0.305	0.152	0.123	-0.442

Table 4.10 Natantia decapod larval family/stage associations with axes.

	RDA1	RDA2	RDA3	RDA4	RDA5	RDA6
Caridean early	0.353	-0.377	0.069	-0.172	0.105	-0.133
Crangonidae. early	-0.576	-1.005	-0.184	-0.063	-0.277	-0.148
Crangonidae. mid	0.648	-0.152	-0.482	-0.278	0.192	-0.032
Crangonidae. late	0.395	0.254	-0.584	0.456	-0.167	-0.153
Crangonidae. post	0.583	-0.146	0.330	0.256	0.014	-0.081
Hippolytidae. early	-0.549	0.675	0.094	-0.137	-0.045	-0.382
Hippolytidae. mid	0.842	0.158	0.185	-0.353	-0.393	-0.064
Hippolytidae. late	0.124	-0.078	0.243	0.277	-0.244	0.104
Hippolytidae. post	0.302	-0.382	0.285	0.207	0.239	-0.260

Table 4.11 Reptantia decapods – Infraorders Brachyura, Anomura, and Thalassinidae. Species-stage combinations, their abundance when present (±SD) and their percent occurrence..

Taxonomic group	Mean abundance when present per $100m^2$	Percent of samples in which group was present
Neotrypaea californiensis late	136.83 (488.92)	21
Neotrypaea californiensis mid	119.04 (349.78)	28
Fabia subquadrata late	83.18 (218.68)	19
Neotrypaea californiensis early	62.93 (114.23)	52
Cancer magister mid	23.98 (27.60)	16
Pagurus spp. mid	18.64 (25.28)	25
Pagurus spp. late	16.78 (29.29)	22
Cancer magister late	15.45 (15.71)	9
Pagurus spp. early	15.02 (16.49)	19
Emerita analoga early	13.86 (13.02)	3
Fabia subquadrata post	13.16 (12.55)	5
Cancer gracilis mid	9.86 (15.67)	3
Pagurus spp. post	8.51 (4.99)	16
Cancer productus/oregonensis post	8.23 (9.50)	32
Cancer magister early	6.16 (6.67)	12
Pugettia spp. mid	5.57 (5.38)	7
Cancer gracilis/antennarius post	5.33 (7.26)	25
Cancer spp. mid	5.24 (5.34)	1
Pugettia spp. early	5.23 (4.28)	20
Cancer productus mid	5.21 (2.56)	3
Cancer productus late	5.03 (0.44)	1
Pachycheles pubescens early	4.77 (3.60)	7
Lophopanopeus bellus early	4.70 (3.76)	18
Pugettia spp. post	4.64 (3.17)	10
Lophopanopeus bellus mid	4.43 (2.53)	8
Fabia subquadrata early	4.04 (2.24)	6
Cancer magister post	3.94 (2.99)	14
Cancer gracilis early	3.28 (1.56)	8
Pugettia gracilis post	3.07 (0.04)	1
Fabia subquadrata mid	2.72 (0.25)	1
Galatheidae early	2.71 (0.97)	3
Cancer antennarius late	2.23 (0.30)	1

Table 4.12 NPMR models of Reptantia decapod larval abundance. The first column contains species and stages. The second and third column contain the cross-validated R^2 value and p-value. Each subsequent pair of columns contain an explanatory variable in the model and the corresponding sensitivity of the explanatory variable. Explanatory variables and sensitivities are ordered by decreasing sensitivity values. Explanatory variables in models include: dissolved oxygen (DO) in ml/L, bottom dissolved oxygen (BDO) in ml/L, distance from shore (Distance) in km, depth to seafloor (Depth) in m, upwelling intensity in $m^3/s/100m$, the slope of cumulative wind stress one week (CWS1w) and two weeks (CWS2w) prior to sampling, temperature (Temp) in °C, salinity (Sal) in ppm, tidal fluctuation in m, and date.

Table 4.12

Taxonomic group	xR^2	P-value	Explanatory Variable 1	Sensitivity	Explanatory Variable 2	Sensitivity	Explanatory Variable 3	Sensitivity	Explanatory Variable 4	Sensitivity
Cancer gracilis P	0.174	0.0198	Depth	0.455	CWS2w	0.139	Date	0.010		
Cancer magister E	0.304	0.0198	Depth	0.195	CWS1w	0.152	Date	0.004		
Cancer magister M	0.464	0.0099	Upwelling	0.397	CWS1w	0.261				
Cancer magister P	0.340	0.0099	Temperature	0.412	BDO	0.380	Depth	0.058	Date	0.014
Cancer productus P	0.339	0.0099	BDO	0.376	Depth	0.164	CWS2w	0.144		
Fabia subquadrata L	0.319	0.0396	Upwelling	0.362	Distance	0.115	Tide	0.080		
Lophopanopeus bellus E	0.216	0.0297	BDO	0.410	DO	0.202	Depth	0.143	CWS2w	0.142
Neotrypaea californiensis E	0.390	0.0099	DO	0.504	Distance	0.400	CWS1w	0.167		
Neotrypaea californiensis M	0.326	0.0099	CWS1w	0.566	Temperature	0.254	Distance	0.130		
Neotrypaea californiensis L	0.422	0.0198	CWS1w	0.295	Distance	0.046	Upwelling	0.022		
Pagurus spp. E	0.201	0.0198	Distance	0.535	Upwelling	0.302				
Pagurus spp. M	0.215	0.0396	CWS1w	0.676	BDO	0.262	Distance	0.130		
Pagurus spp. L	0.297	0.0198	CWS1w	0.387	BDO	0.270	Distance	0.073		
Pagurus spp. P	0.403	0.0099	CWS1w	0.635	Temperature	0.409	Tide	0.142		
Pugettia spp. E	0.076	0.0891	Depth	0.872	BDO	0.338				

Table 4.13 Natantia decapods – Infraorder Caridea. Species-stage combinations, their percent occurrence and their abundance when present.

Taxonomic group	Mean abundance when present per $100m^2$ (±SD)	Percent of samples in which group was present
Crangonidae mid	43.36 (115.78)	69
Hippolytidae mid	31.19 (80.01)	57
Caridean early	20.41 (20.06)	2
Crangonidae early	19.94 (31.35)	31
Crangonidae late	15.96 (30.01)	23
Hippolytidae early	13.44 (23.93)	58
Crangonidae post	5.79 (6.32)	7
Hippolytidae late	4.85 (4.45)	13
Hippolytidae post	1.80 (1.15)	2

Table 4.14 NPMR models of Natantia decapod larval abundance. The first column contains species and stages. The second and third column contain the cross-validated R^2 value and p-value. Each subsequent pair of columns contain an explanatory variable in the model and the corresponding sensitivity of the explanatory variable. Explanatory variables and sensitivities are ordered by decreasing sensitivity values. Explanatory variables in models include: dissolved oxygen (DO) in ml/L, bottom dissolved oxygen (BDO) in ml/L, distance from shore (Distance) in km, depth to seafloor (Depth) in m, upwelling intensity the day of sampling and two days prior to sampling in $m^3/s/100m$, temperature in °C, and salinity in ppm.

Taxonomic group	xR2	P-value	Explanatory Variable 1	Sensitivity	Explanatory Variable 2	Sensitivity	Explanatory Variable 3	Sensitivity
Crangonidae. E	0.448	0.0198	Salinity	0.220	BDO	0.080	Upwelling 2 day prior	0.066
Crangonidae. M	0.293	0.0099	Distance	0.370	Upwelling	0.338	DO	0.219
Crangonidae. L	0.136	0.0198	Upwelling 2 days prior	1.421	Depth	0.409	DO	0.223
Hippolytidae. E	0.104	0.0099	Depth	1.391	Distance	0.386		
Hippolytidae. M	0.338	0.0198	Distance	0.20	Upwelling	0.128	Upwelling 2 days prior	0.075
Hippolytidae. L	0.158	0.0198	Temperature	0.535	Depth	0.199		

Table 4.15 Reptantia and Natantia taxonomic groups and their habitats.

Taxa	Adult habitat
Reptantia (Brachyura, Anomura, Thalassinidae) (Habitat details from Shanks (2001))	
Cancer antennarius	Pacific Rock Crab, found intertidally and subtidally to depths of 91m on gravel bottoms or kelp beds
Cancer gracilis	Graceful crab, found subtidally to depths of 143m on sand or mud
Cancer magister	Dungeness crab, found in eelgrass beds and subtidally on sandy bottoms
Cancer productus	Red Rock Crab, found intertidally and subtidally to depths of 79m on boulder beaches or sandy bottoms
Emerita analoga	Pacific Sand Crab, in sandy beaches in the surf zone
Fabia subquadrata	Mussel crab, lives commensally with mollusks in the intertidal to and subtidally to 220m
Family Galatheidae	Squat lobsters, from the intertidal to abyssal plains in rocky or silty areas.
Lophopanopeus bellus	Black-clawed Crab, from low intertidal to 80m depths under rocks, and sandy or gravel habitats
Neotrypaea californiensis	the Bay Ghost Shrimp, burrows in the middle to low intertidal zone of bays and estuaries.
Pachycheles pubescens	Pubescent Porcelain Crab, found in the intertidal zone to a depth of 55m in the open coast or inshore areas with strong currents
Pagurus spp.	hermit crabs, mostly found in the intertidal
Pugettia spp.	kelp crabs, intertidal to 140m deep
Natantia decapods (Caridea) (habitat details from Bauer (2004))	
Crangonidae	Cold water group. Highly benthic, soft bottom habitats (sand, mud, gravel). Bottom fauna of north temperate to arctic continental shelves.
Hippolytidae	Epibenthic bottom dwellers. Do not burrow. Perch on or under rocks, algae, or cling to sea grasses or sessile invertebrates. Depth distribution is from littoral zone to shelf depths with some deep-sea species.

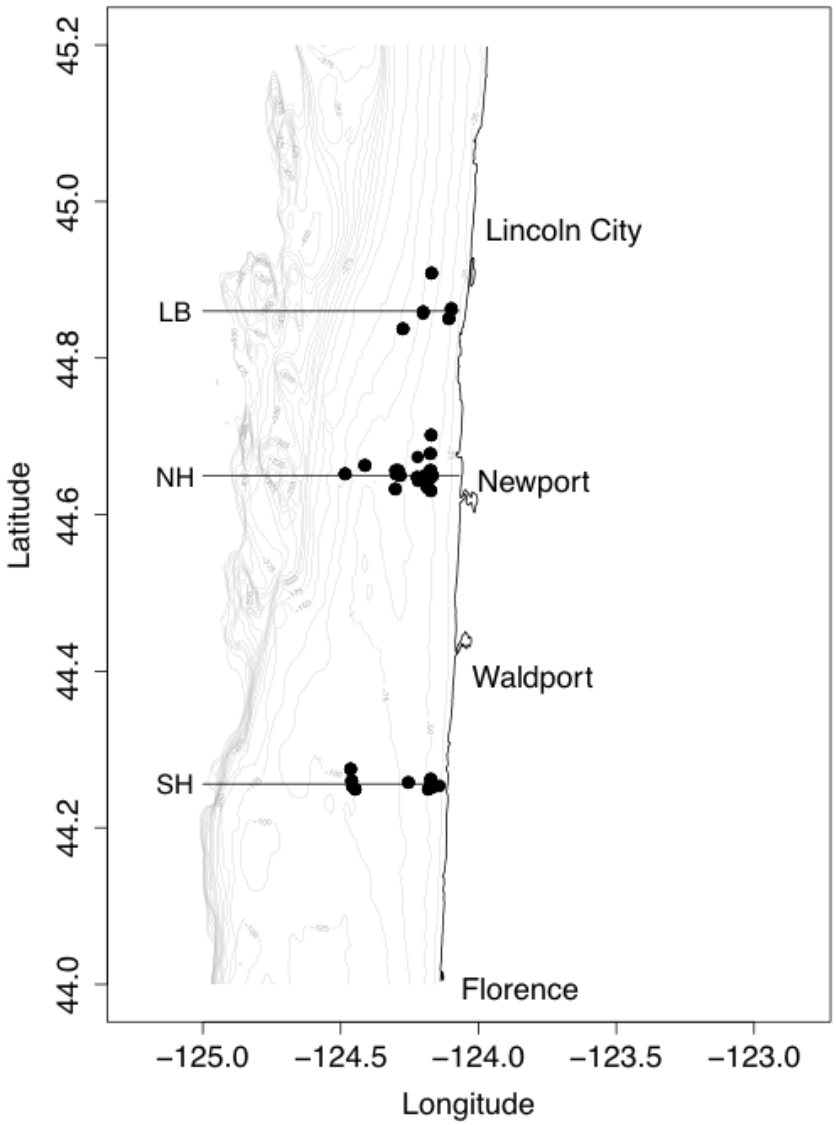

Figure 4.1 Sampling on the Oregon coast occurred along three transect lines: SH (Strawberry Hill), NH (Newport Hydroline), and LB (Lincoln Beach) with the highest frequency of sampling occurring along the NH line.

Figure 4.2 Boxplots of explanatory variables with means (triangles), medians (solid lines), 25% and 75% quantiles, and outliers outside of the interquartile range.

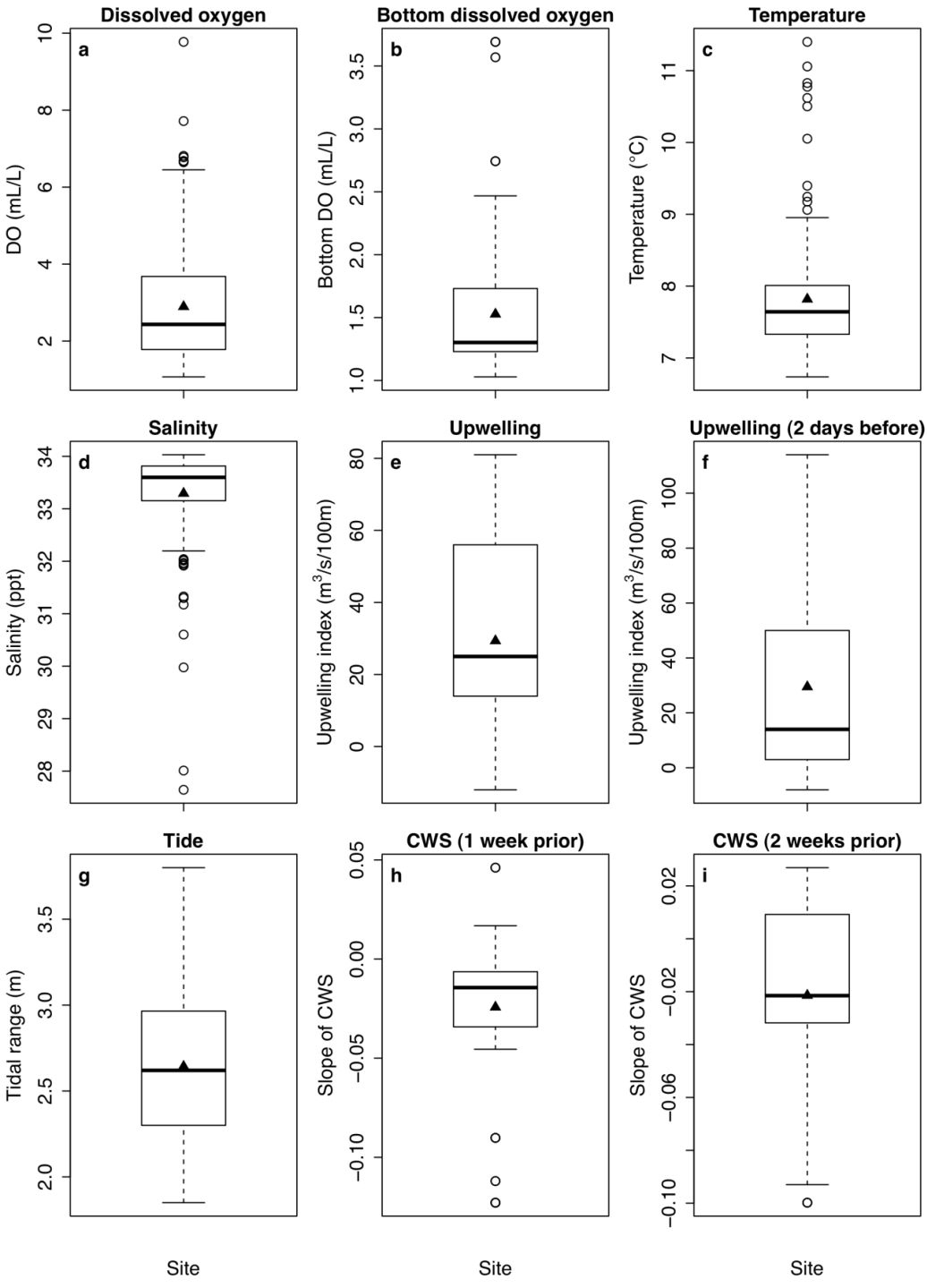
Dissolved oxygen
a
DO (mL/L)
Bottom dissolved oxygen
b
Bottom DO (mL/L)
Temperature
c
Temperature (°C)
Salinity
d
Salinity (ppt)
Upwelling
e
Upwelling index (m3/s/100m)
Upwelling (2 days before)
f
Upwelling index (m3/s/100m)
Tide
g
Tidal range (m)
CWS (1 week prior)
h
Slope of CWS
CWS (2 weeks prior)
i
Slope of CWS
Site
Site
Site

Figure 4.2

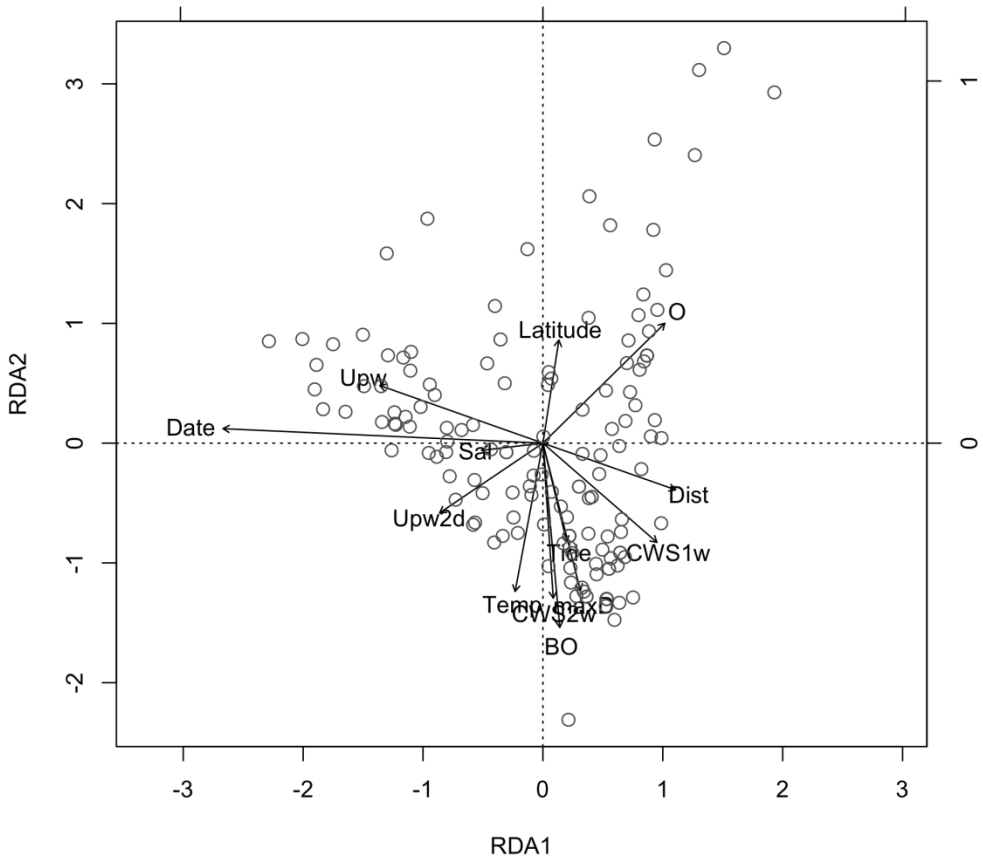

Figure 4.3 Redundancy analysis (RDA) biplot axis 1 and 2 for Reptantia decapods, showing the distribution of individual samples (gray circles) as a function of the environmental factors (black arrows). Environmental factors are: Latitude, dissolved oxygen (O) and bottom oxygen (BO), temperature (Temp), salinity (Sal), date of sampling (Date), distance from shore (Dist), depth to seafloor (maxD), tidal amplitude (Tide) in m, upwelling intensity the day of sampling (Upw) and two days prior to sampling (Upw2dl), and the slope of cumulative wind stress for one week (CWS1w) and two weeks (CWS2w) prior to sampling.

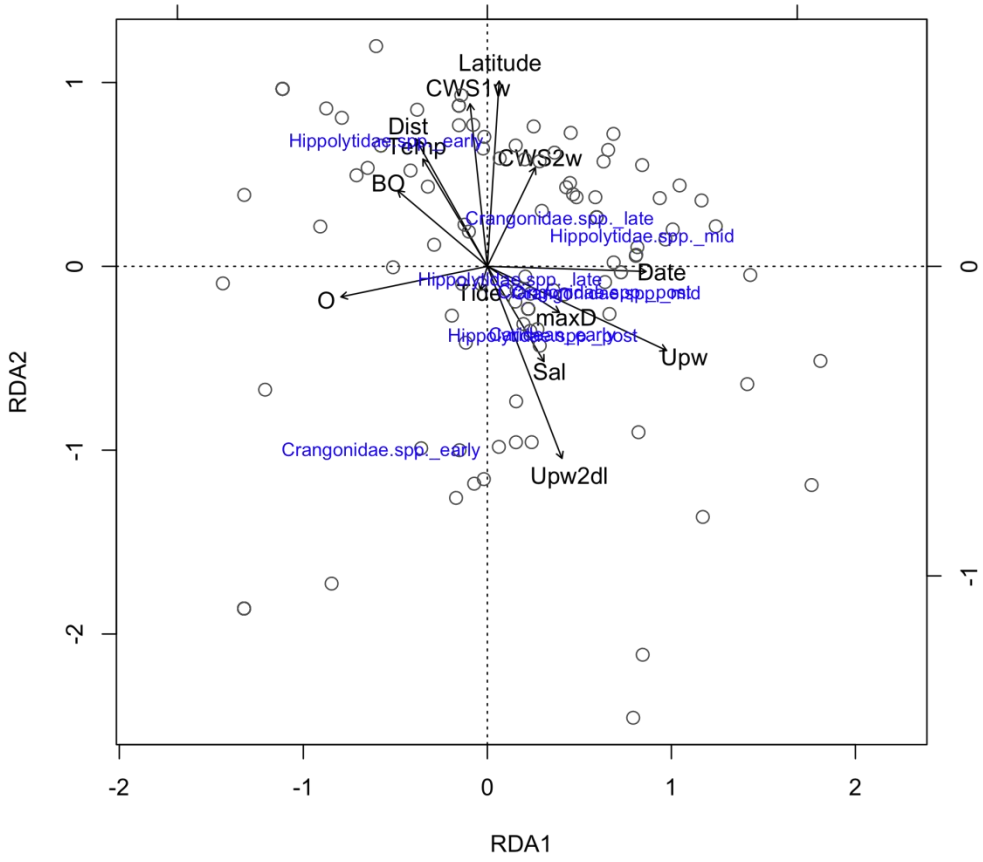

Figure 4.4 Redundancy analysis biplot axis 1 and 2 for Natantia decapods, showing the distribution of individual samples (gray circles) as a function of the environmental factors (black arrows). Environmental factors are: Latitude, dissolved oxygen (O) and bottom oxygen (BO), temperature (Temp), salinity (Sal), date of sampling (Date), distance from shore (Dist), depth to seafloor (maxD), tidal amplitude (Tide) in m, upwelling intensity the day of sampling (Upw) and two days prior to sampling (Upw2dl), and the slope of cumulative wind stress for one week (CWS1w) and two weeks (CWS2w) prior to sampling.

Figure 4.5 Two predictor contour plots for abundance of different species-stages of Reptantia decapod larvae. White spaces are no data. Predictors appearing in plots are distance from shore (Dist) in km, depth to seafloor (Depth) in m, upwelling intensity the day of sampling (Upw) in $m^3/s/100m$, and the slope of cumulative wind stress one week (CWS1w) or two weeks (CWS2w) prior to sampling. Contour plots are presented for the following species-stages a) *C. gracilis* post larvae, b) *C. magister* early larvae, c) *C. magister* mid larvae, d) *C. productus* post larvae, e) *F. subquadrata* late larvae, f) *L. bellus* early larvae, g) *N. californiensis* early larvae, h) *N. californiensis* mid larvae, i) *N. californiensis* late larvae, j) *Pagurus* spp. early larvae.

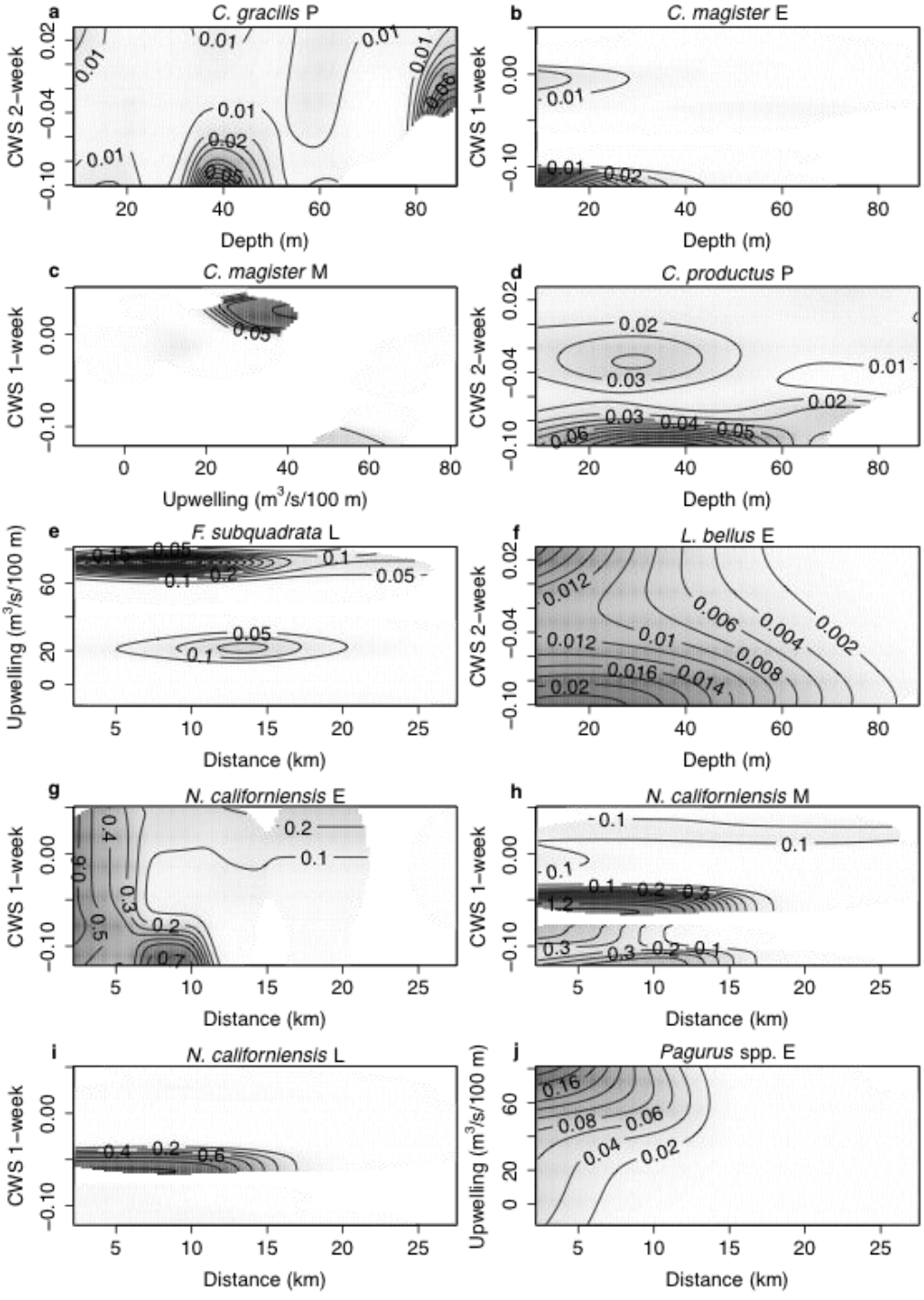
a
C. gracilis P
CWS 2−week
Depth (m)
b
C. magister E
CWS 1−week
Depth (m)
c
C. magister M
CWS 1−week
Upwelling (m3/s/100 m)
d
C. productus P
CWS 2−week
Depth (m)
e
F. subquadrata L
Upwelling (m3/s/100 m)
Distance (km)
f
L. bellus E
CWS 2−week
Depth (m)
g
N. californiensis E
CWS 1−week
Distance (km)
h
N. californiensis M
CWS 1−week
Distance (km)
i
N. californiensis L
CWS 1−week
Distance (km)
j
Pagurus spp. E
Upwelling (m3/s/100 m)
Distance (km)

Figure 4.5

Figure 4.6 Two predictor contour plots for abundance of different species-stages of Reptantia decapod larvae. White spaces are no data. Predictors appearing in plots are distance from shore (Dist) in km, depth to seafloor (Depth) in m, tidal amplitude (Tide) in m, dissolved oxygen (DO) in ml/L, bottom dissolved oxygen (BDO) in ml/L, and temperature (Temp) in ºC. Contour plots are presented for the following species-stages a) *C. magister* post larvae, b) *C. magister* post larvae, c) *C. productus* post larvae, d) *L. bellus* Early larvae, e) *L. bellus* early larvae, f) *N. californiensis* early larvae, g) *N. californiensis* mid larvae, h) *Pagurus* spp. mid larvae, i) *Pagurus* spp. Late larvae, j) *Pagurus* spp. post larvae.

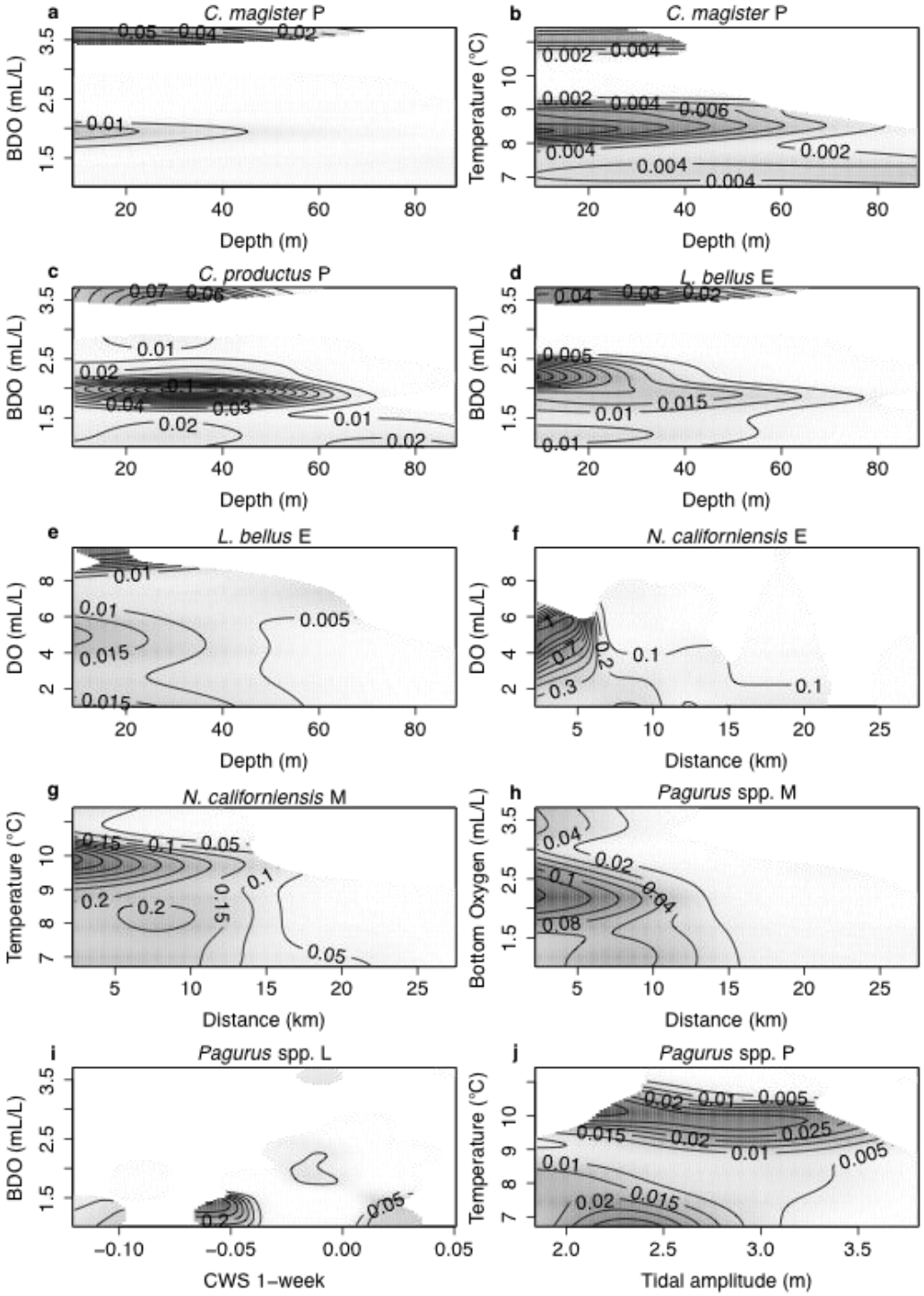
a
C. magister P
BDO (mL/L)
Depth (m)
b
C. magister P
Temperature (°C)
Depth (m)
c
C. productus P
BDO (mL/L)
Depth (m)
d
L. bellus E
BDO (mL/L)
Depth (m)
e
L. bellus E
DO (mL/L)
Depth (m)
f
N. californiensis E
DO (mL/L)
Distance (km)
g
N. californiensis M
Temperature (°C)
Distance (km)
h
Pagurus spp. M
Bottom Oxygen (mL/L)
Distance (km)
i
Pagurus spp. L
BDO (mL/L)
CWS 1−week
j
Pagurus spp. P
Temperature (°C)
Tidal amplitude (m)

Figure 4.6

Figure 4.7 Two predictor contour plots for abundance of different species-stages of Reptantia (a, b) and Natantia decapod larvae (c-j). White spaces are no data. Predictors appearing in plots are distance from shore (Dist) in km, depth to seafloor (Depth) in m, upwelling intensity (Upw) and upwelling intensity two days prior to sampling (Upw2dp) in $m^3/s/100m$, the slope of cumulative wind stress one week (CWS1w) prior to sampling, temperature (Temp) in °C, salinity (Sal) in ppm, and dissolved oxygen and bottom dissolved oxygen (BDO) in ml/L. Contour plots are presented for the following species-stages a) *Pagurus* spp. mid, b) *Pagurus* spp. post, c) Crangonidae mid, d) Crangonidae late, e) Hippolytidae early, f) Hippolytidae mid, g) Hippolytidae late, h) Crangonidae early, i) Crangonidae mid, j) Crangonidae late

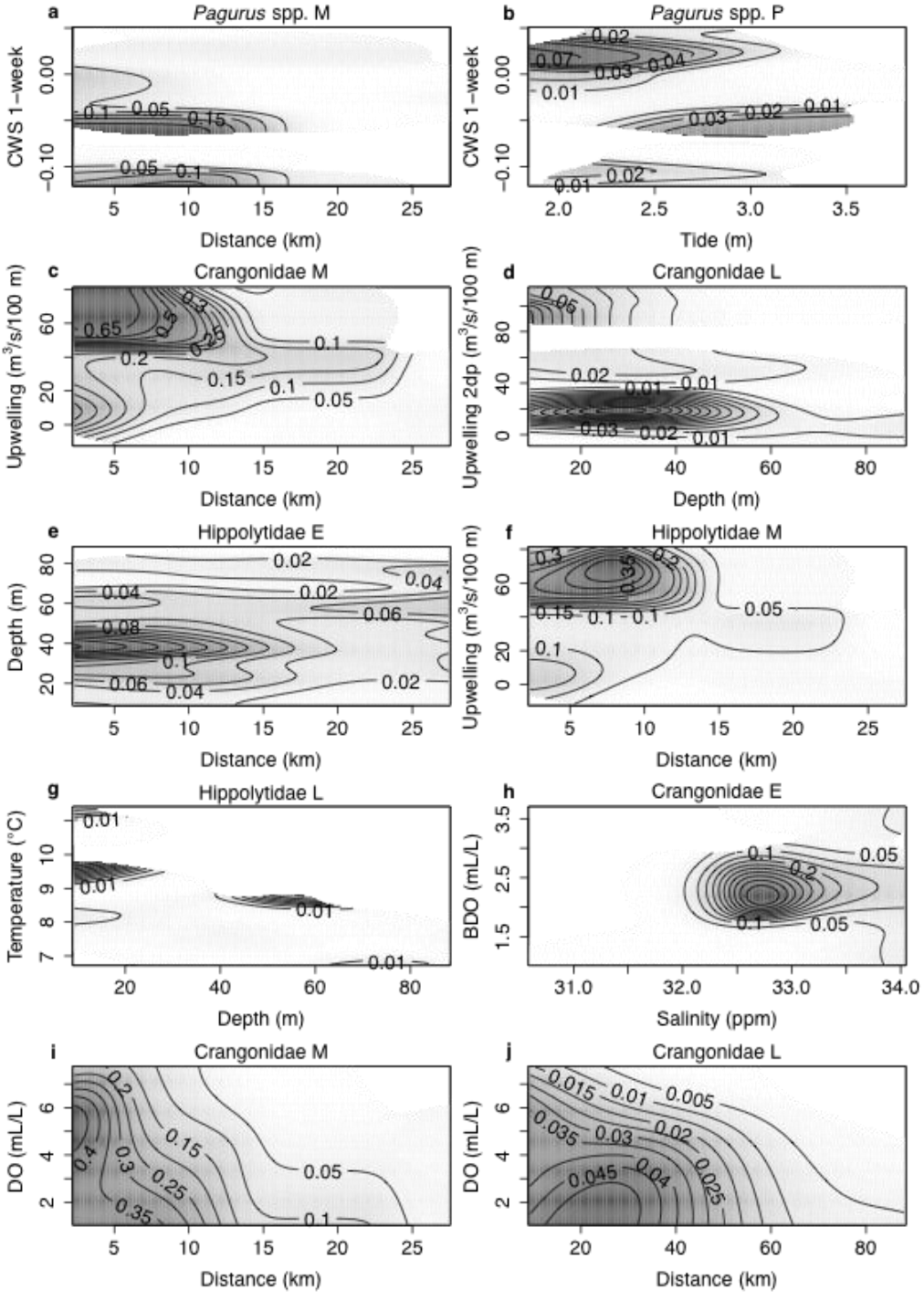
a
Pagurus spp. M
CWS 1−week
Distance (km)
b
Pagurus spp. P
CWS 1−week
Tide (m)
c
Crangonidae M
Upwelling (m3/s/100 m)
Distance (km)
d
Crangonidae L
Upwelling 2dp (m3/s/100 m)
Depth (m)
e
Hippolytidae E
Depth (m)
Distance (km)
f
Hippolytidae M
Upwelling (m3/s/100 m)
Distance (km)
g
Hippolytidae L
Temperature (°C)
Depth (m)
h
Crangonidae E
BDO (mL/L)
Salinity (ppm)
i
Crangonidae M
DO (mL/L)
Distance (km)
j
Crangonidae L
DO (mL/L)
Distance (km)

Figure 4.7

5 – Conclusion

In a framework of changing ocean conditions in the CCS, my research has explored how larval invertebrates relate to their environment. Through both laboratory experiments and field observations, my dissertation research shows that larval invertebrates have differential responses to environmental conditions. In scenarios of hypoxia, laboratory experiments (Chapter 2) reveal that many species are tolerant to six-day exposures of hypoxia and microxia. The crustaceans, however, are highly sensitive and experience significant mortality within twelve hours. This is in agreement with published findings of reduced tolerance of crustaceans to low oxygen conditions (Vaquer-Sunyer and Duarte 2008). Recent years have seen a rise of nearshore hypoxia and anoxia on the Oregon coast. These events have been related to fluctuations in ocean-atmosphere processes that affect upwelling wind stress (Chan et al. 2008). With climate change predictions for an intensification in coastal upwelling winds, the incidence of incidence of hypoxia is predicted to continue to occur in the nearshore waters of coastal upwelling systems (Chan et al. 2008; Bakun et al. 2010). Therefore planktonic communities are likely to experience hypoxia on a seasonal basis. Based on our laboratory findings, differential responses of larval invertebrates to chronic hypoxia or anoxia have the potential to alter the structure and species composition of Meroplankton assemblages and subsequent adult communities in the rocky intertidal.

The rationale behind investigating the relationship of planktonic larval invertebrates to their environment through field studies (Chapters 3 & 4) lies in the climate change predictions for EBUE that forecast an intensification of upwelling, ocean hypoxia, and ocean acidification (Chan et al. 2008; Bakun et al. 2010). Because the larval stage, which links benthic adult communities and planktonic communities, is an important time of development that is impacted by its immediate environment, this research is pertinent. A second reason for this research is that most investigations on the impact of ocean hypoxia on organisms are laboratory studies; field studies are generally lacking (Vaquer-Sunyer and Duarte 2008). For these reasons, field studies on the distribution of larval invertebrates in relation to environmental variables were conducted. While dissolved oxygen during sampling seasons (2008 and 2009) did not reach the hypoxic levels of previous years, the field research still contributes to an understanding of how planktonic larvae are affected by their environment. Field observations revealed that a variety of environmental conditions contribute to community structure and individual abundance of larval invertebrates. However, upwelling related factors (i.e. upwelling intensity and cumulative wind stress) were the most frequently occurring predictors in species abundance models. In Chapter 3 larval abundance models were commonly associated with strong upwelling conditions, and in Chapter 4 models for species abundance were commonly associated with persistent upwelling winds (indicated by cumulative wind stress). The larval abundance models

of Chapter 4 also confirmed literature findings of larvae found closer to shore (Shanks and Shearman 2009; Morgan et al. 2009b).

As climate projections point towards future intensification of upwelling winds, and associated changes in water biogeochemistry, these findings are of importance. Studies such as these will aid our understanding of how changes associated with climate change will affect larval invertebrates during their time in the plankton and the benthic communities that they recruit to. This research makes the following novel contributions:

1) In Chapter 2, hypoxia experiments focus on the impact of hypoxia on species that have not previously been studied. While the majority of laboratory hypoxia studies focus on species of estuaries and bays, our study focuses on species of an open coastal upwelling system.

2) In Chapter 2 the approach of exploring the effects of hypoxia on at a suite of rocky intertidal community players, rather than a single species is new. Most laboratory studies focus on hypoxia impacts on one or a few species, but our focus is on a suite of community members.

3) There are more laboratory studies than field observations on the impact of hypoxia (Vaquer-Sunyer and Duarte 2008), therefore our efforts to relate meroplankton distributions to oxygen levels adds new knowledge (Chapter 3 and 4).

4) Few studies investigate the impact of hypoxia on planktonic organisms (Ekau et al. 2010) therefore, this research is increasing our existing knowledge on the impactsof hypoxia.

5) Meroplankton assemblages of the CCS have mostly been studied with the aim of addressing questions of transport and dispersal. Few studies have focused on other environmental variables that are not aimed at addressing transport/dispersal

Findings from these laboratory experiments and field studies are new additions to our understanding of larval biology in the CCS and indicate towards future directions of research. Further laboratory experiments could expand on the sublethal effects of hypoxia on larval invertebrates and the behavioral responses of larvae to low oxygen conditions. Future explorations of larval water column distributions in the field may focus on finding which components of upwelling (physical transport vs. water temperature/chemistry) drive larval abundance and community composition.

Bibliography

Allen, J. D. 2008. Size-specific predation on marine invertebrate larvae. The Biological Bulletin **214**: 42 -49.

Allen, R. M., and D. J. Marshall. 2010. The larval legacy: cascading effects of recruit phenotype on post- recruitment interactions. Oikos **119**: 1977-1983, doi:10.1111/j.1600-0706.2010.18682.x

Alvariño, A. 1965. Distributional atlas of Chaetognatha in the California Current region, 3rd ed. California Cooperative Oceanic Fisheries Investigations.

Aquarone, M., and S. Adams. 2008. California Current: LME #3, p. 593-604. *In* The UNEP Large Marine Ecosystem Report: A perspective on changing conditions in LMEs of the world's Regional Seas. United Nations Environment Programme.

Armstrong, D. A., C. Rooper, and D. Gunderson. 2003. Estuarine production of juvenile dungeness crab (*Cancer magister*) and contribution to the Oregon-Washington coastal fishery. Estuaries **26**: 1174-1188, doi:10.1007/BF02803372

Armstrong, J. L., J. L. Boldt, A. D. Cross, J. H. Moss, N. D. Davis, K. W. Myers, R. V. Walker, D. A. Beauchamp, and L. J. Haldorson. 2005. Distribution, size, and interannual, seasonal and diel food habits of northern Gulf of Alaska juvenile pink salmon, *Oncorhynchus gorbuscha*. Deep Sea Research Part II: Topical Studies in Oceanography **52**: 247-265, doi:10.1016/j.dsr2.2004.09.019

Auel, H., and H. Verheye. 2007. Hypoxia tolerance in the copepod *Calanoides carinatus* and the effect of an intermediate oxygen minimum layer on copepod vertical distribution in the northern Benguela Current upwelling system and the Angola–Benguela Front.

Journal of Experimental Marine Biology and Ecology **352**: 234-243, doi:10.1016/j.jembe.2007.07.020

Babarro, J. M. F., U. Labarta, and M. J. F. Reiriz. 2007. Energy metabolism and performance of *Mytilus galloprovincialis* under anaerobiosis. Journal of the Marine Biological Association of the UK **87**: 941, doi:10.1017/S0025315407053726

Baden, S. P., L. Loo, L. Pihl, and R. Rosenberg. 1990. Effects of eutrophication on benthic communities including fish - Swedish west coast. AMBIO **19**: 113-122.

Baker, S. M., and R. Mann. 1992. Effects of hypoxia and anoxia on larval settlement, juvenile growth, and juvenile survival of the oyster *Crassostrea virginica*. The Biological Bulletin **182**: 265 -269.

Baker, S. M., and R. Mann. 1994. Feeding ability during settlement and metamorphosis in the oyster *Crassostrea virginica* (Gmelin, 1791) and the effects of hypoxia on post-settlement ingestion rates. Journal of Experimental Marine Biology and Ecology **181**: 239-253, doi:10.1016/0022-0981(94)90131-7

Bakun, A., D. B. Field, A. Redondo-Rodriguez, and S. J. Weeks. 2010. Greenhouse gas, upwelling- favorable winds, and the future of coastal ocean upwelling ecosystems. Global Change Biology **16**: 1213-1228, doi:10.1111/j.1365-2486.2009.02094.x

Bakun, A., and S. J. Weeks. 2004. Greenhouse gas buildup, sardines, submarine eruptions and the possibility of abrupt degradation of intense marine upwelling ecosystems. Ecology Letters **7**: 1015-1023, doi:10.1111/j.1461-0248.2004.00665.x

Baldwin, A. 2011. Infraorder Caridea (Shrimps and Prawns) of British Columbia (Order Decapoda). In: Klinkenberg, Brian. (Editor) 2011. E-Fauna BC: Electronic Atlas of the

Fauna of British Columbia [www.efauna.bc.ca]. Lab for Advanced Spatial Analysis, Department of Geography, University of British Columbia, Vancouver.

Barth, J. A., B. A. Menge, J. Lubchenco, F. Chan, J. M. Bane, A. R. Kirincich, M. A. McManus, K. J. Nielsen, S. D. Pierce, and L. Washburn. 2007. Delayed upwelling alters nearshore coastal ocean ecosystems in the northern California current. Proceedings of the National Academy of Sciences **104**: 3719-3724, doi:10.1073/pnas.0700462104

Baschek, B., and W. J. Jenkins. 2009. Gas ventilation of the Saguenay fjord by an energetic tidal front. Atmosphere-Ocean **47**: 308-318, doi:10.3137/OC314.2009

Bauer, R. T. 2004. Remarkable shrimps: adaptations and natural history of the Carideans, University of Oklahoma Press.

Beamish, R. J., R. M. Sweeting, and C. M. Neville. 2004. Improvement of juvenile Pacific salmon production in a regional ecosystem after the 1998 climatic regime shift. Transactions of the American Fisheries Society **133**: 1163-1175, doi:10.1577/T03-170.1

Becker, B. J., L. A. Levin, F. J. Fodrie, and P. A. McMillan. 2007. Complex larval connectivity patterns among marine invertebrate populations. Proceedings of the National Academy of Sciences **104**: 3267-3272, doi:10.1073/pnas.0611651104

Belgrano, A., M. Vincx, J.-M. Dewarumez, A. Richard, J. A. Craeymeersch, and C. H. R. Heip. 1990. Recruitment of meroplanktonic larvae in the Southern Bight of the North Sea. Océanis **16**: 225-243.

Blanchette, C. A., E. A. Wieters, B. R. Broitman, B. P. Kinlan, and D. R. Schiel. 2009. Trophic structure and diversity in rocky intertidal upwelling ecosystems: A comparison of

community patterns across California, Chile, South Africa and New Zealand. Progress In Oceanography **83**: 107-116, doi:10.1016/j.pocean.2009.07.038

Bograd, S. J., C. G. Castro, E. D. Lorenzo, D. M. Palacios, H. Bailey, W. Gilly, and F. P. Chavez. 2008. Oxygen declines and the shoaling of the hypoxic boundary in the California Current. Geophys. Res. Lett. **35**: 6 PP., doi:200810.1029/2008GL034185

Boldt, J., L, and L. J. Haldorson. 2002. A bioenergetics approach to estimating consumption of zooplankton by juvenile Pink salmon in Prince William Sound, Alaska. Alaska Fisheries Research Bulletin **9**: 111-127.

Brandt, S. B., M. Costantini, S. Kolesar, S. A. Ludsin, D. M. Mason, C. M. Rae, H. Zhang, and C. Kraft. 2011. Does hypoxia reduce habitat quality for Lake Erie walleye (*Sander vitreus*)? A bioenergetics perspective. Canadian Journal of Fisheries and Aquatic Sciences **68**: 857-879, doi:10.1139/f2011-018

Breitburg, D., K. Rose, and J. Cowan. 1999. Linking water quality to larval survival: predation mortality of fish larvae in an oxygen-stratified water column. Marine Ecology Progress Series **178**: 39-54, doi:10.3354/meps178039

Brodeur, R. D., E. A. Daly, R. A. Schabetsberger, and K. L. Mier. 2007. Interannual and interdecadal variability in juvenile coho salmon (*Oncorhynchus kisutch*) diets in relation to environmental changes in the northern California Current. Fisheries Oceanography **16**: 395-408, doi:10.1111/j.1365-2419.2007.00438.x

Brodeur, R. D., S. Ralston, R. L. Emmett, M. Trudel, T. D. Auth, and A. J. Phillips. 2006. Anomalous pelagic nekton abundance, distribution, and apparent recruitment in the

northern California Current in 2004 and 2005. Geophysical Research Letters **33, doi:10.1029/2006GL026614**

Brodeur, R., W. Peterson, T. Auth, H. Soulen, M. Parnel, and A. Emerson. 2008. Abundance and diversity of coastal fish larvae as indicators of recent changes in ocean and climate conditions in the Oregon upwelling zone. Marine Ecology Progress Series 366: 187-202, doi:10.3354/meps07539

Burnett, L. E., and B. R. McMahon. 1987. Gas exchange, hemolymph acid-base status, and the role of branchial water stores during air exposure in three littoral crab species. Physiological Zoology **60**: 27-36.

Burnett, L., N. Terwilliger, A. Carroll, D. Jorgensen, and D. Scholnick. 2002. Respiratory and acid-base physiology of the purple sea urchin, *Strongylocentrotus purpuratus*, during air exposure: Presence and function of a facultative lung. Biological Bulletin **203**: 42-50, doi:10.2307/1543456

Casariego, A., J. Alberti, T. Luppi, and O. Iribarne. 2009. Stage-dependent interactions between intertidal crabs: from facilitation to predation. JOURNAL OF THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM **89**: 781-788, doi:10.1017/S0025315408002324

Castro, J. M., D. A. López, and M. V. Vial. 2001. Physiological responses to hypoxia and anoxia in *Jehlius cirratus* (Darwin, 1854) (Cirripedia, Chthamalidae) in the upper intertidal zone. Crustaceana **74**: 161-170, doi:10.1163/156854001750096265

Chan, F., J. A. Barth, J. Lubchenco, A. Kirincich, H. Weeks, W. T. Peterson, and B. A. Menge. 2008. Emergence of anoxia in the California Current Large Marine Ecosystem. Science **319**: 920, doi:10.1126/science.1149016

Chase, Z., A. van Geen, P. M. Kosro, J. Marra, and P. A. Wheeler. 2002. Iron, nutrient, and phytoplankton distributions in Oregon coastal waters. J. Geophys. Res. **107**: 17 PP., doi:200210.1029/2001JC000987

Chavez, F. P., and M. Messié. 2009. A comparison of Eastern Boundary Upwelling Ecosystems. Progress In Oceanography **83**: 80-96, doi:10.1016/j.pocean.2009.07.032

Checkley Jr., D. M., and J. A. Barth. 2009. Patterns and processes in the California Current System. Progress In Oceanography **83**: 49-64, doi:10.1016/j.pocean.2009.07.028

Chiba, D., and B. Baschek. 2010. Effect of Langmuir cells on bubble dissolution and air-sea gas exchange. J. Geophys. Res. **115**: 13 PP., doi:201010.1029/2010JC006203

Childress, J. J., and B. A. Seibel. 1998. Life at stable low oxygen levels: adaptations of animals to oceanic oxygen minimum layers. Journal of Experimental Biology **201**: 1223 -1232.

Connell, J. H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. Ecology **42**: 710-723, doi:10.2307/1933500

Connolly, S. R., and J. Roughgarden. 1999. Theory of marine communities: Competition, predation, and recruitment-dependent interaction strength. Ecological Monographs **69**: 277-296, doi:10.1890/0012-9615(1999)069[0277:TOMCCP]2.0.CO;2

Cowen, R. K., and S. Sponaugle. 2009. Larval dispersal and marine population connectivity. Annual Review of Marine Science **1**: 443-466, doi:10.1146/annurev.marine.010908.163757

Crim, R. N., J. M. Sunday, and C. D. G. Harley. 2011. Elevated seawater CO_2 concentrations impair larval development and reduce larval survival in endangered northern abalone (*Haliotis kamtschatkana*). Journal of Experimental Marine Biology and Ecology **400**: 272-277, doi:10.1016/j.jembe.2011.02.002

Dauer, D. M. 1993. Biological criteria, environmental health and estuarine macrobenthic community structure. Marine Pollution Bulletin **26**: 249-257, doi:10.1016/0025-326X(93)90063-P

Davenport, J., and S. Irwin. 2003. Hypoxic life of intertidal acorn barnacles. Marine Biology **143**: 555-563, doi:10.1007/s00227-003-1057-0

Dayton, P. K. 1971. Competition, disturbance, and community organization: The provision and subsequent utilization of space in a rocky intertidal community. Ecological Monographs **41**: 351, doi:10.2307/1948498

Dayton, P. K. 1975. Experimental evaluation of ecological dominance in a rocky intertidal algal community. Ecological Monographs **45**: 137-159, doi:10.2307/1942404

Desai, D., L. Khandeparker, and Y. Shirayama. 2006. Larval development and metamorphosis of *Balanus albicostatus* (Cirripedia: Thoracica); implications of temperature, food concentration and energetics. Journal of the Marine Biological Association of the UK **86**: 335, doi:10.1017/S002531540601318X

Desai, D., and S. Prakash. 2009. Physiological responses to hypoxia and anoxia in *Balanus amphitrite* (Cirripedia: Thoracica). Marine Ecology Progress Series **390**: 157-166, doi:10.3354/meps08155

Diaz, R. J. 2001. Overview of hypoxia around the world. J. Environ. Qual. **30**: 275-281.

Diaz, R. J., and R. Rosenberg. 2008. Spreading dead zones and consequences for marine ecosystems. Science **321**: 926 -929, doi:10.1126/science.1156401

Diaz, R., and R. Rosenberg. 1995. Marine benthic hypoxia: A review of its ecological effects and the behavioural responses of benthic macrofauna. Oceanography and Marine Biology - An Annual Review **33**: 245-303.

Díaz-Ochoa, J. A., S. Pantoja, G. J. De Lange, C. B. Lange, G. E. Sánchez, V. R. Acuña, P. Muñoz, and G. Vargas. 2011. Oxygenation variability in Mejillones Bay, off northern Chile, during the last two centuries. Biogeosciences **8**: 137-146, doi:10.5194/bg-8-137-2011

Edwards, M., and A. J. Richardson. 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. Nature **430**: 881-884, doi:10.1038/nature02808

Ekau, W., H. Auel, H.-O. Pörtner, and D. Gilbert. 2009. Impacts of hypoxia on the structure and processes in the pelagic community (zooplankton, macro-invertebrates and fish). Biogeosciences Discuss. **6**: 5073-5144.

Ekau, W., H. Auel, H.-O. Pörtner, and D. Gilbert. 2010. Impacts of hypoxia on the structure and processes in pelagic communities (zooplankton, macro-invertebrates and fish). Biogeosciences **7**: 1669-1699, doi:10.5194/bg-7-1669-2010

Emlet, R. B., S. A. Maslakova, A. L. Shanks, and C. M. Young. 2009. Biological Bulletin virtual symposium: Biology of marine invertebrate larvae. The Biological Bulletin **216**: 201 - 202.

Emlet, R. B., and S. S. Sadro. 2006. Linking stages of life history: How larval quality translates into juvenile performance for an intertidal barnacle (*Balanus glandula*). Integrative and Comparative Biology **46**: 334-346, doi:10.1093/icb/icj023

Feely, R. A., C. L. Sabine, J. M. Hernandez-Ayon, D. Ianson, and B. Hales. 2008. Evidence for upwelling of corrosive "acidified" water onto the continental shelf. Science **320**: 1490-1492, doi:10.1126/science.1155676

Fernandez, M., O. O. Iribarne, and D. A. Armstrong. 1994. Swimming behavior of Dungeness crab, *Cancer magister* Dana, megalopae in still and moving water. Estuaries **17**: 271, doi:10.2307/1352575

Fernández, E., J. Cabal, J. L. Acuña, A. Bode, A. Botas, and C. García-Soto. 1993. Plankton distribution across a slope current-induced front in the southern Bay of Biscay. Journal of Plankton Research **15**: 619 -641, doi:10.1093/plankt/15.6.619

Fréon, P., M. Barange, and J. Arístegui. 2009. Eastern Boundary Upwelling Ecosystems: Integrative and comparative approaches. Progress In Oceanography **83**: 1-14, doi:10.1016/j.pocean.2009.08.001

van Geen, A., R. K. Takesue, J. Goddard, T. Takahashi, J. A. Barth, and R. L. Smith. 2000. Carbon and nutrient dynamics during coastal upwelling off Cape Blanco, Oregon. Deep Sea Research Part II: Topical Studies in Oceanography **47**: 975-1002, doi:10.1016/S0967-0645(99)00133-2

Genin, A., J. S. Jaffe, R. Reef, C. Richter, and P. J. S. Franks. 2005. Swimming against the flow: A mechanism of zooplankton aggregation. Science **308**: 860 -862, doi:10.1126/science.1107834

Gentsch, E., K. H. Wiltshire, and B. Niehoff. 2007. Meroplanktonic larvae in the marine food web - a combination of grazing experiments and stable isotope analyses at Helgoland Roads, North Sea. 4th ICES International Zooplankton Production Symposium, Hiroshima, Japan

Giesecke, R., and H. E. González. 2004. Feeding of *Sagitta enflata* and vertical distribution of chaetognaths in relation to low oxygen concentrations. Journal of Plankton Research **26**: 475 -486, doi:10.1093/plankt/fbh039

Grantham, B. A., F. Chan, K. J. Nielsen, D. S. Fox, J. A. Barth, A. Huyer, J. Lubchenco, and B. A. Menge. 2004. Upwelling-driven nearshore hypoxia signals ecosystem and oceanographic changes in the northeast Pacific. Nature **429**: 749-754, doi:10.1038/nature02605

Hallegraeff, G. M. 2010. Ocean climate change, phytoplankton community responses, and harmful algal blooms: a formidable predictive challenge. Journal of Phycology **46**: 220-235, doi:10.1111/j.1529-8817.2010.00815.x

Hansen, J., M. Sato, R. Ruedy, K. Lo, D. W. Lea, and M. Medina-Elizade. 2006. Global temperature change. Proceedings of the National Academy of Sciences **103**: 14288 -14293, doi:10.1073/pnas.0606291103

Harley, C. D. G., A. Randall Hughes, K. M. Hultgren, B. G. Miner, C. J. B. Sorte, C. S. Thornber, L. F. Rodriguez, L. Tomanek, and S. L. Williams. 2006. The impacts of climate change

in coastal marine systems. Ecology Letters **9**: 228-241, doi:10.1111/j.1461-0248.2005.00871.x

Hastings, A., and L. W. Botsford. 2006. Persistence of spatial populations depends on returning home. Proceedings of the National Academy of Sciences **103**: 6067 -6072, doi:10.1073/pnas.0506651103

Haynes, E. B. 1985. Morphological development, identification, and biology of larvae of Pandalidae, Hippolytidae, and Crangonidae (Crustacea, Decapoda) of the northern North Pacific Ocean. Fishery Bulletin **83**: 253-288.

Helly, J. J., and L. A. Levin. 2004. Global distribution of naturally occurring marine hypoxia on continental margins. Deep Sea Research Part I: Oceanographic Research Papers **51**: 1159-1168, doi:10.1016/j.dsr.2004.03.009

Hendrickx, M. E. 2001. Occurrence of a continental slope decapod crustacean community along the edge of the minimum oxygen zone in the south eastern Gulf of California, Mexico. Belgian Journal of Zoology **31(s2)**: 95-110.

Hendrickx, M. E., and F. D. Estrada-Navarrete. 1989. A checklist of the species of pelagic shrimps (Penaeoidea and Caridea) from the eastern Pacific, with notes on their geographic and depth distribution,.

Hernández- Miranda, E., R. A. Quiñones, G. Aedo, A. Valenzuela, N. Mermoud, C. Román, and F. Yañez. 2010. A major fish stranding caused by a natural hypoxic event in a shallow bay of the eastern South Pacific Ocean. Journal of Fish Biology **76**: 1543-1564, doi:10.1111/j.1095-8649.2010.02580.x

Herreid II, C. F. 1980. Hypoxia in invertebrates. Comparative Biochemistry and Physiology Part A: Physiology **67**: 311-320, doi:10.1016/S0300-9629(80)80002-8

Hicks, D. W., and R. F. McMahon. 2005. Effects of temperature on chronic hypoxia tolerance in the non-indigenous brown mussel, *Perna perna* (Bivalvia : Mytilidae) from the Texas Gulf of Mexico. Journal of Molluscan Studies **71**: 401-408, doi:10.1093/mollus/eyi042

Hsieh, H.-L., L.-F. Fan, C.-P. Chen, J.-T. Wu, and W.-C. Liu. 2010. Effects of semidiurnal tidal circulation on the distribution of holo- and meroplankton in a subtropical estuary. J Plankton Res **32**: 829-841, doi:10.1093/plankt/fbq026

Huyer, A. 1983. Coastal upwelling in the California current system. Progress In Oceanography **12**: 259-284, doi:10.1016/0079-6611(83)90010-1

Iles, A. C., T. C. Gouhier, B. A. Menge, J. S. Stewart, A. J. Haupt, and M. C. Lynch. 2011. Climate- driven trends and ecological implications of event- scale upwelling in the California Current System. Global Change Biology, doi:10.1111/j.1365-2486.2011.02567.x

Ingólfsson, A. 2009. Predators on rocky shores in the northern Atlantic: Can the results of local experiments be generalized on a geographical scale? Estuarine Coastal and Shelf Science **83**: 287-295.

Keeling, R. F., A. Körtzinger, and N. Gruber. 2010. Ocean deoxygenation in a warming world. Annual Review of Marine Science **2**: 199-229, doi:10.1146/annurev.marine.010908.163855

Keeling, R. F., and H. E. Garcia. 2002. The change in oceanic O_2 inventory associated with recent global warming. Proceedings of the National Academy of Sciences **99**: 7848 - 7853, doi:10.1073/pnas.122154899

Keister, J. E., and W. T. Peterson. 2003. Zonal and seasonal variations in zooplankton community structure off the central Oregon coast, 1998–2000. Progress In Oceanography **57**: 341-361, doi:10.1016/S0079-6611(03)00105-8

Kim, S., and J. A. Barth. 2011. Connectivity and larval dispersal along the Oregon coast estimated by numerical simulations. J. Geophys. Res. **116**: 14 PP., doi:201110.1029/2010JC006741

Kimmel, D. G., W. C. Boicourt, J. J. Pierson, M. R. Roman, and X. Zhang. 2010. The vertical distribution and diel variability of mesozooplankton biomass, abundance and size in response to hypoxia in the northern Gulf of Mexico USA. Journal of Plankton Research **32**: 1185 -1202, doi:10.1093/plankt/fbp136

King, M. G., and A. J. Butler. 1985. Relationship of life-history patterns to depth in deep-water caridean shrimps (Crustacea: Natantia). Marine Biology **86**: 129-138, doi:10.1007/BF00399018

Kinlan, B. P., and S. D. Gaines. 2003. Propagule dispersal in marine and terrestrial environments: A community perspective. Ecology **84**: 2007-2020, doi:10.1890/01-0622

Lamb, J., and W. T. Peterson. 2005. Ecological zonation of zooplankton in the COAST study region off central Oregon in June and August 2001 with consideration of retention mechanisms. Journal of Geophysical Research **110, doi:10.1029/2004JC002520**

Large, W. G., and S. Pond. 1981. Open ocean momentum flux measurements in noderate to strong winds. Journal of Physical Oceanography 11: 324-336, doi:10.1175/1520-0485(1981)011<0324:OOMFMI>2.0.CO;2

Legendre, P., and E. Gallagher. 2001. Ecologically meaningful transformations for ordination of species data. Oecologia **129**: 271-280.

Legendre, P., and L. Legendre. 1998. Numerical Ecology, Second English. Elsevier Science B.V.

Levin, L. A., W. Ekau, A. J. Gooday, F. Jorissen, J. J. Middelburg, W. Naqvi, C. Neira, N. N. Rabalais, and J. Zhang. 2009. Effects of natural and human-induced hypoxia on coastal benthos. Biogeosciences Discuss. **6**: 3563-3654, doi:10.5194/bgd-6-3563-2009

Llanso, R. J., and R. J. Diaz. 1994. Tolerance to low dissolved oxygen by the tubicolous polychaete *Loimia medusa*. Journal of the Marine Biological Association of the United Kingdom **74**: 143-148, doi:10.1017/S0025315400035724

López, D. A., J. M. Castro, M. L. González, and R. W. Simpfendörfer. 2003. Physiological responses to hypoxia and anoxia in the Giant Barnacle, *Austromegabalanus psittacus* (Molina, 1782). Crustaceana **76**: 533-545.

Manabe, S., and R. J. Stouffer. 1993. Century-scale effects of increased atmospheric CO_2 on the ocean–atmosphere system. Nature **364**: 215-218, doi:10.1038/364215a0

Manríquez, K., R. Escribano, and P. Hidalgo. 2009. The influence of coastal upwelling on the mesozooplankton community structure in the coastal zone off Central/Southern Chile as assessed by automated image analysis. Journal of Plankton Research **31**: 1075 -1088, doi:10.1093/plankt/fbp053

Manríquez, K., R. Escribano, and R. Riquelme-Bugueño. 2011. Spatial structure of the zooplankton community in the coastal upwelling system off central-southern Chile in spring 2004 as assessed by automated image analysis. Progress In Oceanography, doi:10.1016/j.pocean.2011.07.020

Marques, S. C., U. M. Azeiteiro, F. Martinho, I. Viegas, and M. A. Pardal. 2009. Evaluation of estuarine mesozooplankton dynamics at a fine temporal scale: the role of seasonal, lunar and diel cycles. Journal of Plankton Research **31**: 1249-1263, doi:10.1093/plankt/fbp068

Martin, D., S. Pinedo, and R. Sardá. 1996. Grazing by meroplanktonic polychaete larvae may help to control nanoplankton in the NW Mediterranean littoral: in situ experimental evidence. Mar Ecol Prog Ser **143**: 239-246, doi:10.3354/meps143239

McCune, B. 2006. Non- parametric habitat models with automatic interactions. Journal of Vegetation Science **17**: 819-830, doi:10.1111/j.1654-1103.2006.tb02505.x

McCune, B. 2011. Nonparametric Multiplicative Regression for Habitat Modeling. <http://www.pcord.com/NPMRintro.pdf>.

McCune, B., and M. Mefford. 2009. HyperNiche. Nonparametric multiplicative habitatmodeling,.

McDonald, K. A., and D. Grünbaum. 2010. Swimming performance in early development and the "other" consequences of egg size for ciliated planktonic larvae. Integrative and Comparative Biology **50**: 589 -605, doi:10.1093/icb/icq090

Meehl, G. A., F. Zwiers, J. Evans, T. Knutson, L. Mearns, and P. Whetton. 2000. Trends in extreme weather and climate events: Issues related to modeling extremes in

projections of future climate change. Bulletin of the American Meteorological Society **81**: 427-436, doi:10.1175/1520-0477(2000)081<0427:TIEWAC>2.3.CO;2

Mendelssohn, R., and F. B. Schwing. 2002. Common and uncommon trends in SST and wind stress in the California and Peru–Chile current systems. Progress In Oceanography **53**: 141-162, doi:10.1016/S0079-6611(02)00028-9

Menge, B. 2000. Top-down and bottom-up community regulation in marine rocky intertidal habitats. Journal of Experimental Marine Biology and Ecology **250**: 257-289, doi:10.1016/S0022-0981(00)00200-8

Menge, B. A. 1992. Community Regulation: Under What Conditions Are Bottom-Up Factors Important on Rocky Shores? Ecology **73**: 755-765, doi:10.2307/1940155

Menge, B. A., C. Blanchette, P. Raimondi, T. Freidenburg, S. Gaines, J. Lubchenco, D. Lohse, G. Hudson, M. Foley, and J. Pamplin. 2004. Species interaction strength: testing model predictions along an upwelling gradient. Ecological Monographs **74**: 663-684, doi:10.1890/03-4060

Menge, B. A., F. Chan, K. J. Nielsen, E. D. Lorenzo, and J. Lubchenco. 2009. Climatic variation alters supply-side ecology: impact of climate patterns on phytoplankton and mussel recruitment. Ecological Monographs **79**: 379-395, doi:10.1890/08-2086.1

Menge, B. A., F. Chan, and J. Lubchenco. 2008. Response of a rocky intertidal ecosystem engineer and community dominant to climate change. Ecology Letters **11**: 151-162, doi:10.1111/j.1461-0248.2007.01135.x

Menge, B. A., T. C. Gouhier, T. Freidenburg, and J. Lubchenco. 2011a. Linking long-term, large-scale climatic and environmental variability to patterns of marine invertebrate

recruitment: Toward explaining “unexplained” variation. Journal of Experimental Marine Biology and Ecology **400**: 236-249, doi:10.1016/j.jembe.2011.02.003

Menge, B. A., S. D. Hacker, T. Freidenburg, J. Lubchenco, R. Craig, G. Rilov, M. Noble, and E. Richmond. 2011b. Potential impact of climate-related changes is buffered by differential responses to recruitment and interactions. Ecological Monographs **81**: 493-509, doi:10.1890/10-1508.1

Menge, B. A., and J. P. Sutherland. 1987. Community regulation: Variation in disturbance, competition, and predation in relation to environmental stress and recruitment. The American Naturalist **130**: 730-757, doi:10.1086/284741

Miller, B., and R. Emlet. 1997. Influence of nearshore hydrodynamics on larval abundance and settlement of sea urchins *Strongylocentrotus franciscanus* and *S. purpuratus* in the Oregon upwelling zone. Marine Ecology Progress Series **148**: 83-94, doi:10.3354/meps148083

Minchinton, T. E., and R. E. Scheibling. 1991. The influence of larval supply and settlement on the population structure of barnacles. Ecology **72**: 1867-1879, doi:10.2307/1940984

Monteiro, P. M. S., A. K. van der Plas, J.-L. Mélice, and P. Florenchie. 2008. Interannual hypoxia variability in a coastal upwelling system: Ocean-shelf exchange, climate and ecosystem-state implications. Deep Sea Research Part I: Oceanographic Research Papers **55**: 435-450, doi:10.1016/j.dsr.2007.12.010

Morgan, S. G. 1995. Life and death in the plankton: Larval mortality and adaptation, p. 279-322. *In* Ecology of Marine Invertebrate Larvae, edited by L. McEdward. CRC Press.

Morgan, S. G., J. L. Fisher, A. J. Mace, L. Akins, A. M. Slaughter, and S. M. Bollens. 2009a. Cross-shelf distributions and recruitment of crab postlarvae in a region of strong upwelling. Mar Ecol Prog Ser **380**: 173-185, doi:10.3354/meps07913

Morgan, S. G., J. L. Fisher, S. H. Miller, S. T. McAfee, and J. L. Largier. 2009b. Nearshore larval retention in a region of strong upwelling and recruitment limitation. Ecology **90**: 3489-3502, doi:10.1890/08-1550.1

Munk, P., C. J. Fox, L. J. Bolle, C. J. G. Van Damme, P. Fossum, and G. Kraus. 2009. Spawning of North Sea fishes linked to hydrographic features. Fisheries Oceanography **18**: 458-469, doi:10.1111/j.1365-2419.2009.00525.x

Navarrete, S. A., E. A. Wieters, B. R. Broitman, and J. C. Castilla. 2005. Scales of benthic–pelagic coupling and the intensity of species interactions: From recruitment limitation to top-down control. Proceedings of the National Academy of Sciences of the United States of America **102**: 18046 -18051, doi:10.1073/pnas.0509119102

Nilsson, H., and R. Rosenberg. 1994. Hypoxic response of two marine benthic communities. Marine Ecology Progress Series **115**: 209-217, doi:10.3354/meps115209

O'Donnell, M. J., L. M. Hammond, and G. E. Hofmann. 2008. Predicted impact of ocean acidification on a marine invertebrate: elevated CO_2 alters response to thermal stress in sea urchin larvae. Marine Biology **156**: 439-446, doi:10.1007/s00227-008-1097-6

Paine, R. T. 1966. Food web complexity and species diversity. The American Naturalist **100**: 65-75.

Pechenik, J. A. 1999. On the advantages and disadvantages of larval stages in benthic marine invertebrate life cycles. Marine Ecology Progress Series **177**: 269-297, doi:10.3354/meps177269

Perry, A. L., P. J. Low, J. R. Ellis, and J. D. Reynolds. 2005. Climate change and distribution shifts in marine fishes. Science **308**: 1912 -1915, doi:10.1126/science.1111322

Peterson, W. 1998. Life cycle strategies of copepods in coastal upwelling zones. Journal of Marine Systems **15**: 313-326, doi:doi:16/S0924-7963(97)00082-1

Phillips, J. A., R. D. Brodeur, and A. V. Suntsov. 2009. Micronekton community structure in the epipelagic zone of the northern California Current upwelling system. Progress In Oceanography **80**: 74-92, doi:10.1016/j.pocean.2008.12.001

Phillips, N. E. 2002. Effects of nutrition-mediated larval condition on juvenile performance in a marine mussel. Ecology **83**: 2562-2574, doi:10.1890/0012-9658(2002)083[2562:EONMLC]2.0.CO;2

Queiroga, H., and J. Blanton. 2004. Interactions between behaviour and physical forcing in the control of horizontal transport of decapod crustacean larvae. Advances in Marine Biology **47**: 107-214.

Qureshi, N. A., and N. N. Rabalais. 2001. Distribution of Zooplankton on a Seasonally Hypoxic Continental Shelf, p. 61-76. *In* Coastal Hypoxia: Consequences for Living Resources and Ecosystems. American Geophysical Union.

Rabalais, N. N., R. J. Díaz, L. A. Levin, R. E. Turner, D. Gilbert, and J. Zhang. 2010. Dynamics and distribution of natural and human-caused hypoxia. Biogeosciences **7**: 585-619, doi:10.5194/bg-7-585-2010

Rau, G. H., M. D. Ohman, and A. Pierrot-Bults. 2003. Linking nitrogen dynamics to climate variability off central California: a 51 year record based on $^{15}N/^{14}N$ in CalCOFI zooplankton. Deep Sea Research Part II: Topical Studies in Oceanography **50**: 2431-2447, doi:10.1016/S0967-0645(03)00128-0

Reed, D. C., P. T. Raimondi, M. H. Carr, and L. Goldwasser. 2000. The role of dispersal and disturbance in determining spatial heterogeneity in sedentary organisms. Ecology **81**: 2011-2026, doi:10.1890/0012-9658(2000)081[2011:TRODAD]2.0.CO;2

Richardson, A. J. 2008. In hot water: zooplankton and climate change. ICES Journal of Marine Science: Journal du Conseil **65**: 279 -295, doi:10.1093/icesjms/fsn028

Roman, M. R., A. L. Gauzens, W. K. Rhinehart, and J. R. White. 1993. Effects of low oxygen waters on Chesapeake Bay zooplankton. Limnology and Oceanography **38**: 1603-1614.

Rosenberg, R., B. Hellman, and B. Johansson. 1991. Hypoxic tolerance of marine benthic fauna. Marine Ecology Progress Series **79**: 127-131.

Roughgarden, J., S. Gaines, and H. Possingham. 1988. Recruitment dynamics in complex life cycles. Science **241**: 1460 -1466, doi:10.1126/science.11538249

Rumrill, S., J. Pennington, and F. Chia. 1985. Differential susceptibility of marine invertebrate larvae: Laboratory predation of sand dollar, *Dendraster excentricus* (Eschscholtz), embryos and larvae by zoeae of the red crab, *Cancer productus* Randall. Journal of Experimental Marine Biology and Ecology **90**: 193-208, doi:10.1016/0022-0981(85)90166-2

Rykaczewski, R. R., and D. M. Checkley. 2008. Influence of ocean winds on the pelagic ecosystem in upwelling regions. Proceedings of the National Academy of Sciences **105**: 1965-1970, doi:10.1073/pnas.0711777105

dos Santos, A., A. M. P. Santos, D. V. P. Conway, C. Bartilotti, P. Loureno, and H. Queiroga. 2008. Diel vertical migration of decapod larvae in the Portuguese coastal upwelling ecosystem: implications for offshore transport. Mar Ecol Prog Ser **359**: 171-183, doi:10.3354/meps07341

dos Santos, A., A. Santos, and D. Conway. 2007. Horizontal and vertical distribution of cirripede cyprid larvae in an upwelling system off the Portuguese coast. Marine Ecology Progress Series **329**: 145-155, doi:10.3354/meps329145

Sarmento, H., J. M. Montoya, E. Vázquez-Domínguez, D. Vaqué, and J. M. Gasol. 2010. Warming effects on marine microbial food web processes: how far can we go when it comes to predictions? Philosophical Transactions of the Royal Society B: Biological Sciences **365**: 2137 -2149, doi:10.1098/rstb.2010.0045

Sarmiento, J. L., T. M. C. Hughes, R. J. Stouffer, and S. Manabe. 1998. Simulated response of the ocean carbon cycle to anthropogenic climate warming. Nature **393**: 245-249, doi:10.1038/30455

Schwamborn, R., M. de Meló Júnior, S. N. Leitão, W. Ekau, and M. N. Paranaguá. 2008. Dynamic patterns of zooplankton transport and migration in Catuama Inlet (Pernambuco, Brazil), with emphasis on the decapod crustacean larvae. Latin american journal of aquatic research **36, doi:10.4067/S0718-560X2008000100010**

Schwing, F. B., and R. Mendelssohn. 1997. Increased coastal upwelling in the California Current System. Journal of Geophysical Research 102: 3421-3438, doi:10.1029/96JC03591

Shanks, A. 2001. An identification guide to the larval marine invertebrates of the pacific northwest, Oregon State University Press.

Shanks, A. L. 2009. Pelagic Larval Duration and Dispersal Distance Revisited. The Biological Bulletin **216**: 373 -385.

Shanks, A. L., J. Largier, L. Brink, J. Brubaker, and R. Hooff. 2002. Observations on the distribution of meroplankton during a downwelling event and associated intrusion of the Chesapeake Bay estuarine plume. Journal of Plankton Research **24**: 391 -416, doi:10.1093/plankt/24.4.391

Shanks, A. L., J. Largier, and J. Brubaker. 2003. Observations on the distribution of meroplankton during an upwelling event. Journal of Plankton Research **25**: 645 -667, doi:10.1093/plankt/25.6.645

Shanks, A. L., and L. Brink. 2005. Upwelling, downwelling, and cross-shelf transport of bivalve larvae: test of a hypothesis. Mar Ecol Prog Ser **302**: 1-12, doi:10.3354/meps302001

Shanks, A. L., and R. K. Shearman. 2009. Paradigm lost? Cross-shelf distributions of intertidal invertebrate larvae are unaffected by upwelling or downwelling. Mar Ecol Prog Ser **385**: 189-204, doi:10.3354/meps08043

Shinen, J. S., S. G. Morgan, and A. L. Chan. 2009. Invasion resistance on rocky shores: direct and indirect effects of three native predators on an exotic and a native prey species. Mar Ecol Prog Ser **378**: 47-54, doi:10.3354/meps07870

Sifeddine, A., D. Gutiérrez, L. Ortlieb, H. Boucher, F. Velazco, D. Field, G. Vargas, M. Boussafir, R. Salvatteci, V. Ferreira, M. García, J. Valdés, S. Caquineau, M. Mandeng Yogo, F. Cetin, J. Solis, P. Soler, and T. Baumgartner. 2008. Laminated sediments from the central Peruvian continental slope: A 500 year record of upwelling system productivity, terrestrial runoff and redox conditions. Progress In Oceanography **79**: 190-197, doi:10.1016/j.pocean.2008.10.024

Smith, D. L., and K. B. Johnson. 1996. A Guide to Marine Coastal Plankton and Marine Invertebrate Larvae, 2nd ed. Kendall Hunt Pub Co.

Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, H. L. Miller, and (eds.). 2007. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, 2007, Cambridge University Press.

Sousa, W. P. 1979. Disturbance in Marine Intertidal Boulder Fields: The Nonequilibrium Maintenance of Species Diversity. Ecology **60**: 1225-1239, doi:10.2307/1936969

Stalder, L. C., and N. H. Marcus. 1997. Zooplankton responses to hypoxia: behavioral patterns and survival of three species of calanoid copepods. Marine Biology **127**: 599-607, doi:10.1007/s002270050050

Stillman, J., and G. Somero. 1996. Adaptation to temperature stress and aerial exposure in congeneric species of intertidal porcelain crabs (genus Petrolisthes): correlation of physiology, biochemistry and morphology with vertical distribution. Journal of Experimental Biology **199**: 1845 -1855.

Strathmann, M. F. 1987. Reproduction and Development of Marine Invertebrates of the Northern Pacific Coast, University of Washington Press.

Strathmann, R. 1978. Length of pelagic period in echinoderms with feeding larvae from the northeast Pacific. Journal of Experimental Marine Biology and Ecology **34**: 23-27.

Tankersley, R. A., and M. G. Wieber. 2000. Physiological responses of postlarval and juvenile blue crabs *Callinectes sapidus* to hypoxia and anoxia. Mar Ecol Prog Ser **194**: 179-191, doi:10.3354/meps194179

Tyrrell, T. 2011. Anthropogenic modification of the oceans. Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences **369**: 887 -908, doi:10.1098/rsta.2010.0334

Vaquer-Sunyer, R., and C. M. Duarte. 2008. Thresholds of hypoxia for marine biodiversity. Proceedings of the National Academy of Sciences **105**: 15452-15457, doi:10.1073/pnas.0803833105

Venrick, E. L. 1978. How many cells to count?, p. 167-180. *In* Phytoplankton manual. UNESCO.

Visser, E. P., P. S. McDonald, and D. A. Armstrong. 2004. The impact of yellow shore crabs,*Hemigrapsus oregonensis*, on Early Benthic Phase Dungeness crabs, *Cancer magister*, in intertidal oyster shell mitigation habitat. Estuaries **27**: 699-715, doi:10.1007/BF02907654

Wang, C.-de, and F.-sui Zhang. 1995. Effects of environmental oxygen deficiency on embryos and larvae of bay scallop, *Argopecten irradians irradians*. Chinese Journal of Oceanology and Limnology **13**: 362-369, doi:10.1007/BF02889472

Wang, W. X., and J. Widdows. 1991. Physiological responses of mussel larvae *Mytilus edulis* to environmental hypoxia and anoxia. Marine Ecology Progress Series **70**: 223-236.

Warton, D. I., and F. K. C. Hui. 2011. The arcsine is asinine: the analysis of proportions in ecology. Ecology **92**: 3-10, doi:10.1890/10-0340.1

Yoshinaga, M. Y., P. Y. G. Sumida, I. C. A. Silveira, Á. M. Ciotti, S. A. Gaeta, L. F. C. M. Pacheco, and A. G. Koettker. 2010. Vertical distribution of benthic invertebrate larvae during an upwelling event along a transect off the tropical Brazilian continental margin. Journal of Marine Systems **79**: 124-133, doi:10.1016/j.jmarsys.2009.07.007

Zippay, M. L., and G. E. Hofmann. 2009. Physiological tolerances across latitudes: thermal sensitivity of larval marine snails (*Nucella* spp.). Marine Biology **157**: 707-714, doi:10.1007/s00227-009-1354-3

Zippay, M. L., and G. E. Hofmann. 2010. Studies of ocean acidification: the physiological response of marine larval snails to elevated CO(2). Integrative and Comparative Biology **50**: E318-E318.

de Zwaan, A. 1977. Anaerobic energy metabolism in bivalve mollusks. Oceanogrraphy and Marine Biology Annual Review **15**: 103-187.

APPENDICES

Appendix A – Supplementary Material to Chapter 2

Outlined below is additional information to supplement the methods of the main manuscript. Some of the original information in the manuscript is included in this supplement for context and flow.

A.1. Collection of adults and egg masses – additional information

Spawning, fertilization, larval collection, and culturing techniques followed the methods outlined in Strathmann 1987. For the urchin, S. purpuratus, and mussel, M. californianus, adults were collected in the field and brought back to the lab where they were induced to spawn (see Table S1). Mussels were also conditioned for later experiments by rearing in flow through aquaria at ambient temperatures with supplies of ample food (fed continuously on a diet of 8 x104 cells ml-1 of Isochrysis galbana and Chaetoceros neogracile). In the case of barnacles, B. glandula and P. polymerus, ripe egg lamellae were collected from adults in the field and transported back to the lab where hatching was induced. In the case of gravid female crabs, animals were brought to the lab and each female kept in separate aquarium tank until the larvae hatched. The larger crab, C. antennarius, was kept in a large aquarium (76L) with running seawater. The smaller crabs, Hemigrapsus spp., were kept in individual aquaria (3L) supplied with air bubblers and their water was changed every other day. All crabs were fed Mytilus trossulus daily and monitored more than three times daily

for hatching larvae. Egg masses of the nudibranch, O. bilamellata were collected in the field, brought back to the lab and kept in aquaria with running seawater until time of hatching. Gametes for the anemone, A. xanthogrammica, and the sea star, P. ochraceus, were obtained from spawning captive individuals from a public aquarium at HMSC. These adults had previously been collected along the Oregon coast and were maintained in aquaria with running seawater and fed fish chunks three times a week.

A.2. Larval culture – additional information

With the exception of barnacles, all larval culture methods (including spawning and fertilization) were performed as per the methods outlined in Strathmann (1987) (Table S2). Barnacle cultures followed procedures outlined in Emlet and Sadro (2006). Cultures were intended to consist of the offspring of more than one parent to account for individual variation in the field. This was accomplished by combining the eggs and sperm of two or more females/males or the hatched larvae from more than one egg mass. This was possible for all organisms except Cancer antennarius and Hemigrapsus nudus where only one brooding female was obtained. Cultures were incubated at 8-10oC and kept on a 10:14 hour light:dark photoperiod. The water used for larval rearing was sand and bag filtered to 1 micron and UV filtered. All cultures were reared in 3L glass jars. Cleaning of cultures occurred every other day and was done by reverse sieving. In this process a funnel attached to Tygon tubing and with

micron mesh covering over the mouth of the funnel was used to gently sieve water out of the cultures. Mesh sizes used in reverse sieving were: 30μm mesh for larval stages up to 150μm in size, 100μm for larvae greater than 150μm, and a 250μm mesh for crab larvae. Following reverse sieving, cultures were transferred to clean 3L glass jars containing filtered seawater and the volumes brought up to 3L. Once cultures were cleaned they were fed the appropriate diet. An exception to this feeding regime were anemone cultures, which were fed homogenized brine shrimp (Artemia) prior to cleaning. The Artemia-based food was prepared by hatching 1g of Artemia cysts a day in advance. Twenty-four hours later, hatched brine shrimp were collected, rinsed with filtered seawater, collected on a filter and placed in fresh filtered seawater. They were then homogenized and passed through a 100μm filter. The filtrate was brought to a volume of 800ml and used for feeding anemone larvae. The food was provided in excess (approximately 100ml of homogenate per 3L container) and allowed to sit in the culture for 1-2 hours. Following this period the cultures were cleaned in the same method as other cultures.

A.3. Experimental setup – additional information

All of the containers and tubing used for the experimental setup were built of materials suitable for larval culturing. Tygon tubing was used to carry seawater and gas. Containers that held water that came in contact with larvae were made of either either polypropylene or polycarbonate.

A.4. Experiment – additional information

To create low oxygen conditions, each diffuser tank was bubbled with nitrogen gas. We used liquid nitrogen supplied in a 160L cylinder. Gas flow from the cylinder was set at 5-7.5 scfh, standard cubic feet per hour, and the pressure was set at 10 psi. We built a PVC manifold with ball valves to control the flow of gas into diffusers. From the manifold, gas flowed through Tygon tubing and into glass bonded silica diffusers (Sweetwater Air Diffuser, 9" L x 1.5" W, 1/2" NPT, PE, Aquatic Ecosystems Inc.), which were used for diffusing nitrogen gas into treatment containers. Control of oxygen levels in treatment tanks was achieved through the use of different numbers of diffusers (1 diffuser for control and upwelled water treatments, 3 diffusers and 4 diffusers for hypoxia and microxia treatments respectively) and by adjusting the flow from the PVC manifold via the ball valves. Each time an experimental trial was run, the experimental treatments were assigned randomly to the 50L diffuser tanks. This meant that the location of each treatment alternated through the set of 4 diffuser tanks for each experimental trial. The position of the 1L outflow bottle, connected to one of the four replicate 1L larval containers, for monitoring oxygen and temperature was also assigned randomly, as was the order in which larvae were put into the system for each experiment. Between experiments the whole experimental setup was cleaned thoroughly.

All experiments were run within a temperature range of 8-10oC and kept on a 10:14 hour light:dark photoperiod. Treatments were chosen based on the hypoxic conditions observed on the Oregon coast. There was an extreme low oxygen treatment, called “microxia” (<0.5 ml L-1), a hypoxic treatment called “hypoxia” (>0.5 and <1.4 ml L-1), and a treatment that would represent the oxygen levels of summer upwelled waters called “upwelled water” (1.8-3.6 ml L-1). In addition, there was a control treatment (“control,” 5-7 ml L-1) with oxygen levels representative of dissolved oxygen in the upper 10m of the water column (Chan et al. 2008; Grantham et al. 2004). Oxygen levels were monitored with an YSI Professional Optical Dissolved Oxygen (ProODO) instrument. The sensor in the ProODO is an optical luminescent sensor, which in comparison to traditional electrochemistry sensors has greater stability and less susceptibility to calibration drift (holding its calibration for many months). Calibration of the ProODO to DO % saturation was performed daily following user manual instructions for calibration in water-saturated air. The instrument was also initially calibrated in ml L-1 with a three-point calibration using solutions with known DO concentration (determined by a Winkler Titration). Larvae were not introduced into the system until oxygen levels reached required treatment levels. Once oxygen treatments were set, dissolved oxygen levels remained stable within 10% of the set value and were monitored twice daily.

A.5. Monitoring whether change in pH as a byproduct of low oxygen treatments affects survivorship

Bubbling with nitrogen gas affected the pH of our experiments by raising the pH from 8.1 in the control treatments to 8.3 in the most extreme microxia treatment. To monitor the potential side effects of changing pH as a byproduct of low oxygen treatments we ran an experiment with four treatments including one control (pH 8.1) and three microxic treatments (DO <0.5 ml L-1) of varying pH (7.5, 8.1, 8.3). The first microxic treatment had N2 and enough CO2 gas to reduce pH to 7.5. The second microxic treatment had N2 gas and enough CO2 gas to reduce the pH to 8.1 (the same as the control). The third microxic treatment had only N2 gas and a pH of 8.3. The pH levels were monitored with a Beckman Phi 350 pH meter (Beckman Coulter Inc.). We ran trials on the most sensitive group of larvae – the crabs. We chose Hemigrapsus oregonensis because we had easy access to these individuals.

A mixed model anova with treatment as a fixed effect and date of experimental trial as a random effect showed no significant interaction ($p=0.311$), but there was a significant difference between treatments ($p<0.0001$). Tukey's HSD post hoc test (alpha=0.05) revealed that the control with higher survivorship than microxia treatments was significantly different from the three microxia treatments, but there was no significant difference between any of the microxia treatments with varying pH levels.

Table S1 Collection locations and time of collection. The following table identifies the collection locations and month of collection for spawning or brooding adults and for egg masses of the different species used in experiments. The number of individuals collected is also specified

Species	**Collection location**	**Month of collection**	**Adult, gametes, egg mass**	**Notes**
Anthopleura xanthogrammica	HMSC Aquarium Science Center	June	Gametes	Sperm from three males and eggs from three females collected
Balanus glandula	Seal Rock, Yachats	May, October	Egg mass	Obtained 8 to 12 ripe egg lamellae on each occasion.
Cancer antennarius	Yaquina Bay	May	Gravid adult	Obtained one gravid female
Hemigrapsus nudus	Yaquina Bay	July	Gravid adult	Obtained one gravid female
Hemigrapsus oregonensis	Yaquina Bay	June, August, September	Gravid adult	Obtained four, six, and two gravid females on each occasion
Mytilus californianus	Fogarty Creek	August	Adults	Obtained 50 adults. Twelve were spawned in September, and the remainder were conditioned for spawning in December.
Onchidoris bilamellata	Yaquina Bay	July	Egg mass	Obtained two egg masses
Pisaster ochraceus	HMSC Aquarium Science Center	June	Gametes	Sperm from two males and eggs from three females
Pollicipes polymerus	Yachats	September, October	Egg mass	Obtained four and three ripe egg lamellae on each occasion
Strongylocentrotus purpuratus	Boiler Bay	July	Adults	Obtained 20 adults.

Table S2. Spawning and culturing details. Spawning/hatching procedures, rearing density, rearing setup, and larval culturing diet.

Species	**Spawning/hatching procedure**	**Rearing density**	**Rearing setup**	**Diet**
Anthopleura xanthogrammica	Gametes obtained from spawning individuals at HMSC Aquarium	2 larvae/ml of seawater	Swinging paddle	homogenized *Artemia* nauplii fed the day of *Artemia* hatching
Balanus glandula	Ripe egg lamellae obtained from adults in the field were induced to hatch at the lab by exposing them to fiber optic illumination (see Emlet and Sadro 2006).	2 larvae/ml of seawater	Swinging paddle	$1x10^5$ cells ml^{-1}, 1:1 mixture of *Skeletonema costatum* and *Isochrysis galbana*
Cancer antennarius	Gravid female kept in aquaria; eggs allowed to hatch naturally	1 larva/25ml of seawater	Aerated seawater	*Artemia* nauplii fed the day of hatching
Hemigrapsus nudus	Gravid female kept in aquaria; eggs allowed to hatch naturally	1 larva/25ml of seawater	Aerated seawater	*Artemia* nauplii fed the day of hatching
Hemigrapsus oregonensis	Gravid female kept in aquaria; eggs allowed to hatch naturally	1 larva/25ml of seawater	Aerated seawater	*Artemia* nauplii fed the day of hatching
Mytilus californianus	One-hour immersion in 2-4 mmol/L solution of hydrogen peroxide in seawater brought to pH 9 with 2 mol/L TRIS. Followed by immersion for a few hours in sea water warmed 5-6°C above ambient temperature	5 larvae/ml of seawater	Swinging paddle	$3x10^4$ to $1x10^5$ cells ml^{-1} depending on larval stage, 1:1 mixture of *Isochrysis galbana* and *Chaetoceros neogracile*

Table S2. Spawning and culturing details. (continued)

Species	**Spawning/hatching procedure**	**Rearing density**	**Rearing setup**	**Diet**
Onchidoris bilamellata	Egg mass kept in aquaria and allowed to hatch naturally	5 larvae/ml of seawater	Standing cultures	$1x10^4$ cells ml^{-1}, 1:1 mixture of *Isochrysis galbana* and *Chaetoceros neogracile*
Pisaster ochraceus	Gametes obtained from spawning individuals at HMSC Aquarium	2 larvae/ml of seawater	Swinging paddle	$1x10^4$ cells ml^{-1}, 1:1 mixture of *Isochrysis galbana* and *Rhodomonas salina*
Pollicipes polymerus	Ripe egg lamellae obtained from adults in the field were induced to hatch at the lab by exposing them to fiber optic illumination (see Emlet and Sadro 2006).	2 larvae/ml of seawater	Swinging paddle	$1x10^5$ cells ml^{-1} 1:1 mixture of *Skeletonema costatum* and *Isochrysis galbana*
Strongylocentrotus purpuratus	Injection of 0.5-5ml of 0.53 M KCl into coelom of animal	2 larvae/ml of seawater	Swinging paddle	$1x10^4$ cells ml^{-1}, 1:1 mixture of *Isochrysis galbana* and *Rhodomonas salina*

Table S3. Larval stage or age used in experiments, the number of larvae used in each replicate, the density of larvae in each replicate, and the month when experiments were conducted.

Species	**Larval stage or age**	**Number of larvae**	**Density of larvae**	**Month when conducted experiments**
Anthopleura xanthogrammica	Two-week old anemone planula	100	1 per ml	June
Balanus glandula	Stage IV, V, and VI nauplii	100	1 per ml	May, October, November
Cancer antennarius	Stage I zoea	20	1 per 50ml	June
Hemigrapsus nudus	Stage I zoea	20	1 per 50ml	July
Hemigrapsus oregonensis	Stage I zoea	20	1 per 50ml	June
Mytilus californianus	Pediveligers	1500	3 per 2 ml	September, December
Onchidoris bilamellata	Two-week old veligers	1500	3 per 2 ml	July
Pisaster ochraceus	Bipinnaria, brachiolaria	30	1 per 33ml	June, August
Pollicipes polymerus	Stage IV nauplii	100	1 per ml	October, November
Strongylocentrotus purpuratus	6-arm pluteus and 8-arm pluteus	1500	3 per 2 ml	July, August, September