Adult Demography and Larval Processes in Coastal Benthic Populations: Intertidal Barnacles in Southern California and Baja California

by

Fabián J. Tapia
B.S., University of Concepción, Chile, 1994

Submitted in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

at the

MASSACHUSETTS INSTITUTE OF TECHNOLOGY

and the

WOODS HOLE OCEANOGRAPHIC INSTITUTION

September 2005

Signature of Author ______________________________
Joint Program in Oceanography/Applied Ocean Science and Engineering
Massachusetts Institute of Technology
and Woods Hole Oceanographic Institution
September 2005

Certified by ______________________________
Jesús Pineda
Thesis Supervisor

Accepted by John Waterbury
John Waterbury
Chair, Joint Committee for Biological Oceanography
Woods Hole Oceanographic Institution

To my parents Olga and Luis Alberto.
Their believing in me taught me how to believe in myself.

Adult Demography and Larval Processes in Coastal Benthic Populations: Intertidal Barnacles in Southern California and Baja California

by

Fabián J. Tapia

Joint Program in Oceanography/Applied Ocean Science and Engineering
Massachusetts Institute of Technology and Woods Hole Oceanographic Institution
September 2005

ABSTRACT

The geographic distribution and dynamics of coastal benthic populations are shaped by physical – biological interactions affecting larval dispersal and the demography of juvenile and adult individuals. This thesis focused on nearshore patterns of larval distribution and regional patterns in demography of intertidal barnacles in Southern and Baja California. Horizontal and vertical distributions, and the mortality rates of larvae, were assessed from short term (i.e. days) small-scale observations (0.1-1 km) in nearshore waters. Observations on spatial variability of adult barnacle demography were gathered over 1.5 years at scales of hundreds of kilometers.

Stage-specific horizontal distributions and nearshore current measurements suggested that larvae of *Balanus glandula* and *Chthamalus* spp. may experience limited dispersal. High mortality rates could further limit travel distances and the exchange of individuals among disjunct populations. Data on vertical distributions indicated that nauplii and cyprids of *Balanus nubilus* and *Pollicipes polymerus* occur at different depths. Nauplii remained near the surface at all times, whereas cyprids occurred in the bottom half of the water column. Such distributions, combined with vertical variability in horizontal flows, might cause the observed horizontal segregation of nauplii and cyprids.

Differences in survival, growth rate, size structure, and per capita fertility of adult *Balanus glandula* were observed between Dana Point (Southern California) and Punta Baja (Baja California), a site located near the species' southern limit of distribution. Effects of spatial differences in demography on population persistence were assessed with a stage-structured matrix model. Model analyses indicated that the Punta Baja population is more susceptible to environmental stochasticity and more prone to local extinction than populations located further north.

This thesis emphasizes the importance of characterizing factors that affect the dynamics of benthic populations at multiple spatial-temporal scales, and the usefulness of small scale high-frequency observations of nearshore phenomena, especially in relation with the dispersal of larvae.

Thesis Supervisor :	Jesús Pineda, Associate Scientist Biology Department Woods Hole Oceanographic Institution

ACKNOWLEDGEMENTS

I would like to thank many people who made these years of graduate school possible, and many others who enriched the experience of being here on all levels.

First, it would have been impossible to get here without funding, so I must thank the Chilean MIDEPLAN (Ministerio de Planificación y Cooperación), which provided funds for the first three years of my doctoral studies through a Presidential Fellowship (Beca Presidente de la República). Tuition, stipend, and research funds for the rest of my time as a Joint Program student came from National Science Foundation grants OCE-0083976 and OCE-9986627 to my thesis supervisor (Jesús Pineda), and through the WHOI Academic Programs Office.

Julia, Marsha, and Stacey at the WHOI Academic Programs Office provided all the support I needed through the years. John Farrington and Judy McDowell were always there to listen and to help.

I was lucky to land on a lab where, depending on the lunar phase, time of year, and who knows what other environmental variables, I would find a thesis supervisor, an advisor, a fellow fisherman, or sometimes just a friend to go have a beer with. Jesús was all of that. I learned a lot from him, and I am very grateful for it. Vicke Starczak was many things as well. She was always there, willing to listen to my yapping about the latest plot I had made, to my sometimes untimely statistical questions, and to pretty much any thought that was crossing my mind when I happened to walk into the lab. Claudio DiBacco came to the lab as a post doc and became both a highly regarded colleague and a dear friend, whose feedback on scientific and non-scientific matters was always appreciated. Lynne Davies, Hazel Richmond and Todd Stueckle were important members of this family as well. I am especially grateful to Lynne for her always positive and cheerful attitude towards helping me out with the plankton sorting.

Almost two years of my time as a Woods Hole student were spent in Southern California, where I was lucky to have Jim Leichter host me as a visiting scholar in his lab at the Scripps Institution of Oceanography. Jim provided invaluable logistical and scientific support, and became the advisor away from home and a good friend. Mike Murray, Ed Parnell, Kristin Riser, Catherine Johnson, Luis Vilchis, Carlos Neira, and Falk Feddersen were among the people who made me feel at home at SIO and in the city of San Diego. My work in Baja California would not have been possible without the logistical and moral support provided by Lydia Ladah and Manuel Lopez at CICESE (Ensenada). They had much to do on my getting the work done in a beautiful but sometimes tricky to navigate part of the world.

My dear friends Oscar Pizarro, Sarah Webster, Chris Roman, and Tim Prestero, plus many others I won't even attempt to list here, made me feel part of a community, and thoroughly enjoy every day, season, and year in this town.

Bea deserves a separate paragraph. Her encouragement, boundless generosity, unconditional support, and wonderful company always helped me put things in perspective during this last year of grad school. Contrary to what some people say the last months of a Ph.D. should be like, I really enjoyed the process of finishing my thesis, and Bea had a lot to do with it.

I want to thank my family for their loving support and encouragement. My parents Olga and Luis Alberto have always been my biggest fans. My siblings Margarita, Julio and Luis gave me all the love, attention, and hard times a little brother can handle. Grandpa Rosamel and grandma Margarita watch me get started in this world, and left many wonderful images in my memory. I have been blessed with the environment I grew up in, for it taught me how to enjoy simple things.

Thank you all.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

CHAPTER 1

GENERAL INTRODUCTION

1.1. BACKGROUND AND MOTIVATION OF THIS STUDY

Coastal ecosystems have been modified by human activities over the past centuries (Vitousek et al. 1997; Jackson et al. 2001). A large fraction of the world population is concentrated around coastal areas, which are heavily exploited for food, recreation, and waste disposal. Marine biological communities have been directly affected by these uses, especially by overfishing and habitat degradation (Botsford et al. 1997; Jackson et al. 2001), and will likely be impacted by future changes in global climate (Sagarin et al. 1999). Such changes may affect the distribution and abundance of species, altering the composition of coastal communities and making some species more prone to local extinction, while facilitating the colonization of others. Many species have disappeared from coastal habitats due to natural and human-induced changes in the physical and biological environment (Jackson et al. 2001; Lotze and Milewski 2004), and reports of invasive or exotic species in coastal habitats have recently increased (Ruiz et al. 2000; Orensanz et al. 2002; Castilla et al. 2005). Marine reserves have been established over the last decade as a means to protect habitats and biodiversity, as well as to manage marine resources under exploitation (Dayton et al. 2000; Lubchenco et al. 2003). Underlying the concept of a marine reserve is the principle that an area can be defined such that it encompasses the spatial scale at which population renewal takes place. The size of this "home range" is given by the scale of dispersal of its individuals, which in turn is a function of a species' life cycle and the scale of dominant physical processes (Shanks et al. 2003).

Many species of coastal invertebrates and fish produce larvae that spend minutes to months in the plankton (Levin and Bridges 1995), where they undergo morphological, behavioral and physiological changes before reaching a stage that is competent to metamorphose into a juvenile individual. During their time in the plankton, larvae may be transported by currents and disperse over long distances (Scheltema 1968, 1986), joining the adult population at localities that are often far from their parental sites. Thus, the supply and settlement of larvae onto a given population may be decoupled from its reproductive output. To assess the extent to which population renewal is decoupled from local reproductive output, and to estimate the spatial scales at which disjunct populations exchange individuals (i.e. scales of connectivity), it is necessary to characterize the interaction between larval biology and hydrodynamic processes affecting their dispersal. For instance, increases in the rate of larval mortality with respect to residual current velocities may greatly reduce dispersal distances (Ellien et al. 2004). On the other hand, differences in vertical distribution and swimming behavior may result in distinct patterns of dispersal for different stages of larval development under similar advective regimes (e.g. Bousfield 1955; Rothlisberg and Miller 1983).

Invertebrate larvae vary in size and morphology (Levin and Bridges 1995). Size ranges from tens to thousands of microns, whereas morphology and body architecture include a variety of swimming appendages, calcareous shells, chitinous carapaces, spines, as well as structures that increase buoyancy, facilitate locomotion, or might protect against predators (Morgan 1995). A similarly wide range of variability is found for swimming speeds, which may range from less than 1 cm s^{-1} in ciliated larvae to 2-8 cm s^{-1} in some crustacean larvae (Chia et al. 1984). Horizontal current velocities in coastal waters are typically greater than these swimming speeds (Largier 2003, p. S75 and references therein), hence most invertebrate larvae are unable to determine their position by horizontal swimming. However, vertical shear in horizontal currents may determine specific patterns of circulation and generate differences in the dispersal patterns of larvae occurring at different depths in the water column (Hannah et al. 1997; Hill 1998). For instance, it has been suggested that a number of coastal and estuarine larvae may take advantage of vertical shear and control their horizontal displacements by moving up and down the water column at various times of the tidal or diurnal cycle (e.g. Bousfield 1955;

Forward 1988; DiBacco et al. 2001; Poulin et al. 2002). Neustonic larvae may be transported by onshore-moving warm fronts (Pineda 1994), whereas the larvae of other taxa may be transported by responding to transient hydrodynamic features such as internal bores (Pineda 1999; Helfrich and Pineda 2003). Thus, there are many cases where larvae do not behave as passive particles, and dispersal cannot be predicted simply from mean flows without information on the behavior and vertical distribution of larvae.

It has been suggested that variability in mortality rates may greatly constrain the dispersal distances of invertebrate larvae (e.g. Ellien et al. 2004). However, despite its importance for dispersal and connectivity, available estimates of larval mortality remain scarce and highly uncertain (Rumrill 1990; Morgan 1995). Larval mortality can be estimated directly when larval aggregations are tracked over time, using the observed change in larval abundance to compute a mortality rate averaged over that period. Although such tracking may be feasible in closed or semi-enclosed environments (e.g. Lamare and Barker 1999; Arnold et al. 2005), in open coastal waters it requires observations at spatial and temporal scales that are seldom achieved (e.g. Natunewicz et al. 2001). Thus, laboratory (Johnson and Brink 1998) and indirect field methods are usually employed to estimate mortality from ratios of local larval production to recruitment (e.g. Thorson 1950; Connell 1970) or from information on the stage composition of larvae over a given area (Aksnes et al. 1997).

While the physical and biological processes that affect larval dispersal and mortality may define the potential limits of a species geographic range, the factors that ultimately determine its persistence and demography at a given site are those affecting post-settlement survival (see Gosselin and Qian 1997) and the subsequent recruitment of settlers into reproductive adults. Regional differences in these factors must affect the spatial variability of a population's structure and vital rates and, by extension, its geographic distribution.

1.2. SYNOPSIS

The motivation of this thesis is to understand the processes that affect the nearshore distribution of larval invertebrates and their potential effect on distribution, connectivity, and persistence of coastal benthic populations. Intertidal barnacles were chosen as model species because of their abundance, accessibility and wide distribution in coastal environments, and the extensive body of knowledge on their morphology, reproductive biology, larval development and population dynamics accumulated in the literature for over 100 years (e.g. Darwin 1854; Hatton 1938; Barnes and Barnes 1956; Crisp 1962; Hines 1979; Crisp and Bourget 1985; Barnes 1989; Crisp et al. 1991; Barnes 1999; Wethey 2002). Results presented in following chapters focus on the larvae and adults of the acorn barnacle *Balanus glandula* Darwin, 1854, and on the larvae of *Chthamalus fissus* Darwin 1854, *Pollicipes polymerus* Sowerby, 1833, and *Balanus nubilus* Darwin, 1854. The first three species are numerically dominant on intertidal habitats in Southern California and Baja California. *Balanus glandula* occurs in the high to middle intertidal zone along the west coast of North America from the Aleutian Islands to San Quintín, Baja California (Newman and Abbott 1980). *Chthamalus fissus* is found in the high and upper middle intertidal zone between San Francisco and Baja California (Newman and Abbott 1980). Its distribution occasionally overlaps with that of *Chthamalus dalli* Pilsbry 1916, a northern species found from Alaska to a southern limit that fluctuates between Point Conception (Wares 2001) and San Diego (Newman and Abbott 1980). *Pollicipes polymerus* is found in the middle intertidal zone of wave-swept rocky shores from British Columbia to Punta Abreojos, Baja California (Newman and Abbott 1980), whereas *Balanus nubilus* occurs from the lower intertidal to 90 m depths, and from La Jolla, Southern California, to Alaska (Newman and Abbott 1980).

Observations on the adults and larvae of these species were gathered at regional (10-100 km) and local scales (0.1-1 km), and aimed at addressing questions regarding the effect of nearshore physical processes on larval distribution, dispersal and mortality, as well as the geographic distribution and persistence of adults.

In Chapter 2, I attempt to characterize the small-scale distribution and mortality of larval barnacles in nearshore waters. Stage-specific spatial distributions of *Balanus glandula* and *Chthamalus* spp. larvae were observed daily over seven days. The results are used to discuss the potential for dispersal of larvae in nearshore waters. Chapter 3 presents observations on the vertical distribution of larvae in nearshore waters over a 48 hour period, showing that different stages of development occur at different depths in the water column. These patterns do not change between day and night and, combined with vertical variability in horizontal flows, may explain the horizontal segregation of nauplii and cyprids observed in Chapter 2. The role of onshore winds as a physical mechanism forcing the nearshore distribution of surface material, and possibly of neustonic larvae, is discussed in the publication included as Appendix A.

Chapter 4 focuses on a regional analysis of the population structure and demography of *Balanus glandula* in Southern California and Baja California. Field observations on size structure, growth rates, survival and per capita fertility were combined with a stage-structured matrix population model to assess the effect that spatial changes in demography and environmental variability may have on population persistence and geographic distribution.

Finally, general conclusions from the results of this thesis and recommendations for future research are presented on Chapter 5.

1.3. REFERENCES

Aksnes DL, Miller CB, Ohman MD, Wood SN (1997) Estimation techniques used in studies of copepod population dynamics - A review of underlying assumptions. Sarsia 82: 279-296

Arnold WS, Hitchcock GL, Frischer ME, Wanninkhof R, Sheng YP (2005) Dispersal of an introduced larval cohort in a coastal lagoon. Limnology and Oceanography 50: 587-597

Barnes H, Barnes M (1956) The general biology of *Balanus glandula* Darwin. Pacific Science 10: 415-422

Barnes M (1989) Egg production in cirripedes. Oceanography and Marine Biology Annual Review 27: 91-166

Barnes M (1999) The mortality of intertidal cirripedes. Oceanography and Marine Biology Annual Review 37: 153-244

Botsford LW, Castilla JC, Peterson CH (1997) The management of fisheries and marine ecosystems. Science 277: 509-515

Bousfield EL (1955) Ecological control of the occurrence of barnacles in the Miramichi Estuary. Bulletin of the National Museum of Canada Biological Series 137: 1-65

Castilla JC, Uribe M, Bahamonde N, Clarke M, Desqueyroux-Faundez R, Kong I, Moyano H, Rozbaczylo N, Santelices B, Valdovinos C, Zavala P (2005) Down under the southeastern Pacific: marine non-indigenous species in Chile. Biological Invasions 7: 213-232

Chia F-S, Buckland-Nicks J, Young CM (1984) Locomotion of marine invertebrate larvae: a review. Canadian Journal of Zoology 62: 1205-1222

Connell JH (1970) A predator-prey system in the marine intertidal region. I. *Balanus glandula* and several predatory species of *Thais*. Ecological Monographs 40: 49-78

Crisp DJ (1962) The planktonic stages of the cirripedia *Balanus balanoides* (L.) and *Balanus balanus* (L.) from North temperate waters. Crustaceana 3: 207-221

Crisp DJ, Bourget E (1985) Growth in barnacles. Advances in Marine Biology 22: 199-244

Crisp DJ, Hill EM, Holland DL (1991) A review of the hatching process in barnacles Crustacean Egg Production, pp 57-68

Darwin C (1854) A monograph on the Subclass Cirripedia, with figures of all the species. The Balanidae, the Verrucidae, etc. Ray Society, London

Dayton PK, Sala E, Tegner MJ, Thrush S (2000) Marine reserves: parks, baselines, and fishery enhancement. Bulletin of Marine Science 66: 617-634

DiBacco C, Sutton D, McConnico L (2001) Vertical migration behavior and horizontal distribution of brachyuran larvae in a low-inflow estuary: implications for bay-ocean exchange. Marine Ecology Progress Series 217: 191-206

Ellien C, Thiebaut E, Dumas F, Salomon J-C, Nival P (2004) A modelling study of the respective role of hydrodynamic processes and larval mortality on larval dispersal and recruitment of benthic invertebrates: example of *Pectinaria koreni* (Annelida: Polychaeta) in the Bay of Seine (English Channel). Journal of Plankton Research 26: 117-132

Forward RBJ (1988) Diel vertical migration: zooplankton photobiology and behaviour. Oceanography and Marine Biology Annual Review 26: 361-393

Gosselin LA, Qian P-Y (1997) Juvenile mortality in benthic marine invertebrates. Marine Ecology Progress Series 146: 265-282

Hannah CG, Naimie CE, Loder JW, Werner FE (1997) Upper-ocean transport mechanisms from the Gulf of Maine to Georges Bank, with implications for *Calanus* supply. Continental Shelf Research 17: 1887-1911

Hatton H (1938) Essais de bionomie explicative sur quelques espèces intercotidales d'algues et d'animaux. Annls Inst Océanogr Monaco 17: 241-348

Helfrich KR, Pineda J (2003) Accumulation of particles in propagating fronts. Limnology and Oceanography 48: 1509-1520

Hill AE (1998) Diel vertical migration in stratified tidal flows: Implications for plankton dispersal. Journal of Marine Research 56: 1069-1096

Hines AH (1979) The comparative reproduction ecology of three species of intertidal barnacles. In: Stancyk SE (ed) Reproductive Ecology of Marine Invertebrates. University of South Carolina Press, Columbia, pp 213-234

Jackson JBC, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, Bradbury RH, Cooke R, Erlandson J, Estes JA, Hughes TP, Kidwell S, Lange CB, Lenihan HS, Pandolfi JM, Peterson CH, Steneck RS, Tegner MJ, Warner RR (2001) Historical overfishing and the recent collapse of coastal ecosystems. Science 293: 629-638

Johnson KB, Brink LA (1998) Predation on bivalve veligers by polychaete larvae. Biological Bulletin 194: 297-303

Lamare MD, Barker MF (1999) *In situ* estimates of larval development and mortality in the New Zealand sea urchin *Evechinus chloroticus* (Echonodermata: Echinoidea). Marine Ecology Progress Series 180: 197-211

Largier JL (2003) Considerations in estimating larval dispersal distances from oceanographic data. Ecological Applications 13: S71-S89

Levin LA, Bridges TS (1995) Pattern and diversity in reproduction and development. In: McEdward L (ed) Ecology of Marine Invertebrate Larvae. CRC Press, Boca Raton, pp 1-48

Lotze HK, Milewski I (2004) Two centuries of multiple human impacts and successive changes in a North Atlantic food web. Ecological Applications 14: 1428-1447

Lubchenco J, Palumbi SR, Gaines SD, Andelman S (2003) Plugging a hole in the ocean: the emerging science of marine reserves. Ecological Applications 13: S3-S7

Morgan SG (1995) Life and death in the plankton: larval mortality and adaptation. In: McEdward L (ed) Ecology of Marine Invertebrate Larvae. CRC Press, Boca Raton, FL, pp 279-321

Natunewicz CC, Epifanio CE, Garvine RW (2001) Transport of crab larval patches in the coastal ocean. Marine Ecology Progress Series 222: 143-154

Newman WA, Abbott DP (1980) Cirripedia: the barnacles. In: Morris RH, Abbott DP, Haderlie EG (eds) Intertidal Invertebrates of California. Stanford University Press, Stanford, pp 502-535

Orensanz JM, Schwindt E, Pastorino G, Bortolus A, Casas G, Darrigran G, Elias R, Lopez Gappa JJ, Obenat S, Pascual M, Penchaszadeh P, Piriz ML, Scarabino F, Spivak ED, Vallarino EA (2002) No longer the pristine confines of the world ocean: A survey of exotic marine species in the Southwestern Atlantic. Biological Invasions 4: 115-143

Pineda J (1994) Internal tidal bores in the nearshore: warm-water fronts, seaward gravity currents and the onshore transport of neustonic larvae. Journal of Marine Research 52: 427-458

Pineda J (1999) Circulation and larval distribution in internal tidal bore warm fronts. Limnology and Oceanography 44: 1400-1414

Poulin E, Palma AT, Leiva G, Narvaez D, Pacheco R, Navarrete SA, Castilla JC (2002) Avoiding offshore transport of competent larvae during upwelling events: The case of the gastropod *Concholepas concholepas* in Central Chile. Limnology and Oceanography 47: 1248-1255

Rothlisberg PC, Miller CB (1983) Factors affecting the distribution, abundance, and survival of *Pandalus jordani* (Decapoda, Pandalidae) larvae off the Oregon coast. Fishery Bulletin 81: 455-472

Ruiz GM, Fofonoff PW, Carlton JT, Wonham MJ, Hines AH (2000) Invasion of coastal marine communities in North America: Apparent patterns, processes, and biases. Annual Review of Ecology and Systematics 31: 481-531

Rumrill SS (1990) Natural mortality of marine invertebrate larvae. Ophelia 32: 163-198

Sagarin RD, Barry JP, Gilman SE, Baxter CH (1999) Climate-related change in an intertidal community over short and long time scales. Ecological Monographs 69: 465-490

Scheltema RS (1968) Dispersal of larvae by Equatorial ocean currents and its importance to the zoogeography of shoal-water tropical species. Nature 217: 1159-1162

Scheltema RS (1986) On dispersal and planktonic larvae of benthic invertebrates: An eclectic overview and summary of problems. Bulletin of Marine Science 39: 290-322

Shanks AL, Grantham BA, Carr MH (2003) Propagule dispersal distance and the size and spacing of marine reserves. Ecological Applications 13: S159-S169

Thorson G (1950) Reproductive and larval ecology of marine bottom invertebrates. Biological Reviews 25: 1-45

Vitousek PM, Mooney HA, Lubchenco J, Melillo JM (1997) Human domination of earth's ecosystems. Science 277: 494-499

Wares JP (2001) Patterns of speciation inferred from mitochondrial DNA in North American *Chthamalus* (Cirripedia: Blanomorpha: Chthamaloidea). Molecular Phylogenetics and Evolution 18: 104-116

Wethey DS (2002) Biogeography, competition, and microclimate: The barnacle *Chthamalus fragilis* in New England. Integrative and Comparative Biology 42: 872-880

2. CHAPTER 2

LIMITED DISPERSAL AND HIGH MORTALITY OF BARNACLE LARVAE IN THE NEARSHORE

2.1. ABSTRACT

The stage-specific spatial distribution and mortality of *Balanus glandula* and *Chthamalus* spp. larvae were assessed from a series of daily vertical plankton tows collected off La Jolla, Southern California, on 6-12 March 2003. Sampling stations were located within 1.1 km of the shoreline, at depths of 10 – 45 meters. Vertical distributions of temperature and current velocities were recorded at an average depth of 16 m. For both species, a spatial segregation of naupliar stages and cyprids was observed, although the differences were statistically significant for *Chthamalus* spp. only. Earlier naupliar stages (NII-NIII) were more abundant at the inshore stations, whereas later stages (NIV-NVI) were more abundant at the offshore. Cyprid concentrations were higher at the inshore stations. These structured spatial distributions suggest limited dispersal of intertidal barnacle larvae in the nearshore. Trajectories computed from current measurements, and a set of assumptions regarding the vertical distribution of larvae, predicted short dispersal distances (2-8 km) over a 7-day period. Vertical life tables were used to estimate naupliar mortality from daily stage distributions. Average estimates for the instantaneous rate of larval mortality in *B. glandula* and *Chthamalus* spp. were 0.329 d^{-1} (SD=0.045 d^{-1}) and 0.232 d^{-1} (SD=0.033 d^{-1}), respectively. These mortality estimates are substantially higher than previously assumed for these species. I discuss the limitations of these data, as well as the implications of limited dispersal and high larval mortality for the connectivity among populations of intertidal barnacles and other coastal species with a similar life cycle.

2.2. INTRODUCTION

Many coastal benthic invertebrates have complex life cycles. Sedentary adults release larvae into the pelagic environment, where development is completed within days to months (Levin and Bridges 1995). Larvae may be transported over long distances during their development (Scheltema 1968, 1986), which often results in recruitment being decoupled from adult abundance at any given site. Coastal populations are thus considered open in terms of their reproductive output and local demography. To assess how much of the local recruitment is determined by local reproductive output, the rates of dispersal and mortality of early larval stages must be known. The speed, trajectory and vertical variability of horizontal currents play an important role on larval dispersal, especially for species whose vertical distribution changes over the course of development (e.g. Bousfield 1955).

Intertidal barnacles are conspicuous members of coastal communities around the world. Their high abundance, wide geographical distribution, and sessile adult stage make them good model species for the study of interactions between larval dispersal and the openness of a population. Past studies have focused on mesoscale patterns of adult and larval distribution (i.e. tens to hundreds of km), as well as their dependence on physical variability at similar scales. Mathematical models that couple benthic and oceanic processes have been used in a series of influential studies (Roughgarden et al. 1988; Possingham and Roughgarden 1990; Alexander and Roughgarden 1996; Connolly and Roughgarden 1998; Gaylord and Gaines 2000) to assess the effect of biological and physical variables on mesoscale patterns of barnacle distribution. Central to all of these studies is the idea that larvae are swept away from their parental, intertidal populations by along-shore and cross-shore advection, determined by mesoscale coastal circulation and Ekman transport, respectively (Roughgarden et al. 1988). In this framework, the openness and connectivity of intertidal barnacle populations are determined by the survival of larvae in the plankton, the intensity of onshore transport, and substrate availability.

Extensive research has been done on the influence of substrate type and availability on larval settlement and recruitment (e.g. Raimondi 1988; Pineda 1994b; Pineda and Caswell 1997), as well as the physical mechanisms that mediate the onshore transport of larvae. Patterns of larval settlement have been linked to the occurrence of internal waves (Shanks 1983), internal tidal bores (Pineda 1991, 1994a), persistent onshore winds (Bertness et al. 1996), and the cross-shore displacement of surface waters during relaxation of wind-induced upwelling (Farrel et al. 1991; Wing et al. 1995). Contrastingly, the survival and dispersal of early larval stages in the nearshore have not been investigated extensively (but see Natunewicz et al. 2001), although retention and self-recruitment might be more prevalent than previously thought (Cowen et al. 2000; Sponaugle et al. 2002; Warner and Cowen 2002). Assessing the scales of dispersal and the mortality of larvae in the nearshore is thus necessary for understanding the interactions between nearshore hydrodynamics and the openness of coastal populations.

In this contribution I examine the small-scale (~1 km from shore) horizontal distribution and estimate the mortality rate of larval *Balanus glandula* and *Chthamalus* spp., the two most abundant species of intertidal barnacles on the US West Coast. Persistent patterns of spatial distribution were observed, with a horizontal segregation of late naupliar stages and cyprids. These observations and a series of particle trajectories predicted from nearshore current velocities suggest a limited larval dispersal larvae. Larval mortality estimates for both species were substantially higher than the rates previously assumed (see Gaylord and Gaines 2000, p. 774). I discuss the limitations of these results in relation to local physical variability and larval behavior, as well as the assumptions underlying the estimation of larval mortality rates.

2.3. MATERIALS AND METHODS

2.3.1. Study site and species

The survey was conducted in nearshore waters off the Scripps Institution of Oceanography (SIO) pier in La Jolla, Southern California, between 6-13 March 2003 (hereafter Days 1-8 of the survey). Intertidal barnacles on which this study was based are two of the most abundant species found on the US West Coast. The acorn barnacle *Balanus glandula* Darwin, 1854 occurs in the high to middle intertidal zone along the west coast of North America from the Aleutian Islands to San Quintín, Baja California (Newman and Abbott 1980). *Chthamalus fissus* is found between San Francisco and Baja California (Newman and Abbott 1980), and dominates the high to upper middle intertidal in La Jolla. Its distribution, however, occasionally overlaps with that of *C. dalli,* a northern species found from Alaska to a southern limit that fluctuates between Point Conception (Wares 2001) and San Diego (Newman and Abbott 1980). Although adult *C. fissus* and *C. dalli* can be identified by dissection and microscopic examination (Newman and Abbott 1980), their larvae are morphologically identical (Miller et al. 1989). Thus, chthamalid larvae will be referred to as *Chthamalus* spp., as larval identification was based solely on morphological criteria (see below).

Timing of the survey was based on the known reproductive cycle of *B. glandula* and *C. fissus*, and aimed at finding their larvae in nearshore waters. *Chthamalus* settlers can be found year round at a wide range of tidal heights in Central and Southern California (Hines 1979; Pineda 1994b and unpublished observations). Individuals reach sexual maturity ca. 2 months after settlement, after which up to 16 small broods are continuously produced each year (Hines 1976). Adult *B. glandula*, in contrast, produce 2 to 6 broods over a reproductive season that extends from early winter to late spring (Barnes and Barnes 1956; Hines 1979; Newman and Abbott 1980). Settlement takes place between late winter and early summer (Hines 1979 and author's unpublished observations).

2.3.2. Sampling procedure

Plankton samples were collected daily over 7 days from 3 stations located within 0.3, 0.6 and 1.1 km of the shoreline, at depths of 10 – 40 m (Fig. 2.1). Plankton was collected by vertically towing a 110 μm mesh net (0.75 m diameter, 2.75 m length) from bottom to surface. The water volume sampled at each station was estimated using a mechanical flowmeter (General Oceanics 2030). Samples were taken into the laboratory and preserved in 95% ethanol.

Concurrently with the plankton survey, I monitored settlement of *B. glandula* and *Chthamalus* spp. larvae on collectors deployed within the vertical range of adult distribution at a nearby intertidal site (Dike Rock, Fig. 2.1). Collectors were made out of 11-cm long pieces of white PVC pipe (2.54 cm diameter), which were cut in half lengthwise and grooved in three areas. A hole was drilled in the center, so that the collectors could be attached to the substrate using stainless steel screws that were cemented into holes drilled in the rock. Settlement collectors were first deployed on Day 1 and recovered/replaced daily during the daytime low tide until Day 8. Tidal height and wave action precluded the recovery of collectors on Day 4. Barnacles on recovered collectors were identified and enumerated using a dissecting microscope. Only larvae that settled within *ca.* 0.16 mm of the intersection between the groove bottom and wall were counted, since settlement rarely occurs outside this area. Hence, the area of substrate per collector was ~1.9 cm^2 (Pineda 1994b). Settlement rates were computed as number of settlers per day of deployment.

2.3.3. Identification of larvae and analysis of spatial patterns

The classification of larvae by species and stage was based on morphological descriptions for *Balanus glandula* (Branscomb and Vedder 1982; Brown and Roughgarden 1985) and *Chthamalus* spp. larvae (Miller et al. 1989), as well as for other species that occur in the study area (Lewis 1975; Miller and Roughgarden 1994). Abundances of naupliar stages NII through NVI are reported only, as NI larvae molt into NII within hours of hatching at the temperatures recorded in the survey area (Brown and Roughgarden 1985; Miller et al. 1989).

Spatial patterns in the distribution of different larval stages were analyzed using a two-way Analysis of Variance (ANOVA) without replicates, in which sampling stations and days were used as factors. To achieve homogeneity of variances prior to the analysis, concentrations of nauplii and cyprids were transformed as $\log(x+1)$ and $-1/(x+1)$, respectively.

2.3.4. Environmental variables

From Day 1, temperature in the water column was recorded at 1 minute intervals with Onset Stowaway XTI loggers (response time < 15 sec), located at the surface and at 1, 2, 4, 6, 8, 10, 12 and 14 meters above the bottom (mab). The string of loggers was deployed at a depth of ca. 18 m (Fig. 2.1). Horizontal and vertical currents were measured with a bottom-mounted 1,200 kHz Acoustic Doppler Current Profiler (ADCP, RD Instruments, USA), deployed on Day 1 near Station 2 at a depth of ca. 16 m (Fig. 2.1). Measurements were recorded in 1 meter bins at 1-min intervals (60 pings per ensemble). Due to the temporal variability in water depth introduced by tidal fluctuations, surface wave action, and side lobbing, data collected from the surface bins had to be discarded. The uppermost bin with reliable data was at 14 mab, which was on average 2 m below the surface.

Data on hourly wind velocity and direction were obtained from the SIO Coastal Data Information Program website (http://cdip.ucsd.edu). The wind gauge (Qualimetrics Skyvane anemometer) was located at 20.2 m above Mean Lower Low Water (MLLW), on the west end of the SIO Pier. Wind data were rotated and aligned to the average shoreline orientation (21° with respect to true north) and then decomposed into along-shore and cross-shore components. ADCP data were aligned to the main axis of variability for horizontal currents (24.7° with respect to true north), which roughly paralleled the shoreline orientation. The orientation of this axis was given by the major eigenvector of a covariance matrix computed for depth-averaged east and north velocities.

2.3.5. Assessment of potential dispersal – Progressive Vector Diagrams

Hypotheses regarding the nearshore distribution of barnacle larvae were formulated using Progressive Vector Diagrams (PVD). The construction of these diagrams is based on the strong assumption that horizontal currents measured at a single point are representative of a larger area. PVDs were used as a first-order approach to project the trajectory of particles found in nearshore waters at the study area. The goal of this analysis was to assess how likely it is for a particle to remain in nearshore waters within the time scale of this study (7 days). Near-surface current velocities from moored current meters might fail to predict the trajectory of particles found in the uppermost layer of the water column (Tapia et al. 2004, Appendix A). However, it was assumed that the depth range for which reliable current meter data were available (2-14 mab) was representative of the vertical range of larval distribution.

PVDs were computed as predicted (x, y) positions at time t_n :

$$x(t_n) = \Delta t \sum_{i=1}^{n} u(t_i) \qquad y(t_n) = \Delta t \sum_{i=1}^{n} v(t_i) \tag{2.1}$$

where $u(t)$ and $v(t)$ are the east and north current speeds measured by the current meter at a given depth at time t, and Δt is the sampling interval (Emery and Thomson 1998, p. 165). PVDs were computed for the duration of the study, and for six different patterns of larval vertical distribution. First, it was assumed that larvae are uniformly distributed in the water column, and their trajectory was predicted using depth-averaged current velocities. For the second through fourth alternative patterns, it was assumed that larvae remain at mid depths (7-9 mab), near the bottom (2-4 mab), and near the surface (12-14 mab) at all times. In the last two cases, larvae were assigned behavior in the form of diurnal vertical migrations (DVM), so that they occur near the bottom during the day (defined as 6:00-18:00 PST) and near the surface at night. In one case (Two-layer DVM) larvae were assumed to move between the upper and lower half of the water column, whereas in the final example (Extreme DVM) larvae moved between a 3-m thick layer near the surface (12-14 mab) and a layer of similar thickness near the bottom (2-4 mab).

2.3.6. Estimation of larval mortality

Vertical life tables (Aksnes and Ohman 1996) were used to estimate the mortality of nauplius larvae. The method yields estimates of mortality at the transitions between contiguous larval stages, and is recommended for cases where advection is expected to affect the horizontal distribution of larvae (Aksnes et al. 1997). Mortality is estimated from instantaneous stage distributions (i.e. obtained at one point in time), hence it is not necessary to track a particular larval aggregation. Instead, the stage distribution must be representative of the population under study, and spatial coverage and resolution should be large enough to compensate for the effect of small-scale patchiness.

Derivations of the method presented by Aksnes and Ohman (1996, p. 1462) are summarized below. Three main assumptions are made : (1) daily recruitment (ρ_i) to a given stage i is constant over the duration of that stage, (2) the duration of a stage (α_i) is constant and equal for all individuals in the same stage, and (3) the mortality over that period (θ_i) is constant. Thus, the number of nauplii in stage i at time $t = x$ can be expressed as:

$$n_i = \rho_i \int_{x-\alpha_i}^{x} \exp[-\theta_i(x-t)]dt = \frac{\rho_i}{\theta_i}[1-\exp(-\theta_i\alpha_i)] \tag{2.2}$$

which is equal to the number of larvae that recruited during the last α_i days and survived (Aksnes and Ohman 1996). If it is also assumed that the mortality rate is constant for a period equal to the duration of two consecutive stages i and i+1, then the number of nauplius larvae in stage i+1 at day x is :

$$n_{i+1} = \rho_{i+1} \int_{x-\alpha_{i+1}}^{x} \exp[-\theta(x-t)]dt = \frac{\rho_{i+1}}{\theta}[1-\exp(-\theta\alpha_{i+1})] \tag{2.3}$$

The number of cyprid larvae, for which the stage duration α_c is assumed infinite by the analysis, can be expressed as :

$$n_c = \rho_c \int_{-\infty}^{x} \exp[-\theta_c(x-t)]dt = \frac{\rho_c}{\theta_c} \tag{2.4}$$

Finally, the rate of recruitment to a stage i+1 is the product of recruitment to the previous stage i and the stage-specific survival :

$$\rho_{i+1} = \rho_i \exp(-\theta_i\alpha_i) \tag{2.5}$$

An equation that relates the relative abundance of two consecutive stages with their duration and mortality rate can be obtained by combining Eqs. 2.2, 2.3, and 2.5, and by setting $\theta_i = \theta$:

$$\frac{n_i}{n_{i+1}} = \frac{\exp(\theta\alpha_i)-1}{1-\exp(-\theta\alpha_{i+1})} \tag{2.6}$$

Similarly, an equation that relates the number of nauplius VI and cyprid larvae can be obtained by combining Eqs. 2.2, 2.4, and 2.5.

$$\theta = \frac{1}{\alpha_{VI}} \ln\left(\frac{n_{VI}}{n_C} + 1\right) \tag{2.7}$$

Equation 2.6 was solved iteratively to obtain estimates of the mortality rate at the transition between naupliar stages NII-NV. The estimated mortality of NVI larvae was obtained directly from Equation 2.7. Estimates of the number of individuals per stage for each day with plankton observations (Days 1-7) were obtained by pooling larval counts recorded at the three stations. An average stage duration of 3 days was used for *Chthamalus* spp. (Miller et al. 1989), whereas durations of 1, 2, 2, 3, and 3 days were used for *B. glandula* NII, NIII, NIV, NV, and NVI, respectively (Brown and Roughgarden 1985).

2.4. RESULTS

2.4.1. *Spatial-temporal distribution of larval stages*

Patterns of spatial distribution for different larval stages were consistent for both species. In general, earlier naupliar stages (NII and NIII) were more abundant at the inshore stations, whereas later stages (NV-NVI) increased in abundance towards the offshore station (Fig. 2.2, 2.3). The statistical analysis of stage-specific distributions indicated no significant between-station differences for all but one larval stage in *Balanus glandula* (NII, Table 2.1). Conversely, the analysis of *Chthamalus* spp. distributions indicated significant spatial differences in all but one case (NII, Table 2.1). The concentration of *B. glandula* NII larvae at the offshore station was significantly lower than at the inshore stations (Table 2.1). On the other hand, concentrations of *Chthamalus* spp. NIV, NV, and NVI larvae were significantly higher at the offshore station. Although not statistically significant for *B. glandula*, cyprid concentrations were higher at the inshore stations (Fig. 2.2f, 2.3f) and resembled the distributions of NII rather than, for instance, NVI.

High concentrations of cyprids relative to NVI larvae at the inshore station suggest that cyprids were advected from an adjacent source, or that their distribution was dictated by a different set of physical and behavioral factors. These high concentrations of cyprids at the inshore station could also be the result of accumulation over an undetermined number of days. Patchiness in larval distribution appeared to be species specific. For example, on Day 1 the concentration of *B. glandula* NII decreased steadily from 14.5 to 1.5 indiv m^{-3} between the inshore and offshore station (Fig. 2.2a), whereas *Chthamalus* spp. NII peaked at Station 2 with 108 indiv m^{-3}. This concentration was two orders of magnitude higher than observed at the other two stations (Fig. 2.3a).

2.4.2. Temporal variability in stage distribution

Daily stage distributions for *B. glandula* and *Chthamalus* spp. (Fig. 2.4a-g, 2.4h-n) were obtained by pooling larval counts from the three sampling stations. All stages of larval development in *B. glandula* were observed on all but one day of the survey (Fig. 2.4f). Stage distributions of *B. glandula* were dominated by NII and NIV during the first three days of the survey (Fig. 2.4a-c). The distributions observed on subsequent days were dominated by NII (Fig. 2.4d-g), suggesting a constant input of newly hatched larvae, either released by local adults of advected into the study area from adjacent populations. Stage distributions of *Chthamalus* spp. larvae were dominated by NII on five out of seven days of observations (Fig. 2.4h-n), but most notably on days 5-7 (Fig. 2.4k-n). This suggests a continuous input of larvae released locally or at a site from which they can be advected within the time it takes for the NII-NIII transition to occur (~3 days, Miller et al. 1989). A high abundance of cyprid larvae on days 3-5 and 7, relative to the abundance of NVI larvae (Fig. 2.4j-l,n), suggests that cyprids are either transported into the study area from an external source or accumulated over time.

2.4.3. Settlement at Dike Rock

Larvae of both species settled at Dike Rock throughout the survey (Fig. 2.5), suggesting that cyprids found in the plankton samples were competent to settle. In general, and consistent with their higher abundance in the plankton (Fig. 2.3f), *Chthamalus* spp. cyprids settled at higher rates than those of *B. glandula* (Fig. 2.5a). While the timing of settlement in *B. glandula* was not correlated with changes in cyprid abundance in the nearshore (Fig. 2.5b), daily changes in the rate of settlement of *Chthamalus* spp. larvae were positively correlated with daily changes in their concentration at the inshore station (Fig. 2.5c).

2.4.4. Environmental variables

Wind data for March 2003 indicated that the survey was conducted during a relatively calm period (Fig. 2.6a, inset). Cross-shore wind speeds ranged from –2.5 to 3.2 m s^{-1} (positive is onshore, 111° east of true north), whereas along-shore speeds ranged between –2.0 and 2.8 m s^{-1} (positive is 21° east of true north). Fluctuations in cross-shore wind velocities, up to 3 m s^{-1} in amplitude (Fig. 2.6a), followed a diurnal cycle that was consistent with the daily sea breeze.

Horizontal currents measured during the survey were dominated by along-shore flows (Fig. 2.6b). Along-shore currents were more energetic (up to 17 cm s^{-1}) and uniformly distributed through the water column than cross-shore currents ($\leq$ 10 cm s^{-1}), where most of the energy was concentrated near the surface (Fig. 2.6c). Variability in the along-shore flow was dominated by the barotropic tide, with semidiurnal changes in current direction throughout the water column (Fig. 2.6b). The vertical structure of cross-shore flows, on the other hand, was consistent with the structure of mode one internal motions, often showing two layers of variable thickness that were flowing in opposite directions (Fig. 2.6c).

Temperature measurements showed a stratified water column, with differences between the surface and the bottom that reached ca. 5°C on Day 7 (Fig. 2.6d). Semidiurnal fluctuations in temperature distribution, associated with the tidal cycle, occurred throughout the survey. A propagating internal tidal bore warm front was observed in the afternoon of Day 3 (Fig. 2.6d). The occurrence of this bore coincided with an increase in the velocity of onshore currents throughout the water column, especially near the bottom (Fig. 2.6c), as well as a change in the vertical structure of along-shore velocities (Fig. 2.6b). Although a high tide made it impossible to record settlement immediately after such feature occurred (Day 4), maximum *Chthamalus* spp. settlement was observed on the following day (Fig. 2.5a).

2.4.5. Progressive Vector Diagrams

In no instance did the PVD produce trajectories that suggest an offshore dispersal of larvae (Fig. 2.7). According to the predicted trajectories, larvae would remain within ca. 2 km of their release point in all but one case. Only when larvae were assumed to occur near the bottom at all times did the PVD predict a longer, northward trajectory that intersected with the shoreline ~8 km north of the starting point (Fig. 2.7b). Trajectories predicted when PVD computations were started at different phases of the tidal cycle (symbols in Fig. 2.7) suggested that the tidal phase during which particles are released should not affect the expected range of dispersal distances.

2.4.6. Mortality estimates

Highly variable daily stage distributions (Fig. 2.4) precluded the estimation of mortality for all transitions between naupliar stages. Larval counts were pooled for the contiguous stages NII-NIII and NIV-NV, so that reported mortality estimates correspond to the transitions NII+NIII → NIV+NV, NIV+NV → NVI, and NVI → C (Table 2.2). Average mortality estimates ranged between 0.298 d^{-1} and 0.396 d^{-1} for *B. glandula*, and between 0.176 d^{-1} and 0.309 d^{-1} for *Chthamalus* spp.. There was no trend in the average values or in the variability of mortality estimates with stage transitions (Fig. 2.8). Average mortality rates computed across stage transitions and days were 0.329 d^{-1} (SE=0.045 d^{-1}) for *B. glandula* larvae, and 0.232 d^{-1} (SE=0.033 d^{-1}) for *Chthamalus* spp.

2.5. DISCUSSION

I have shown stage-specific patterns of spatial distribution that point to a limited dispersal of intertidal barnacle larvae in the nearshore, and estimated mortality rates that are substantially higher than previously assumed. However, large daily fluctuations in the observed stage distributions suggest that the spatial coverage and resolution of the survey were insufficient to compensate for nearshore advection and small-scale patchiness. Thus, the basic assumption of the mortality estimation method may have not been met. Despite the apparent effect of advection on the observed stage structures, spatial distributions of late larval stages suggested that larvae may complete their development within a short distance from shore. The generality of these results should be tested at sites with different coastal configuration and bathymetry, as two submarine canyons flanking the study area may have played a role in the nearshore retention of larvae. Horizontal flows and their variability at scales of kilometers, together with stage-specific patterns of vertical distribution, must be better described before any conclusions can be drawn as to dispersal distances expected for these larvae.

2.5.1. Spatial distribution and settlement of larvae

Observed temporal changes in stage distributions suggested a continuous input of early nauplii (NII) into nearshore waters, especially after Day 4 (Fig. 2.4). Consistently higher concentrations of NII larvae at Stations 1 and 2 could indicate a continuous production of larvae at the study area, superimposed with continuous input of larvae produced at neighboring populations. Food availability and water temperature affect the rate of development in barnacle larvae (Barnes and Barnes 1958; Scheltema and Williams 1982). Assuming that food concentration is sufficiently high, it should take 2-3 days for NII larvae to molt into NIII at the average temperature of ca. 15°C recorded during this study (Brown and Roughgarden 1985; Miller et al. 1989). During such time, a passive particle in the area could have been transported 2.4 - 3.6 km northward, based on a depth-averaged mean velocity of 1.4 cm s^{-1} computed from alongshore current measurements. Thus, intertidal populations located within a few kilometers of each other could be connected through the dispersal of early larval stages, assuming that their behavior resembles that of a passive particle more closely than that of later stages.

Cyprid concentrations at the inshore station were higher than those of NVI larvae, suggesting that some of the observed cyprids did not settle immediately after molting from a NVI larva and were accumulated over an undetermined number of days. Nauplii and cyprids are likely to exhibit different behaviors, especially in terms of their response to transient hydrodynamic features that could transport them onshore (Pineda 1999; Helfrich and Pineda 2003). Cyprids collected at the inshore station may have also been transported from an adjacent population, or from an offshore source located beyond Station 3. Current velocities recorded during this study, and the change in relative importance of advective versus diffusive forces as a function of distance to shore (see Largier 2003), suggest that advection by currents is more likely to affect the along-shore distribution of larvae. Thus, higher concentrations of cyprid larvae at the inshore station are probably the result of an interaction between stage-specific behavior, duration of the cyprid stage, and the variability of cross-shore flows. Vertical distributions of cyprids and their responses to transient hydrodynamic features must be assessed in order to further investigate this question.

Cross-shore flows of opposite directions, dominated by the internal tide, were often observed in the current meter data, whereas along-shore flows were predominately uniform throughout the water column. Under such conditions, vertically migrating larvae may be able to control their distance to shore, but unable to control their position on the along-shore axis, which would be strongly affected by the energetic flows associated with the barotropic tide. Net alongshore transport may be restricted due to the oscillatory nature of tidal flows, although it has been shown that oscillating along-shore flows can generate complex spatial-temporal patterns of larval distribution (Richards et al. 1995).

An increase in the abundance of later stages at the offshore station towards the end of the survey could be ascribed to an accumulation of larvae produced at a number of neighboring populations, rather than to the retention of larvae released only at the study area. No conclusion can be reached, however, without knowledge on the ontogenetic patterns in vertical distribution and migration behavior of these larvae.

Another factor that could contribute to the observed patterns of cross-shore larval distribution is the effect of wind forcing on the transport of surface materials. As previously observed at a similar site in the region (Tapia et al. 2004), cross-shore winds blew onshore during the day and slightly reversed their direction at night. Although at this point it is not known whether late larval stages occur close enough to the surface to be affected by onshore winds, larval settlement observed at the appropriate frequencies could provide a means to test for this potential association. The frequency of settlement observations in this study did not allow us to test for a correlation with diurnal changes in wind forcing. Had settlement been monitored at a semi-diurnal frequency (e.g. at dawn and dusk), significantly higher numbers of settlers should have been observed at dusk if cross-shore winds have any effect on the distribution of competent larvae.

2.5.2. Assessing larval dispersal in nearshore waters

As larvae develop in the plankton, they acquire behaviors that could either increase dispersal or facilitate retention. For example, crustacean larvae use diurnal vertical migrations or other vertical swimming behaviors to exploit vertical shear in horizontal currents to move in and out of estuaries (Forward 1988) or bays (DiBacco et al. 2001), or to remain close to shore (Sponaugle et al. 2002, p. 349). Mortality and dilution, on the other hand, cause a decrease in the abundance of larvae in nearshore waters to an extent that is currently unknown for most species (but see Ellien et al. 2004). Estimating these rates in the field requires tracking aggregations of larvae with a spatial and temporal resolution that is rarely achieved (e.g. Natunewicz et al. 2001; Arnold et al. 2005).

Tagging larvae to estimate mortality and dispersal through a mark-recapture approach has numerous disadvantages and logistical limitations (see Levin 1990), especially for larvae that are as small and abundant as the larvae of intertidal barnacles. Natural or environmentally-induced tags have provided a means to assess larval dispersal over temporal scales of days to months (e.g. Swearer et al. 1999; DiBacco and Levin 2000; Becker et al. 2005). However, the applicability of this approach to tracking barnacle larvae is very limited, given the duration of their planktonic life and the loss of hard structures during ecdysis. Nauplius I larvae, for instance, molt into NII within hours of hatching (Brown and Roughgarden 1985; Miller et al. 1989). Therefore, in order to assess the dispersal of barnacle larvae over temporal scales of days to weeks we must resort to a high-frequency characterization of nearshore circulation patterns and plankton distribution.

Although more spatial coverage is required to characterize horizontal flows and their variability in the study area, it was assumed that horizontal current velocities measured at the study site were representative of nearshore conditions. This assumption is critical when interpreting results of the PVD analysis, which pointed to a limited dispersal (1-10 km) of larval barnacles in nearshore waters off Southern California. Before these results can be extrapolated to other sites in the region, the spatial variability of nearshore flows must be assessed. It is also necessary to investigate the role of two submarine canyons flanking the sampling area (Fig. 2.1) on the retention and/or aggregation of larvae. Furthermore, hypotheses regarding vertical migration behavior, ontogenetic changes in the range of vertical distribution, and swimming responses to transient hydrodynamic features, remain to be tested.

2.5.3. Mortality estimates

Using vertical life tables to estimate mortality at every transition between larval stages yielded a large number of estimates that were negative, zero, or greater than one (results not shown). Such values are clearly outside the range of values expected for a closed system, or for a stage distribution that is representative of the larval population. Although it would not be correct to use these values, for instance, to parameterize a population model, it is possible to use them to infer how open the area was in terms of larval dispersal over the duration of our study.

On four out of seven days, mortality estimates for the NII-NIII transition in *Balanus glandula* were greater than one, suggesting that an input of NII and/or a loss of NIII larvae had occurred. Estimates for the NIII-NIV transition in *B. glandula* were either negative or zero on four out of seven days, suggesting a loss of NIII, or an input of NIV larvae. Negative or zero estimates for the transitions NII-NIII (2 out of 7) and NIII-NIV (5 out of 7) in *Chthamalus* spp. also suggested a loss of NIII, and probably of NII, during the first two days. This is probably related to ontogenetic differences in swimming abilities and vertical distribution. Perhaps NII-NIII larvae are less able to determine their position within the water column, becoming easily entrained in along-shore flows.

The estimated rates of larval mortality presented here were clearly affected by insufficient spatial coverage and resolution of our sampling. Although the vertical life table method does not require tracking an individual larval aggregation, instantaneous stage structures utilized in the estimation of mortality are assumed to represent the population's stage composition (Aksnes and Ohman 1996). Daily stage distributions observed in this study were highly variable, and suggested that the plankton survey lacked the spatial coverage needed to compensate for small-scale patchiness and advection of early naupliar stages. Furthermore, the assumption of constant and equal development time for all larvae in a given stage (Aksnes and Ohman 1996) could be unrealistic for the larvae of *B. glandula* and *Chthamalus* spp., which have shown an increase in the variability of stage duration between early and late naupliar stages (Brown and Roughgarden 1985; Miller et al. 1989).

The results suggest that average mortality rates of barnacle nauplii in nearshore waters fluctuate around 20-40% per day (Fig. 2.8). These values are substantially higher than previously assumed for *B. glandula* and *Chthamalus* spp. (Connolly and Roughgarden 1998, p. 323), but within the range of mortality estimates found in the literature for other benthic invertebrate larvae (Rumrill 1990; Morgan 1995; Lamare and Barker 1999). A nominal mortality rate of 0.05 d^{-1} has been used repeatedly in modeling studies that describe the distribution and population dynamics of *B. glandula* and *Chthamalus* spp. from Northern California and Oregon (see Gaylord and Gaines 2000, p. 774). This estimate was reportedly obtained from stage-specific counts of *Semibalanus balanoides* larvae, collected on 3 occasions over a period of 20 days from a pier in Millport, Scotland (Pyefinch 1949). The characteristics of my sampling design and target species make the data presented in this contribution more likely to provide a realistic estimate for the mortality of *B. glandula* and *Chthamalus* spp. larvae in nearshore waters. However, similar surveys must be conducted at other sites in the region to contrast and validate these estimates.

A four- to six-fold increase in mortality rates would have a substantial effect on the number of larvae completing their planktonic development. When constant mortality rates of 20 – 40% d^{-1} are used together with a simple exponential decay function to project the numbers of larvae in a closed system after 2.5 weeks (average development time for barnacle larvae at ~15 °C), the numbers of larvae expected to complete their development are 15 – 450 times smaller than the number expected with a 5% d^{-1} mortality. Depending on larval duration, such increases in mortality rates could change the relevant larval transport mechanisms, shorten the mean expected travel distances (e.g. Ellien et al. 2004), and ultimately affect the scales of connectivity among populations.

Results presented in this paper have implications for the current view on population openness and connectivity in coastal marine invertebrates. If the high mortality rates and potential for limited larval dispersal inferred from these data are characteristic of intertidal populations in the region, the distances at which populations are connected by larval exchange could be no longer than 1-10 km. If populations with a similar life cycle are indeed disconnected at such scales, future efforts to model the relationship between local population dynamics and hydrodynamics must shift from an emphasis on mesoscale processes to a better description of nearshore processes and spatial changes in dispersal and self-recruitment.

2.6. ACKNOWLEDGEMENTS

I am indebted to J. Leichter (Scripps Institution of Oceanography) for his invaluable scientific and logistical support during my time at SIO. Field work was greatly facilitated by M. Murray and E. Parnell (SIO). Bathymetric data for La Jolla used in Fig. 2.1 were provided by S. Elgar (WHOI). Comments by V. Starczak, J. Jarrett, and B. Mouriño substantially improved an earlier version of this manuscript. This research was supported by a National Science Foundation grant to Jesús Pineda (WHOI).

2.7. REFERENCES

Aksnes DL, Miller CB, Ohman MD, Wood SN (1997) Estimation techniques used in studies of copepod population dynamics - A review of underlying assumptions. Sarsia 82: 279-296

Aksnes DL, Ohman MD (1996) A vertical life table approach to zooplankton mortality estimation. Limnology and Oceanography 41: 1461-1469

Alexander SE, Roughgarden J (1996) Larval transport and population dynamics of intertidal barnacles: a coupled benthic/oceanic model. Ecological Monographs 66: 259-275

Arnold WS, Hitchcock GL, Frischer ME, Wanninkhof R, Sheng YP (2005) Dispersal of an introduced larval cohort in a coastal lagoon. Limnology and Oceanography 50: 587-597

Barnes H, Barnes M (1956) The general biology of *Balanus glandula* Darwin. Pacific Science 10: 415-422

Barnes H, Barnes M (1958) The rate of development of *Balanus balanoides* (L.) larvae. Limnology and Oceanography 3: 29-32

Becker BJ, Fodrie FJ, McMillan PA, Levin LA (2005) Spatial and temporal variation in trace elemental fingerprints of mytilid mussel shells: A precursor to invertebrate larval tracking. Limnology and Oceanography 50: 48-61

Bertness MD, Gaines SD, Wahle RA (1996) Wind-driven settlement patterns in the acorn barnacle *Semibalanus balanoides*. Marine Ecology Progress Series 137: 103-110

Bousfield EL (1955) Ecological control of the occurrence of barnacles in the Miramichi Estuary. Bulletin of the National Museum of Canada Biological Series 137: 1-65

Branscomb ES, Vedder K (1982) A description of the naupliar stages of the barnacles *Balanus glandula* Darwin, *Balanus cariosus* Pallas, and *Balanus crenatus* Bruguière (Cirripedia, Thoracica). Crustaceana 42: 83-95

Brown SK, Roughgarden J (1985) Growth, morphology, and laboratory culture of larvae of *Balanus glandula* (Cirripedia: Thoracica). Journal of Crustacean Biology 5: 574-590

Connolly SR, Roughgarden J (1998) A latitudinal gradient in northeast Pacific intertidal community structure: evidence for an oceanographically based synthesis of marine community theory. American Naturalist 151: 311-326

Cowen RK, Lwiza KMM, Sponaugle S, Paris CB, Olson DB (2000) Connectivity of marine populations: open or closed? Science 287: 857-859

DiBacco C, Levin LA (2000) Development and application of elemental fingerprinting to track the dispersal of marine invertebrate larvae. Limnology and Oceanography 45: 871-880

DiBacco C, Sutton D, McConnico L (2001) Vertical migration behavior and horizontal distribution of brachyuran larvae in a low-inflow estuary: implications for bay-ocean exchange. Marine Ecology Progress Series 217: 191-206

Ellien C, Thiebaut E, Dumas F, Salomon J-C, Nival P (2004) A modelling study of the respective role of hydrodynamic processes and larval mortality on larval dispersal and recruitment of benthic invertebrates: example of *Pectinaria koreni* (Annelida: Polychaeta) in the Bay of Seine (English Channel). Journal of Plankton Research 26: 117-132

Emery WJ, Thomson RE (1998) Data Analysis Methods in Physical Oceanography. Pergamon Press, New York

Farrel TM, Bracher D, Roughgarden J (1991) Cross-shelf transport causes recruitment to intertidal populations in central California. Limnology and Oceanography 36: 279-288

Forward RBJ (1988) Diel vertical migration: zooplankton photobiology and behaviour. Oceanography and Marine Biology Annual Review 26: 361-393

Gaylord B, Gaines SD (2000) Temperature or transport? Range limits in marine species mediated solely by flow. American Naturalist 155: 769-789

Helfrich KR, Pineda J (2003) Accumulation of particles in propagating fronts. Limnology and Oceanography 48: 1509-1520

Hines AH (1976) Comparative reproductive ecology of three species of intertidal barnacles. Ph.D. Zoology Department, Berkeley

Hines AH (1979) The comparative reproduction ecology of three species of intertidal barnacles. In: Stancyk SE (ed) Reproductive Ecology of Marine Invertebrates. University of South Carolina Press, Columbia, pp 213-234

Lamare MD, Barker MF (1999) *In situ* estimates of larval development and mortality in the New Zealand sea urchin *Evechinus chloroticus* (Echonodermata: Echinoidea). Marine Ecology Progress Series 180: 197-211

Largier JL (2003) Considerations in estimating larval dispersal distances from oceanographic data. Ecological Applications 13: S71-S89

Levin LA (1990) A review of methods for labeling and tracking marine invertebrate larvae. Ophelia 32: 115-144

Levin LA, Bridges TS (1995) Pattern and diversity in reproduction and development. In: McEdward L (ed) Ecology of Marine Invertebrate Larvae. CRC Press, Boca Raton, pp 1-48

Lewis CA (1975) Development of the gooseneck barnacle *Pollicipes polymerus* (Cirripedia: Lepodomorpha): fertilization through settlement. Marine Biology 32: 141-153

Miller KM, Blower SM, Hedgecock D, Roughgarden J (1989) Comparison of larval and adult stages of *Chthamalus dalli* and *Chthamalus fissus* (Cirripedia: Thoracica). Journal of Crustacean Biology 9: 242-256

Miller KM, Roughgarden J (1994) Descriptions of the larvae of *Tetraclita rubescens* and *Megabalanus californicus* with a comparison of the common barnacle larvae of the central California coast. Journal of Crustacean Biology 14: 579-600

Morgan SG (1995) Life and death in the plankton: larval mortality and adaptation. In: McEdward L (ed) Ecology of Marine Invertebrate Larvae. CRC Press, Boca Raton, FL, pp 279-321

Natunewicz CC, Epifanio CE, Garvine RW (2001) Transport of crab larval patches in the coastal ocean. Marine Ecology Progress Series 222: 143-154

Newman WA, Abbott DP (1980) Cirripedia: the barnacles. In: Morris RH, Abbott DP, Haderlie EG (eds) Intertidal Invertebrates of California. Stanford University Press, Stanford, pp 502-535

Pineda J (1991) Predictable upwelling and the shoreward transport of planktonic larvae by internal tidal bores. Science 253: 548-551

Pineda J (1994a) Internal tidal bores in the nearshore: warm-water fronts, seaward gravity currents and the onshore transport of neustonic larvae. Journal of Marine Research 52: 427-458

Pineda J (1994b) Spatial and temporal patterns in barnacle settlement rate along a southern California rocky shore. Marine Ecology Progress Series 107: 125-138

Pineda J (1999) Circulation and larval distribution in internal tidal bore warm fronts. Limnology and Oceanography 44: 1400-1414

Pineda J, Caswell H (1997) Dependence of settlement rate on suitable substrate area. Marine Biology 129: 541-548

Possingham H, Roughgarden J (1990) Spatial population dynamics of a marine organism with a complex life cycle. Ecology 71: 973-985

Raimondi PT (1988) Rock type affects settlement, recruitment, and zonation of the barnacle *Chthamalus anisopoma* Pilsbury. Journal of Experimental Marine Biology and Ecology 123: 253-267

Richards SA, Possingham HP, Noye BJ (1995) Larval dispersion along a straight coast with tidal currents: complex distribution patterns from a simple model. Marine Ecology Progress Series 122: 59-71

Roughgarden J, Gaines SD, Possingham H (1988) Recruitment dynamics in complex life cycles. Science 241: 1460-1466

Rumrill SS (1990) Natural mortality of marine invertebrate larvae. Ophelia 32: 163-198

Scheltema RS (1968) Dispersal of larvae by Equatorial ocean currents and its importance to the zoogeography of shoal-water tropical species. Nature 217: 1159-1162

Scheltema RS (1986) On dispersal and planktonic larvae of benthic invertebrates: An eclectic overview and summary of problems. Bulletin of Marine Science 39: 290-322

Scheltema RS, Williams IP (1982) Significance of temperature to larval survival and length of development in *Balanus eburneus* (Crustacea: Cirripedia). Marine Ecology Progress Series 9: 43-49

Shanks AL (1983) Surface slicks associated with tidally forced internal waves may transport pelagic larvae of benthic invertebrates and fishes shoreward. Marine Ecology Progress Series 13: 311-315

Sponaugle S, Cowen RK, Shanks A, Morgan SG, Leis JM, Pineda J, Boehlert GW, Kingsford MJ, Lindeman KC, Grimes C, Munro JL (2002) Predicting self-recruitment in marine populations: biophysical correlates and mechanisms. Bulletin of Marine Science 70: 341-375

Swearer SE, Caselle JE, Lea DW, Warner RR (1999) Larval retention and recruitment in an island population of a coral-reef fish. Nature 402: 799-802

Tapia FJ, Pineda J, Ocampo-Torres FJ, Fuchs HL, Parnell PE, Montero P, Ramos S (2004) High-frequency observations of wind-forced onshore transport at a coastal site in Baja California. Continental Shelf Research 24: 1573-1585

Wares JP (2001) Patterns of speciation inferred from mitochondrial DNA in North American *Chthamalus* (Cirripedia: Blanomorpha: Chthamaloidea). Molecular Phylogenetics and Evolution 18: 104-116

Warner RR, Cowen RK (2002) Local retention of production in marine populations: evidence, mechanisms, and consequences. Bulletin of Marine Science 70: 245-249

Wing SR, Botsford LW, Largier JL, Morgan LE (1995) Spatial structure of relaxation events and crab settlement in the northern California upwelling system. Marine Ecology Progress Series 128: 199-211

2.8. TABLES

Table 2.1

Results of two-way ANOVAs used to test for spatial (between-station) differences in the concentration of each larval stage. Different days of the study were treated as repeat observations (*df* = 2,6 for all tests). Significant between-station differences are indicated in bold. The results of Tukey pair-wise comparisons, performed for each test with a significant between-station effect, are shown on the third column for each species (* : P<0.05; ** : P<0.01).

Stage	***Balanus glandula***			***Chthamalus* spp.**		
	$F_{2,6}$	***p***	**Pairwise differences**	**$F_{2,6}$**	***p***	**Pairwise differences**
NII	10.973	**0.002**	St1 > St3*, St2 > St3**	3.120	0.089	
NIII	3.168	0.082		6.508	**0.015**	St2 > St 1*
NIV	1.254	0.323		25.373	**0.000**	St3 > St 1**, St2 > St 1**
NV	1.872	0.200		32.301	**0.000**	St3 > St 1**, St2 > St 1**
NVI	3.533	0.065		28.256	**0.000**	St3 > St 1**, St2 > St 1**
Cyprids	2.451	0.132		10.326	**0.004**	St 1 > St 3**

Table 2.2

Estimates of mortality obtained for each day and stage transition. Empty cells correspond to days/transitions for which the estimated mortality rate was zero or negative.

Stage Transition	**MORTALITY ESTIMATES (d^{-1})**						
	Day 1	**Day 2**	**Day 3**	**Day 4**	**Day 5**	**Day 6**	**Day 7**
Balanus glandula							
II+III → IV+V	0.279	0.043	0.128	0.421	0.288	0.322	0.603
IV+V → VI	0.393	0.282	0.366	0.036	0.311	0.108	-
VI → C	0.123	0.629	0.558	0.210	0.462	-	0.693
***Chthamalus* spp.**							
II+III → IV+V	0.239	-	-	0.083	0.119	0.243	0.320
IV+V → VI	0.441	0.224	0.300	0.475	0.315	0.149	0.262
VI → C	0.082	0.501	0.135	0.015	0.086	0.327	0.089

2.9. FIGURES

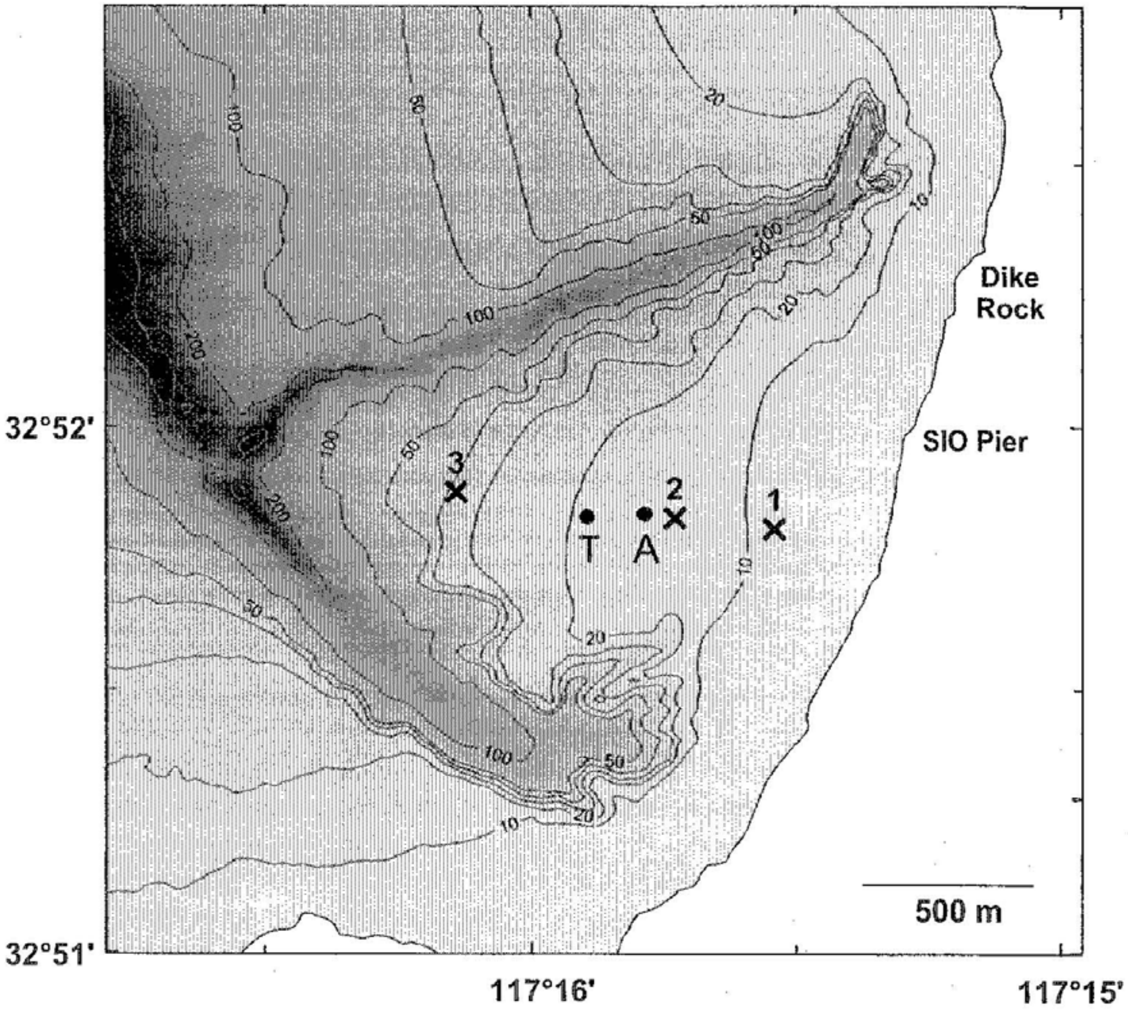

Figure 2.1

Study area in La Jolla, Southern California. The numbered crosses indicate the sampling stations. The letters A and T show the location of the Doppler current meter (32°51.833'N, 117°15.786'W) and temperature mooring (32°51.827'N, 117°15.894'W). Contour lines indicate depth in meters.

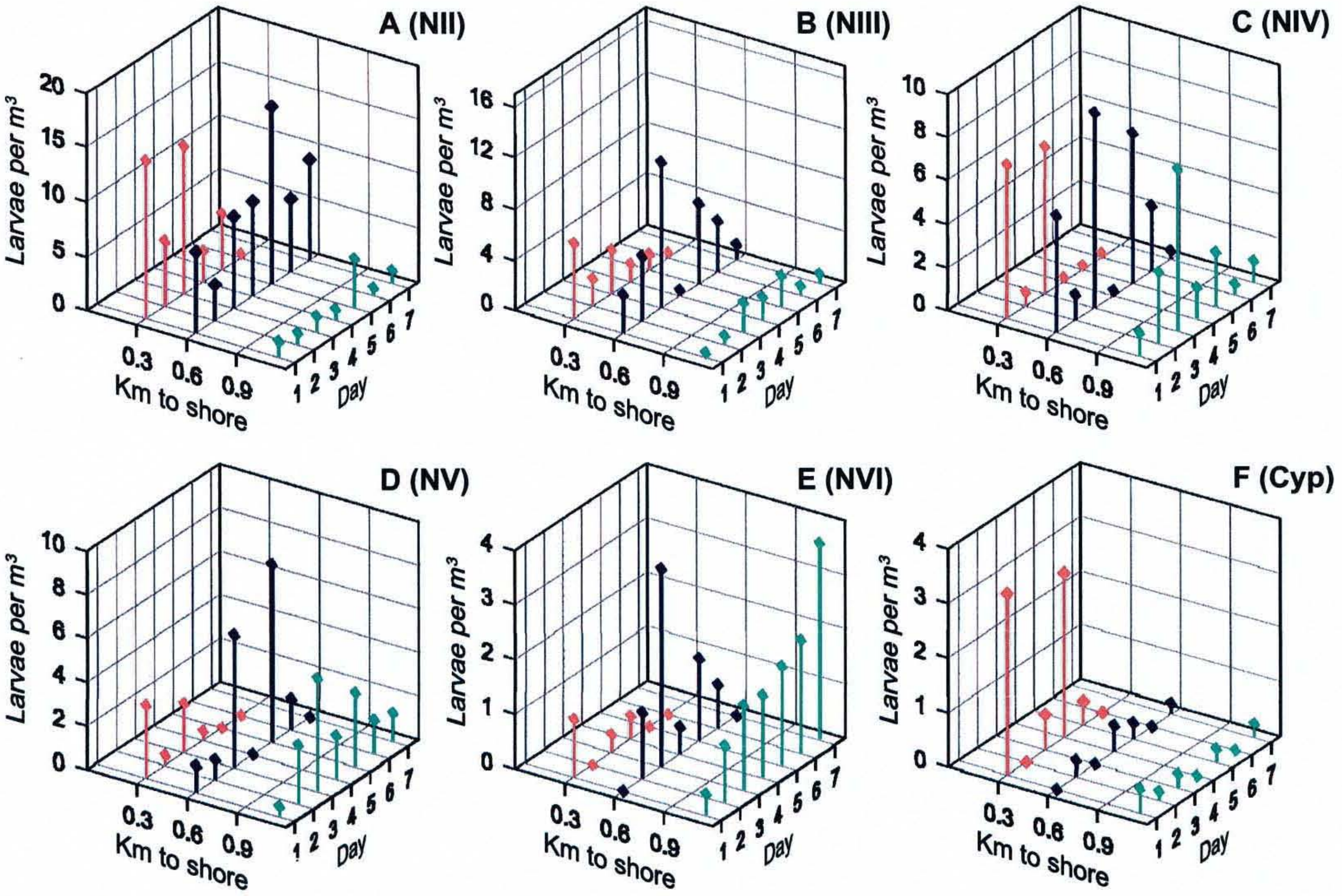

Figure 2.2

Temporal variability in the stage-specific spatial distributions of *Balanus glandula* larvae.

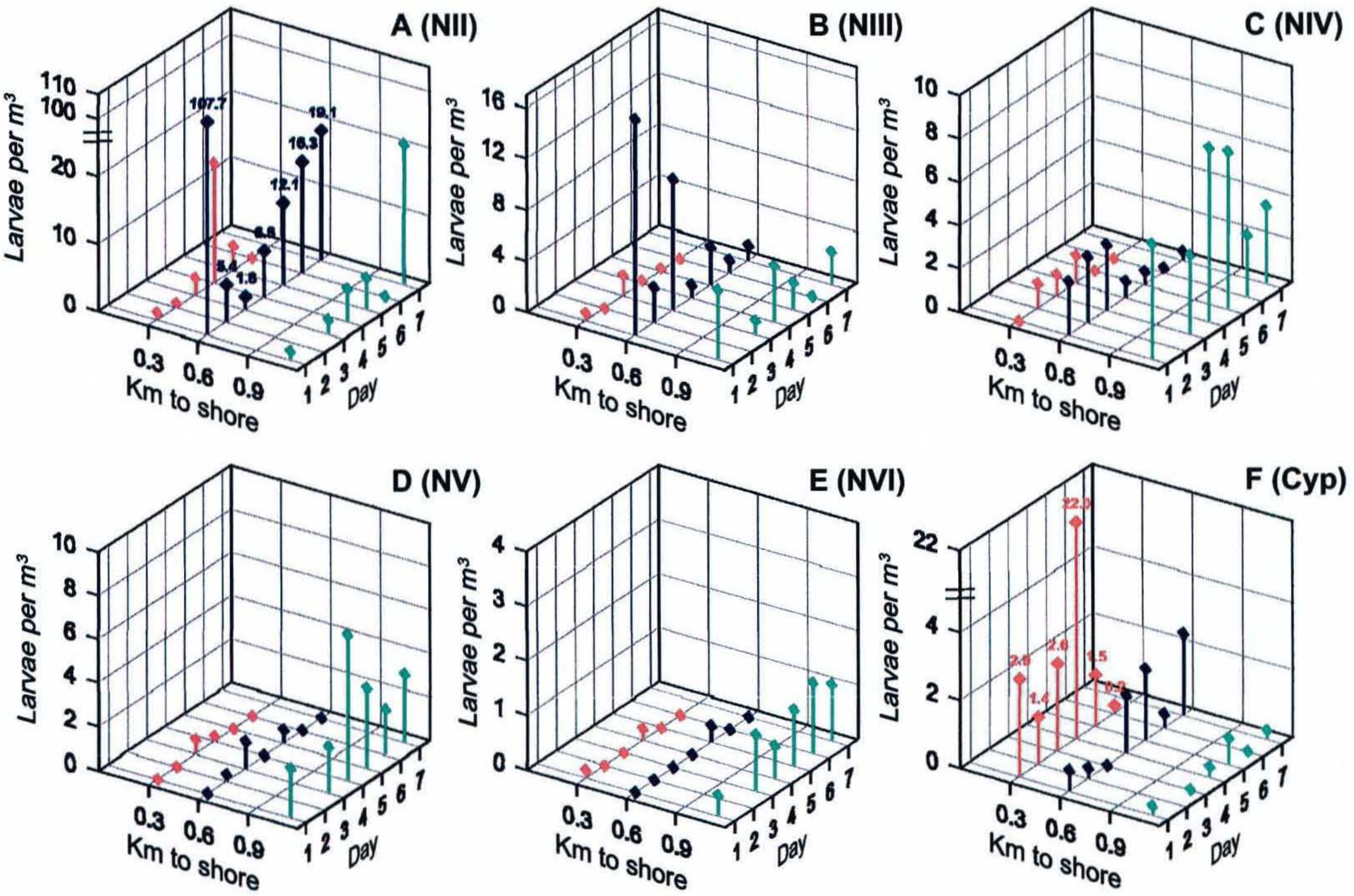

Figure 2.3

Temporal variability in the stage-specific spatial distributions of *Chthamalus* spp. larvae.

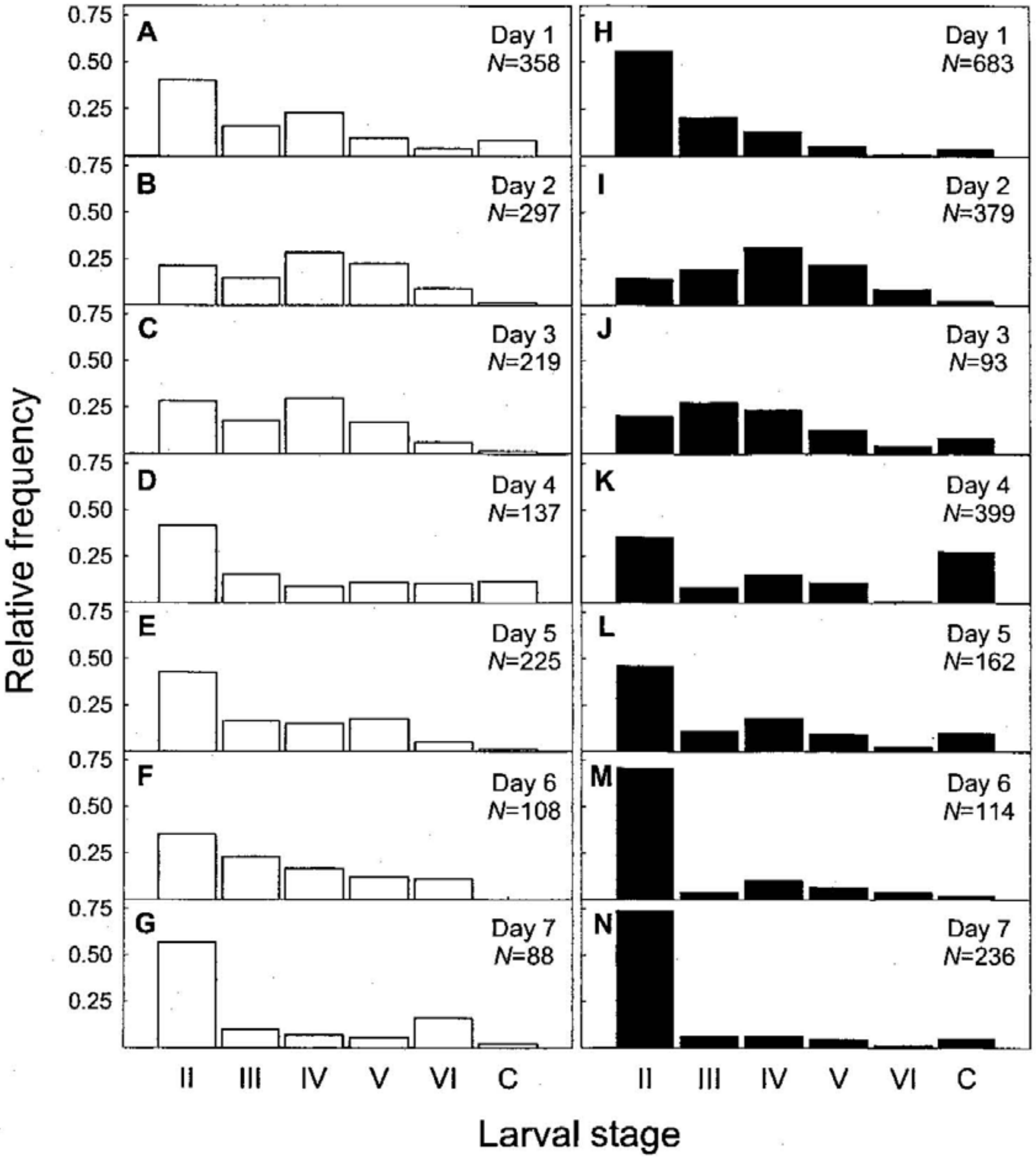

Figure 2.4

Stage distributions of *Balanus glandula* (A-G) and *Chthamalus* spp. (H-N) larvae for each day of the survey (Day 1 = 6 March 2003). Relative stage frequencies were computed from total counts of larvae (*N*) at the three sampling stations.

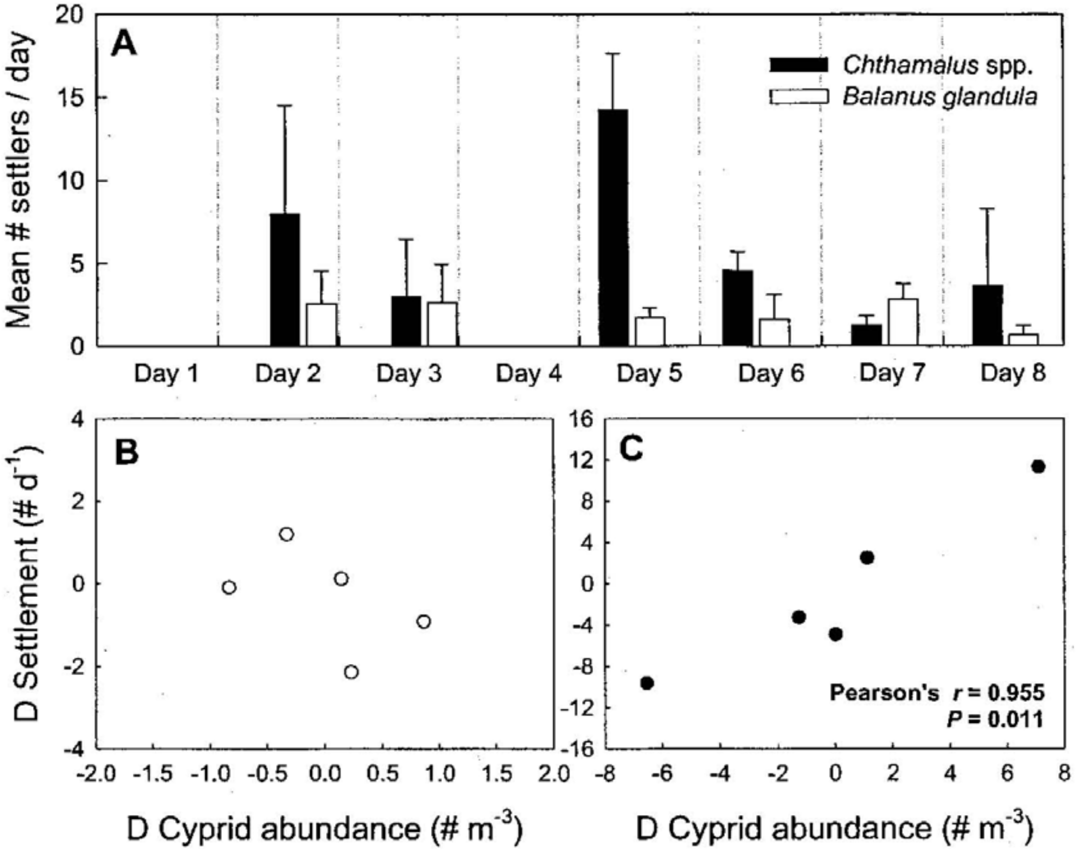

Figure 2.5

Larval settlement at Dike Rock (A), and the correlation between daily changes in settlement and daily changes in nearshore cyprid concentration for *B. glandula* (B) and *Chthamalus* spp. (C).

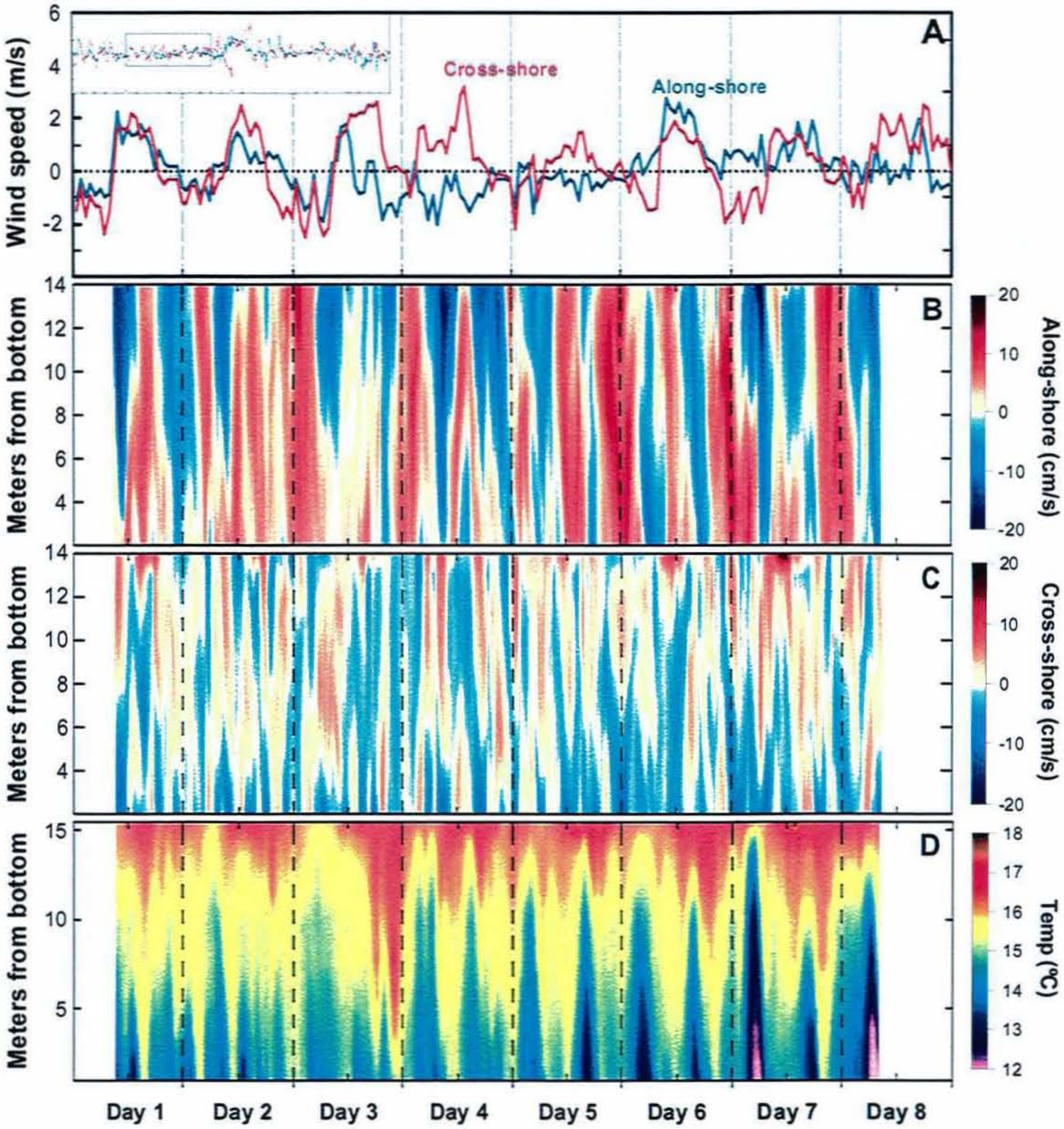

Figure 2.6

Time series of environmental variables measured at the study area. Along-shore and cross-shore winds (**A**) were computed from hourly measurements gathered at the Scripps Institution of Oceanography pier for the month of March 2003 (inset). Box in inset corresponds to **A**. The series of along-shore and cross-shore horizontal currents (**B** and **C**, both in cm s^{-1}), and temperature distribution (**D**), were plotted using low-pass filtered series of 10-point (i.e. 10 min) running means.

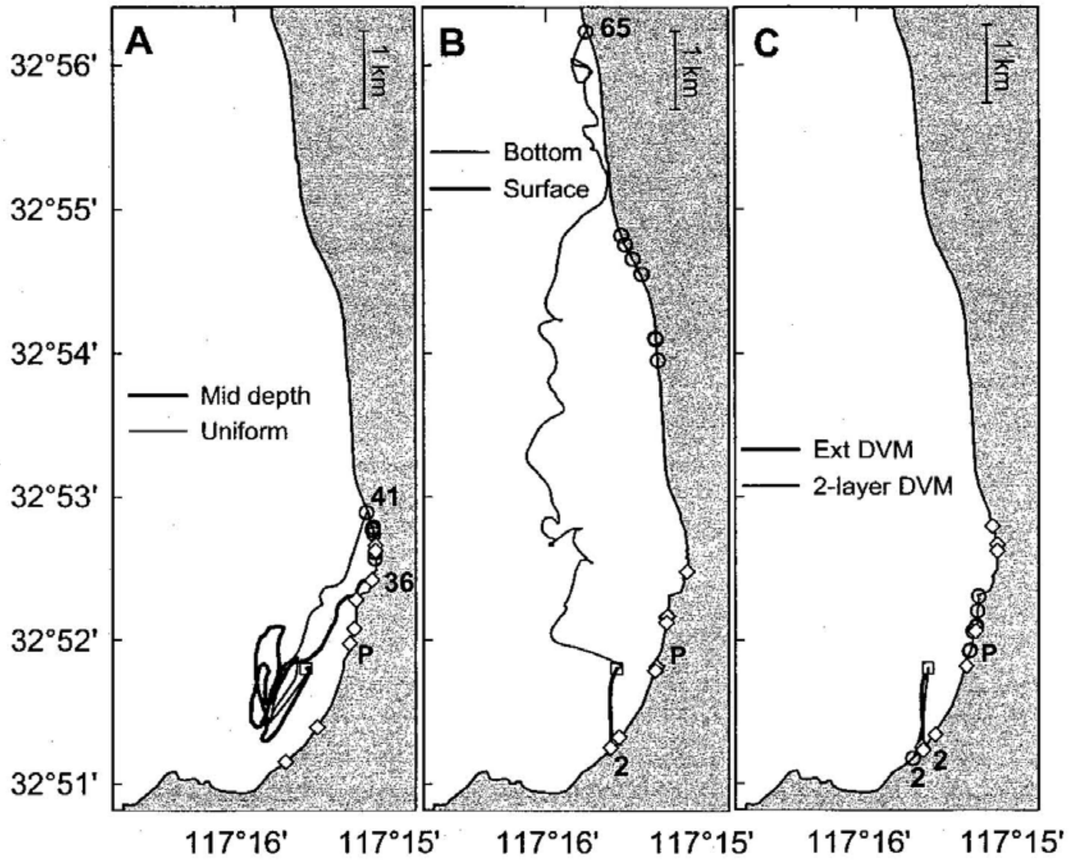

Figure 2.7

Progressive Vector Diagrams (PVD) computed from current meter data collected during this study. Results are presented in three panels for clarity. All trajectories (lines) started from Station 1 (square), and were computed for six cases of larval vertical distribution (see Materials and Methods). Numbers at the end of each trajectory correspond to the approximate time (in hours) after which a particle would have collided with the shore. Symbols along the shore correspond to the endpoints of PVDs computed at different times during a tidal cycle. Circles and diamonds correspond to the thin and thick lines, respectively. The Scripps Institution of Oceanography pier is indicated by P.

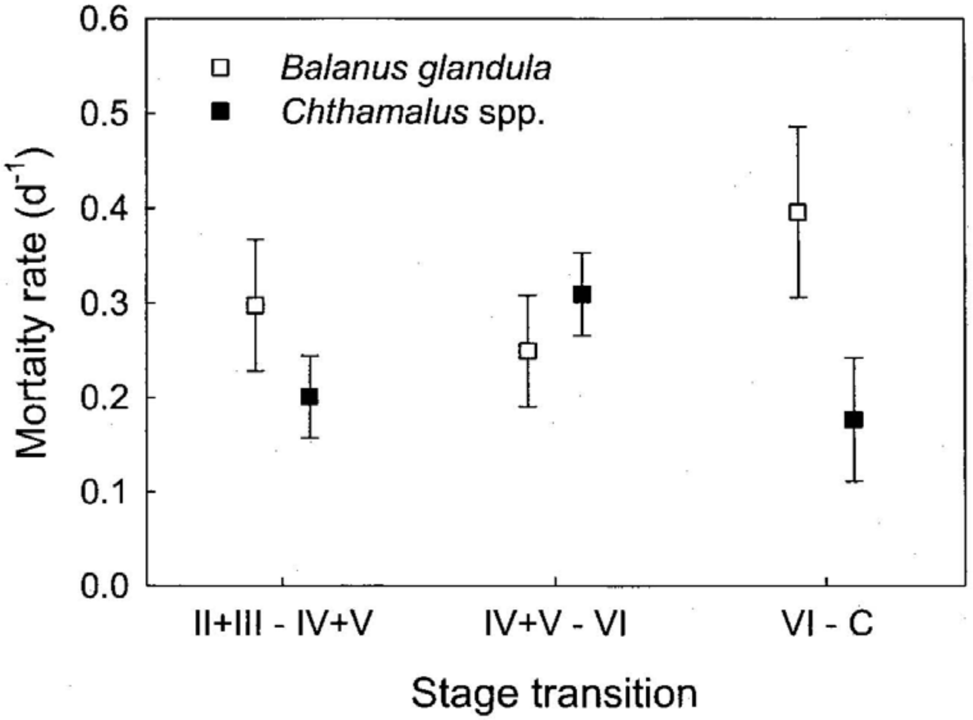

Figure 2.8

Average estimates of larval mortality rate (± SE=SD/√*n*) for three stage transitions in *Balanus glandula* and *Chthamalus* spp. Negative and zero values (see Table 2.2) were not included in the computations.

3. CHAPTER 3

STAGE-SPECIFIC VERTICAL DISTRIBUTIONS OF BARNACLE LARVAE IN THE NEARSHORE

3.1. ABSTRACT

The vertical distribution of barnacle larvae was monitored at a nearshore station off Southern California over a 48-hour period in June 2003. Counts of nauplii and cyprids were tested for the existence of between-stage differences, as well as diurnal changes in the vertical distribution of these stages. Plankton samples were collected every 2 hours from 3 depth intervals (0.5-9, 11-19, and 21-29 m). Environmental information was collected from CTD casts conducted immediately after each plankton station. Collected larvae were enumerated and identified to species and stage of development. Nauplii of the intertidal barnacle *Chthamalus* spp. were numerically dominant (81.7%) and present at all stages of larval development, yet cyprids of this species were absent from our samples. Most collected cyprids (84.2%) were identified as the subtidal barnacle *Balanus nubilus*, which only accounted for 5.6% of total nauplii. Distinct patterns of distribution were found when species-specific distributions of nauplii and cyprids were compared. Naupliar stages of all species occurred near the surface, whereas cyprids were concentrated within the bottom half of the water column at all times. These vertical patterns, which did not change between day and night or across species, are considered in relation to previously observed differences in the horizontal distribution of nauplii and cyprids. I review the factors that are likely to explain this vertical separation and their implications for the dispersal of larval stages in the nearshore.

3.2. INTRODUCTION

The life cycle of many benthic invertebrates includes a dispersive larval stage (Thorson 1950). Sedentary adults produce larvae that spend from hours to months in the plankton before they become competent to settle on adult habitats (Levin and Bridges 1995). During that time they can disperse over potentially long distances (Scheltema 1968, 1986), and larvae that survive to settle often do so in habitats that are far from their parental populations. Larval dispersal is thus the mechanism by which many disjunct populations of benthic invertebrates are demographically and genetically connected. The spatial scale of such exchange of individuals is relevant for understanding recruitment variability (Sponaugle et al. 2002) and for the design of marine reserves (Gaines et al. 2003). Dispersal of planktonic larvae also allows sedentary species to re-colonize and invade coastal habitats. Therefore, the characterization of factors that control the horizontal distribution and dispersal of larvae is key to understanding species geographic ranges and rates of invasion in coastal environments.

Swimming abilities of most invertebrate larvae are limited relative to the horizontal velocities of coastal currents. Swimming speeds range from less than 1 cm s^{-1} in ciliated larvae to a maximum of 2-8 cm s^{-1} in the larvae of some crustaceans (Chia et al. 1984), whereas typical velocities of alongshore currents may fluctuate between 10 and 30 cm s^{-1} (Largier 2003 and references therein). However, the majority of larvae do not behave as passive particles, and dispersal cannot be predicted simply from mean flows without information on their behavior and vertical distribution. Vertical shear in horizontal currents can generate large differences in the dispersal patterns of larvae occurring at different depths in the water column (Rothlisberg et al. 1995; Hannah et al. 1997; Hill 1998). For instance, it has been suggested that a number of coastal and estuarine larvae can control their horizontal displacements by moving up and down the water column at various times of the tidal or diurnal cycle (e.g. Bousfield 1955; DiBacco et al. 2001). Consequently, knowledge of the vertical distribution of invertebrate larvae is essential to understand patterns of dispersal and horizontal distribution.

Intertidal and subtidal barnacles are conspicuous members of coastal communities around the world. Their high abundance, wide geographic distribution, and accessibility make them ideal organisms to study the interaction between nearshore physical processes and larval dispersal. Extensive information is available on the reproductive cycle, ecology and larval development of a number of intertidal species (e.g. Barnes and Barnes 1956; Crisp 1962; Hines 1979; Crisp and Bourget 1985; Barnes 1989; Crisp et al. 1991; Barnes 1999; Wethey 2002). Most adult barnacles are cross-fertilizing hermaphrodites that maintain fertilized eggs in the mantle cavity for several weeks and release up to tens of thousands of nauplius larvae into the plankton (e.g. Hines 1976). Most nauplii must feed on microalgae and undergo six molts before attaining a cyprid stage, which is the non-feeding larva that eventually settles onto hard substrata and metamorphoses into a juvenile barnacle.

Recent observations in Southern California show substantial differences in the horizontal distribution of cyprids and the naupliar stages that precede them (see Chapter 2), suggesting that nauplii and cyprids are affected by different sets of advective forces in the nearshore. Differences in the vertical distribution of nauplii and cyprids may have contributed to the observed horizontal segregation of barnacle larval stages. Here I document temporal patterns in the vertical distribution of barnacle larvae observed in nearshore waters off Southern California over a 48-hour period. The objective of this study was to test for the existence of (1) between-stage differences in vertical distribution and (2) diurnal changes in the vertical distribution of these stages. The results indicate that nauplii and cyprids of the subtidal *Balanus nubilus* and the intertidal gooseneck barnacle *Pollicipes polymerus* occur at different depths, and that their vertical distributions do not change between day and night.

3.3. MATERIALS AND METHODS

Sampling was conducted in June 2003 onboard the R/V Robert Gordon Sproul of the Scripps Institution of Oceanography (SIO). The ship was anchored for 48 hours, starting on 8 June at 23:00 Pacific Daylight Time (PDT), at a coastal station located at a depth of 30 m and approximately 2 km off Del Mar (32°55.91'N, 117°16.79'W) in Southern California, USA (Fig. 3.1). Plankton samples were collected every 2 hours from 3 depth intervals (0.5-9, 11-19, and 21-29 meters) using a semi-vortex AC pump (Ebara DVS, Ebara Corp.). To insure an even sampling of water, the pump was hauled up and down within each depth interval at ca. 1 m s^{-1} for approximately 20 min, until 6 m^3 of water were filtered through a 110 μm mesh net. Volume of water filtered was measured with a digital flow meter attached to the pump hose. Plankton samples were preserved onboard using buffered 4% formaldehyde, and sorted under a dissecting microscope in the laboratory.

A CTD-Rosette (Seabird SBE9) equipped with a fluorometer (Seatech) was lowered down to 29 m immediately after a plankton station was completed. Additional environmental data was obtained from the SIO Coastal Data Information Program website (http://cdip.ucsd.edu). Hourly data recorded at the SIO pier (32°52.00'N, 117°15.42'W, ca. 8 km SE of the ship's position) were used to compute alongshore and cross-shore components of wind. Winds were rotated in order to align them with the shoreline orientation in the area (350° relative to true North). Data on wave significant height and direction recorded every 30 min at a nearby buoy (32°57.72'N, 117°16.38'W, Fig. 3.1) were obtained from the same database.

All barnacle larvae in the samples were enumerated. Nauplii and cyprids were identified to the lowest possible taxonomic level. The species identification and staging of nauplius larvae were based on morphological criteria given by Lewis (1975), Standing (1980), Brown and Roughgarden (1985), Miller et al. (1989), and Miller and Roughgarden (1994). Chthamalid larvae encountered in our samples were probably those of *Chthamalus fissus*, a species that occurs between San Francisco and Baja California (Newman and Abbott 1980) and that numerically dominates the high to upper middle intertidal in La Jolla. However, I refer to the larvae in our samples as *Chthamalus* spp. because the geographic distribution of *C. fissus* occasionally overlaps with that of *C. dalli*, a northern species with a southern limit that fluctuates between Point Conception and San Diego (Newman and Abbott 1980; Wares 2001). Adult *C. fissus* and *C. dalli* can be identified upon dissection and microscopic examination, but their larvae are morphologically identical (Miller et al. 1989).

Counts of nauplii and cyprids for each species were used to test for between-stage differences in vertical distribution, as well as day/night differences within stages. I used a statistical test that allows for comparisons of vertical plankton distributions in the presence of patchiness and when multiple replicates are available (Beet et al. 2003). Samples taken at different times were pooled into two sets of observations, daytime and nighttime, and considered as replicates. Three plankton profiles collected at transition times (i.e. dawn or dusk) were not used in the analysis.

I tested the null hypothesis that means of larval abundance at each depth under one condition (i.e. daytime) are the same as the means under another condition (i.e. nighttime), using the test statistic

$$B = n\sum_{i=1}^{2}\sum_{j=1}^{3}\frac{\left(\overline{Y}_{ij}-\hat{\mu}_{ij}\right)^2}{\hat{\mu}_{ij}\left(1+\hat{c}\hat{\mu}_{ij}\right)} \tag{3.1}$$

where $\overline{Y}_{ij}$ is the average count of *n* replicates for condition *i* and depth *j*, and $\hat{\mu}_{ij}$ and $\hat{c}$ are maximum likelihood estimates of the mean ($\square_{ij}$) and dispersion coefficient (c_{ij}) of a negative binomial distribution, which is recommended to describe count data with a variance to mean ratio greater than one (Hayek and Buzas 1997). The log-likelihood function and details on the procedure used to obtain the maximum likelihood estimates are given by Beet et al. (2003).

To correct for potential effects of serial autocorrelation within groups (i.e. day and night), statistical comparisons of vertical distributions were performed using subsets of plankton profiles selected at random from the pooled datasets. This procedure was repeated ten times for each comparison, and ranges of values obtained for the test statistic B and its corresponding probability under the null hypothesis (i.e. p-values) are reported below. The same sub-sampling scheme was used when the vertical distributions of nauplii and cyprids were compared.

Finally, temporal changes in the vertical distribution of nauplii and cyprids were compared with those observed for temperature and chlorophyll-a in the water column using the Mean Depth of Distribution (MDD) of each larval group. MDDs were calculated for each plankton profile j as the weighted average

$$MDD_j = \frac{1}{N_j} \sum_{i=1}^{3} z_i n_{ji} \qquad (3.2)$$

where z_i is the mean depth of interval i, n_{ji} is the number of nauplii or cyprids collected within that interval, and N_j is the total number of nauplii or cyprids found at time j.

3.4. RESULTS

Total larval counts showed large and persistent differences in the abundance of nauplii and cyprids throughout the sampling period (Fig. 3.2). Nauplii were more abundant near the surface (Fig. 3.2a), with 89% of total nauplii collected between 0.5-9 m. In contrast, most cyprids were found away from the surface (Fig. 3.2b), with 34% and 59% of the total counts collected within the mid-depth and near-bottom intervals, respectively.

Chthamalus spp. represented 78% of the total nauplii found at any given depth interval (Fig. 3.3). Nauplii of the intertidal gooseneck barnacle *Pollicipes polymerus* and the subtidal species *Balanus nubilus* occurred with lower abundance and were mostly found near the surface (Fig. 3.3). A contrasting species composition was observed in cyprids, with a numerical dominance of *B. nubilus* (84.2% of total cyprids) and the absence of *Chthamalus* spp. (Fig. 3.3). All naupliar stages of *Chthamalus* spp. were observed at the near-surface depth interval, with a shift in stage composition over the 48 hours of sampling (Fig. 3.4). The stage structures of *P. polymerus* and *B. nubilus* nauplii, on the other hand, were dominated by early stages (i.e. NII-NIV) throughout the observation period (Fig. 3.4).

Mean fractions of nauplii and cyprids computed from species-specific counts showed no day/night differences within each group, but suggested a consistent difference in the distributions of nauplii and cyprids (Fig. 3.5). This was confirmed by the statistical comparisons of vertical profiles, which showed that the distributions of nauplii or cyprids do not significantly change between day and night, but are significantly different from each other at all times (Table 3.1). This vertical separation between nauplii and cyprids was also apparent when total counts were used to compute mean depths of distribution (MDD). At all times during the observation period, the majority of cyprids were found at a greater depth than nauplii (Fig. 3.6). There was no obvious correspondence between the observed temporal changes in MDD of nauplii or cyprids and fluctuations in cross-shore or alongshore winds (Fig. 3.6c), wave action or tidal height (data not shown). Temperature and chlorophyll contours from CTD measurements showed that the majority of cyprids remained below the surface mixed layer at all times (Fig. 3.6a), and that the MDD of naupliar stages did not overlap with depths at which maximum chlorophyll concentrations were detected (Fig. 3.6b).

3.5. DISCUSSION

Significant differences were found in the vertical distributions of nauplii and cyprids of *Balanus nubilus* and *Pollicipes polymerus*. No day/night differences were observed in the distribution of sampled larval stages for *B. nubilus*, *Chthamalus* spp., and *P. polymerus*. A majority of the collected cyprids (84.2%) were those of *Balanus nubilus*, a subtidal barnacle that occurs from the low intertidal to depths of 90 m (Newman and Abbott 1980). This species accounted for only 5.6% of total nauplii. In contrast, nauplii of the intertidal barnacle *Chthamalus* spp. were numerically dominant (81.7%) and present at all stages of development, yet cyprids of this species were not found in the samples. This absence of *Chthamalus* spp. cyprids, despite the abundance of their nauplii, is an intriguing result that I discuss below.

3.5.1. Larval distribution in relation to environmental variables

Mean Depths of Distribution (MDD) computed for total nauplii did not appear to track the vertical distribution of chlorophyll concentration. Although the observed chlorophyll values were rather low for coastal waters (e.g. Barnett and Jahn 1987; Phillips 2005), nauplii were expected to occur at depths with the highest pigment concentration if their constant vertical distribution is to be interpreted as an adaptation for feeding. Transient increases in near-surface and mid-depth chlorophyll fluorescence associated with high-frequency (≥ 2 cycles h^{-1}) internal waves have been observed during spring and summer in this area (Lennert-Cody and Franks 2002). Given the sampling frequency and short duration of this study, such features cannot be ruled out as a potential source of food for nauplii in near-surface depths.

Forcing of surface layers by wind may have a potential effect on the horizontal distribution of larvae (e.g. Bertness et al. 1996; Garland et al. 2002). The cross-shore component of wind at our study site was either positive or just below zero, and a signal corresponding to the onshore sea breeze could be detected during the daytime hours (Fig. 3.6c). This persistent onshore breeze could have an influence on the horizontal distribution of near-surface material (Tapia et al. 2004). However, its effect on the position of larvae with respect to shore can only be speculated at this point.

3.5.2. Stage-specific differences in distribution

Differences in the vertical distributions of barnacle nauplii and cyprids appeared consistent with observations previously reported for coastal and estuarine waters. Over 4 years of sampling at a site ca. 50 km north of our sampling station, Barnett and Jahn (1987) found that total cyprids (species not identified) were consistently more abundant near the bottom and within 4 km from shore. Pineda (1991) found unidentified cyprids that were more abundant near the bottom than at the surface in shallow waters (4-16 m) off La Jolla, Southern California. Bousfield (1955) observed that early nauplii of *Balanus improvisus* and *Balanus crenatus* in the Miramichi Estuary occurred closer to the surface, whereas nauplius VI and cyprids were concentrated near the bottom. At a shallow bay in New Brunswick, Canada, cyprids of *Semibalanus balanoides* were most abundant within the bottom half of the water column and showed no apparent day/night difference in their vertical distribution (Miron et al. 1999, Fig. 3). A contrasting distribution was found for cyprids of the intertidal barnacle *Verruca stroemia* at tens of kilometers off the west coast of Brittany (Le Fèvre and Bourget 1991). Cyprids occurred predominantly in the upper meter of the water column, whereas nauplii had a more uniform distribution. This suggests that differences in the vertical distribution of nauplii and cyprids are probably species specific, and that vertical differences observed in this study for *B. nubilus* and *P. polymerus* cannot be extrapolated to *Chthamalus* spp. until both nauplii and cyprids are observed over similar temporal scales.

The absence of *Chthamalus* spp. cyprids, despite high concentrations of nauplii, could be due to differences in the behavior and swimming abilities of these stages. In

March 2003, Tapia and Pineda (submitted, see Chapter 2) observed consistently higher concentrations (up to 22 per m^3) of *Chthamalus* spp. cyprids within 300 m of shore, at ca. 10 m depth, over a 7-day period in La Jolla, approximately 10 km SE of our sampling station. Concentrations declined to almost zero at a station located 1.1 km offshore (ca. 40 m depth). Thus, it is possible that *Chthamalus* spp. cyprids were not found in this study because at a station located ca. 2 km offshore their concentrations were too low to be detected. Differences in behavior and perhaps swimming abilities between *Chthamalus* spp. cyprids and nauplii might explain these low concentrations, as cyprids could be better able to move shorewards and to aggregate near adult habitats. Cyprids might accomplish this by responding to cross-shore moving hydrodynamic features (Pineda 1999; Helfrich and Pineda 2003).

The above argument must be qualified by the fact that different sampling gear was utilized in the present study and that conducted by Tapia and Pineda (see Chapter 2). Plankton samples taken by Tapia and Pineda corresponded to vertical tows of a 75 cm diameter net with 110 μm mesh size. Average volumes of water filtered ranged from 8.25 m^3 at the nearshore station to 18.15 m^3 at the station located 1.1 km from shore. Samples taken for the present study were collected by filtering 6 m^3 of water with a pump that was lowered to a maximum depth of 29 m, at a site with an average depth of 30 m. It could be argued that *Chthamalus* spp. cyprids were not collected because they occurred within the space between maximum pumping depth and the bottom. However, Pineda (1999) collected cyprids of *Chthamalus* spp. and *Pollicipes polymerus* using the same type of pump to filter 4 m^3 of water at maximum depths of 4 m below the surface, at least 2 m above the bottom. Thus, it is unlikely that the absence of *Chthamalus* spp. cyprids was due to low sampling efficiency. Still, confirming their absence from our sampling station does not prove that their horizontal distribution resembled that observed by Tapia and Pineda in La Jolla (see Chapter 2), and a future study that includes spatial replication is needed to verify these patterns.

3.5.3. Implications for larval horizontal distribution

The occurrence, forcing factors, and ecological implications of vertical movements in the plankton have been the subject of extensive research for the past 70 years (e.g. Hardy 1936; Forward 1988). Diurnal vertical migrations, in which planktonic organisms move between near-bottom and near-surface waters at dawn and dusk, have been interpreted as a predator avoidance behavior (e.g. Zaret and Suffern 1976; Ohman and Cohen 1983), as well as a mechanism by which many planktonic taxa control their position with respect to shore (e.g. Shanks 1986; Rothlisberg et al. 1995; Poulin et al. 2002). Numerous examples are available in the literature where the vertical motions of certain taxa, mostly coastal, are such that vertical differences in horizontal flows allow them to remain in, or to move out of a given area (e.g. Bousfield 1955; Pineda 1999; DiBacco et al. 2001). Ontogenetic changes in vertical distribution could result from changes in swimming and feeding behavior. It has been suggested that earlier stages may spend more time in near-surface waters due to a phototactic response enhanced by starvation (e.g. Singarajah et al. 1967), whereas later stages may spend more time in deeper waters to avoid visual predators (e.g. Hays 1995). Transient shifts in the vertical distribution of barnacle cyprids can result from a behavioral response to transient hydrodynamic features (Pineda 1999). It has been shown for copepods that individual variability in energy reserves, measured as lipid storage, can explain intra-specific differences in the amplitude of vertical migrations (Hays et al. 2001).

Why do cyprids remain close to the bottom, whereas nauplii occur in the upper half of the water column? The studies cited above suggest that energetic advantages and behavioral differences between cyprids and nauplii could be invoked to answer this question. First, cyprids are non-feeding larvae, hence feeding cannot be considered as a mechanism forcing their vertical distribution. Second, lower temperatures in bottom waters might reduce the consumption rate of lipid reserves, thus allowing cyprids to remain competent for longer periods of time. Laboratory and field observations indicate that low temperatures, or even freezing, can lengthen the competency period for some species (Pechenik et al. 1993; Pineda et al. 2005). Near-bottom waters at the sampling station were ca. 7°C colder than surface waters throughout the 48-h survey, and similar vertical differences have been recorded at La Jolla through the spring and summer (e.g. Pineda and López 2002, Fig. 4). A near-bottom habitat could thus increase the competency time of cyprids, and therefore increase their chance to find suitable substrate and settle. Also, bottom waters may provide cyprids with better conditions to remain in the nearshore. Wind-driven cross-shelf transport of bottom waters (Garland et al. 2002) and onshore moving features such as internal tidal bores (Pineda 1999) could aid these larvae in reaching a suitable substrate to settle. Observations presented here on the vertical distribution of cyprids, and their apparent concentration in nearshore waters (Chapter 2) raise the question of whether cyprids of intertidal barnacles found tens of kilometers offshore (e.g. Roughgarden et al. 1988; Le Fèvre and Bourget 1991) are likely to return to adult habitats and settle successfully during their competency period. Perhaps larvae found at such distances from shore have been lost from the pool of potential settlers, and should not be considered as viable propagules in models that integrate mesoscale physical processes and the dynamics of benthic populations (e.g. Alexander and Roughgarden 1996).

In summary, I have presented distinct patterns of vertical distribution for different stages of barnacle larvae in nearshore waters. Nauplii occur near the surface, whereas the non-feeding cyprids are concentrated in the bottom half of the water column. These vertical patterns, which did not appear to change between day and night or across species, suggest that previously observed differences in the horizontal distribution of larvae may be caused by ontogenetic changes in vertical distribution, and probably behavior, that allow cyprids to respond to transient hydrodynamic features and to move shorewards more effectively than nauplii.

3.6. ACKNOWLEDGEMENTS

I gratefully acknowledge the help of many people who made this work possible. The captain and crew of the R/V Sproul (SIO) provided all the assistance and expertise we could possibly need. T. Stueckle, S. Dean, J. Hernandez-Leon, R. Bermudez, J. Acosta, N. Olivares, and F. Miranda assisted with the collection of samples. L. Davies was of great help with the sorting and enumeration of larvae. A. Beet and A. Solow (WHOI) provided valuable advice on the data analysis. This work was funded by NSF grants to Jesús Pineda (WHOI).

3.7. REFERENCES

Alexander SE, Roughgarden J (1996) Larval transport and population dynamics of intertidal barnacles: a coupled benthic/oceanic model. Ecological Monographs 66: 259-275

Barnes H, Barnes M (1956) The general biology of *Balanus glandula* Darwin. Pacific Science 10: 415-422

Barnes M (1989) Egg production in cirripedes. Oceanography and Marine Biology Annual Review 27: 91-166

Barnes M (1999) The mortality of intertidal cirripedes. Oceanography and Marine Biology Annual Review 37: 153-244

Barnett AM, Jahn AE (1987) Pattern and persistence of a nearshore planktonic ecosystem off Southern California. Continental Shelf Research 7: 1-25

Beet A, Solow AR, Bollens SM (2003) Comparing vertical plankton profiles with replication. Marine Ecology Progress Series 262: 285-287

Bertness MD, Gaines SD, Wahle RA (1996) Wind-driven settlement patterns in the acorn barnacle *Semibalanus balanoides*. Marine Ecology Progress Series 137: 103-110

Bousfield EL (1955) Ecological control of the occurrence of barnacles in the Miramichi Estuary. Bulletin of the National Museum of Canada Biological Series 137: 1-65

Brown SK, Roughgarden J (1985) Growth, morphology, and laboratory culture of larvae of *Balanus glandula* (Cirripedia: Thoracica). Journal of Crustacean Biology 5: 574-590

Chia F-S, Buckland-Nicks J, Young CM (1984) Locomotion of marine invertebrate larvae: a review. Canadian Journal of Zoology 62: 1205-1222

Crisp DJ (1962) The planktonic stages of the cirripedia *Balanus balanoides* (L.) and *Balanus balanus* (L.) from North temperate waters. Crustaceana 3: 207-221

Crisp DJ, Bourget E (1985) Growth in barnacles. Advances in Marine Biology 22: 199-244

Crisp DJ, Hill EM, Holland DL (1991) A review of the hatching process in barnacles Crustacean Egg Production, pp 57-68

DiBacco C, Sutton D, McConnico L (2001) Vertical migration behavior and horizontal distribution of brachyuran larvae in a low-inflow estuary: implications for bay-ocean exchange. Marine Ecology Progress Series 217: 191-206

Forward RBJ (1988) Diel vertical migration: zooplankton photobiology and behaviour. Oceanography and Marine Biology Annual Review 26: 361-393

Gaines SD, Gaylord B, Largier JL (2003) Avoiding current oversights in marine reserve design. Ecological Applications 13: S32-S46

Garland ED, Zimmer CA, Lentz SJ (2002) Larval distributions in inner-shelf waters: The roles of wind-driven cross-shelf currents and diel vertical migrations. Limnology and Oceanography 47: 803-817

Hannah CG, Naimie CE, Loder JW, Werner FE (1997) Upper-ocean transport mechanisms from the Gulf of Maine to Georges Bank, with implications for Calanus supply. Continental Shelf Research 17: 1887-1911

Hardy AC (1936) Plankton ecology and the hypothesis of animal exclusion. Proceedings of the Linnean Society 148: 64-70

Hayek LA, Buzas MA (1997) Surveying natural populations. Columbia University Press, New York

Hays GC (1995) Ontogenetic and seasonal variation in the diel vertical migration of the copepods *Metridia lucens* and *Metridia longa*. Limnology and Oceanography 40: 1461-1465

Hays GC, Kennedy H, Frost BW (2001) Individual variability in diel vertical migration of a marine copepod: Why some individuals remain at depth while others migrate. Limnology and Oceanography 46: 2050-2054

Helfrich KR, Pineda J (2003) Accumulation of particles in propagating fronts. Limnology and Oceanography 48: 1509-1520

Hill AE (1998) Diel vertical migration in stratified tidal flows: Implications for plankton dispersal. Journal of Marine Research 56: 1069-1096

Hines AH (1976) Comparative reproductive ecology of three species of intertidal barnacles. Ph.D. Zoology Department, Berkeley

Hines AH (1979) The comparative reproduction ecology of three species of intertidal barnacles. In: Stancyk SE (ed) Reproductive Ecology of Marine Invertebrates. University of South Carolina Press, Columbia, pp 213-234

Largier JL (2003) Considerations in estimating larval dispersal distances from oceanographic data. Ecological Applications 13: S71-S89

Le Fèvre J, Bourget E (1991) Neustonic niche for cirripede larvae as a possible adaptation to long-range dispersal. Marine Ecology Progress Series 74: 185-194

Lennert-Cody CE, Franks PJS (2002) Fluorescence patches in high-frequency internal waves. Marine Ecology Progress Series 235: 29-42

Levin LA, Bridges TS (1995) Pattern and diversity in reproduction and development. In: McEdward L (ed) Ecology of Marine Invertebrate Larvae. CRC Press, Boca Raton, pp 1-48

Lewis CA (1975) Development of the gooseneck barnacle *Pollicipes polymerus* (Cirripedia: Lepodomorpha): fertilization through settlement. Marine Biology 32: 141-153

Miller KM, Blower SM, Hedgecock D, Roughgarden J (1989) Comparison of larval and adult stages of *Chthamalus dalli* and *Chthamalus fissus* (Cirripedia: Thoracica). Journal of Crustacean Biology 9: 242-256

Miller KM, Roughgarden J (1994) Descriptions of the larvae of *Tetraclita rubescens* and *Megabalanus californicus* with a comparison of the common barnacle larvae of the central California coast. Journal of Crustacean Biology 14: 579-600

Miron G, Boudreau B, Bourget E (1999) Intertidal barnacle distribution: a case study using multiple working hypotheses. Marine Ecology Progress Series 189: 205-219

Newman WA, Abbott DP (1980) Cirripedia: the barnacles. In: Morris RH, Abbott DP, Haderlie EG (eds) Intertidal Invertebrates of California. Stanford University Press, Stanford, pp 502-535

Ohman MD, Cohen EB (1983) Reverse diel vertical migration: An escape from invertebrate predators. Science 220: 1404-1407

Pechenik JA, Rittschof D, Schmidt AR (1993) Influence of delayed metamorphosis on survival and growth of juvenile barnacles *Balanus amphitrite*. Marine Biology 115: 287-294

Phillips NE (2005) Growth of filter-feeding benthic invertebrates from a region with variable upwelling intensity. Marine Ecology Progress Series 295: 79-89

Pineda J (1991) Predictable upwelling and the shoreward transport of planktonic larvae by internal tidal bores. Science 253: 548-551

Pineda J (1999) Circulation and larval distribution in internal tidal bore warm fronts. Limnology and Oceanography 44: 1400-1414

Pineda J, DiBacco C, Starczack V (2005) Barnacle larvae in ice: Survival, reproduction, and time to postsettlement metamorphosis. Limnology and Oceanography In Press

Pineda J, López M (2002) Temperature, stratification and barnacle larval settlement in two Californian sites. Continental Shelf Research 22: 1183-1198

Poulin E, Palma AT, Leiva G, Narvaez D, Pacheco R, Navarrete SA, Castilla JC (2002) Avoiding offshore transport of competent larvae during upwelling events: The case of the gastropod *Concholepas concholepas* in Central Chile. Limnology and Oceanography 47: 1248-1255

Rothlisberg PC, Church JA, Fandry CB (1995) A mechanism for near-shore concentration and estuarine recruitment of post-larval *Penaeus plebejus* Hess (Decapoda, Penaeidae). Estuarine, Coastal and Shelf Science 40: 115-138

Roughgarden J, Gaines SD, Possingham H (1988) Recruitment dynamics in complex life cycles. Science 241: 1460-1466

Scheltema RS (1968) Dispersal of larvae by Equatorial ocean currents and its importance to the zoogeography of shoal-water tropical species. Nature 217: 1159-1162

Scheltema RS (1986) On dispersal and planktonic larvae of benthic invertebrates: An eclectic overview and summary of problems. Bulletin of Marine Science 39: 290-322

Shanks AL (1986) Vertical migration and cross-shelf dispersal of larval *Cancer* spp. and *Randallia ornata* (Crustacea: Brachyura) off the coast of southern California. Marine Biology 92: 189-199

Singarajah KV, Moyse J, Knight-Jones EW (1967) The effect of feeding upon the phototactic behaviour of cirripede nauplii. Journal of Experimental Marine Biology and Ecology 1: 144-153

Sponaugle S, Cowen RK, Shanks A, Morgan SG, Leis JM, Pineda J, Boehlert GW, Kingsford MJ, Lindeman KC, Grimes C, Munro JL (2002) Predicting self-recruitment in marine populations: biophysical correlates and mechanisms. Bulletin of Marine Science 70: 341-375

Standing JD (1980) Common inshore barnacle cyprids of the Oregonian faunal province (Crustacea: Cirripedia). Proceedings of the Biological Society of Washington 93: 1184-1203

Tapia FJ, Pineda J, Ocampo-Torres FJ, Fuchs HL, Parnell PE, Montero P, Ramos S (2004) High-frequency observations of wind-forced onshore transport at a coastal site in Baja California. Continental Shelf Research 24: 1573-1585

Thorson G (1950) Reproductive and larval ecology of marine bottom invertebrates. Biological Reviews 25: 1-45

Wares JP (2001) Patterns of speciation inferred from mitochondrial DNA in North American *Chthamalus* (Cirripedia: Blanomorpha: Chthamaloidea). Molecular Phylogenetics and Evolution 18: 104-116

Wethey DS (2002) Biogeography, competition, and microclimate: The barnacle *Chthamalus fragilis* in New England. Integrative and Comparative Biology 42: 872-880

Zaret TM, Suffern JS (1976) Vertical migration in zooplankton as a predator avoidance mechanism. Limnology and Oceanography 21: 804-813

3.8. TABLES

Table 3.1

Comparisons of vertical distributions for species-specific and total counts of barnacle larvae. The test statistic *B* (Beet et al. 2003) and its corresponding *p*-value were computed ten times for each comparison. The range of observed values is reported. Asterisks indicate comparisons were significant differences were found ($\alpha=0.05$).

Comparison	*B*	*p*
Balanus nubilus		
Nauplii day vs Nauplii night	0.0000 - 2.9288	0.2312 - 1.0000
Cyprids day vs Cyprids night	0.0976 - 1.6367	0.4412 - 0.9524
Nauplii day vs Cyprids day *	9.6415 - 15.666	0.0004 - 0.0081
Nauplii night vs Cyprids night *	15.589 - 21.426	0.0000 - 0.0004
Pollicipes polymerus		
Nauplii day vs Nauplii night	0.4864 - 2.4200	0.2982 - 0.7841
Nauplii day vs Cyprids day *	14.630 - 19.584	0.0000 - 0.0007
Chthamalus spp.		
Nauplii day vs Nauplii night	0.3087 - 3.1196	0.2102 - 0.8570
Total counts		
Nauplii day vs Nauplii night	0.8009 - 4.3161	0.1156 - 0.6700
Cyprids day vs Cyprids night	0.0002 - 1.2561	0.5336 - 0.9999

3.9. FIGURES

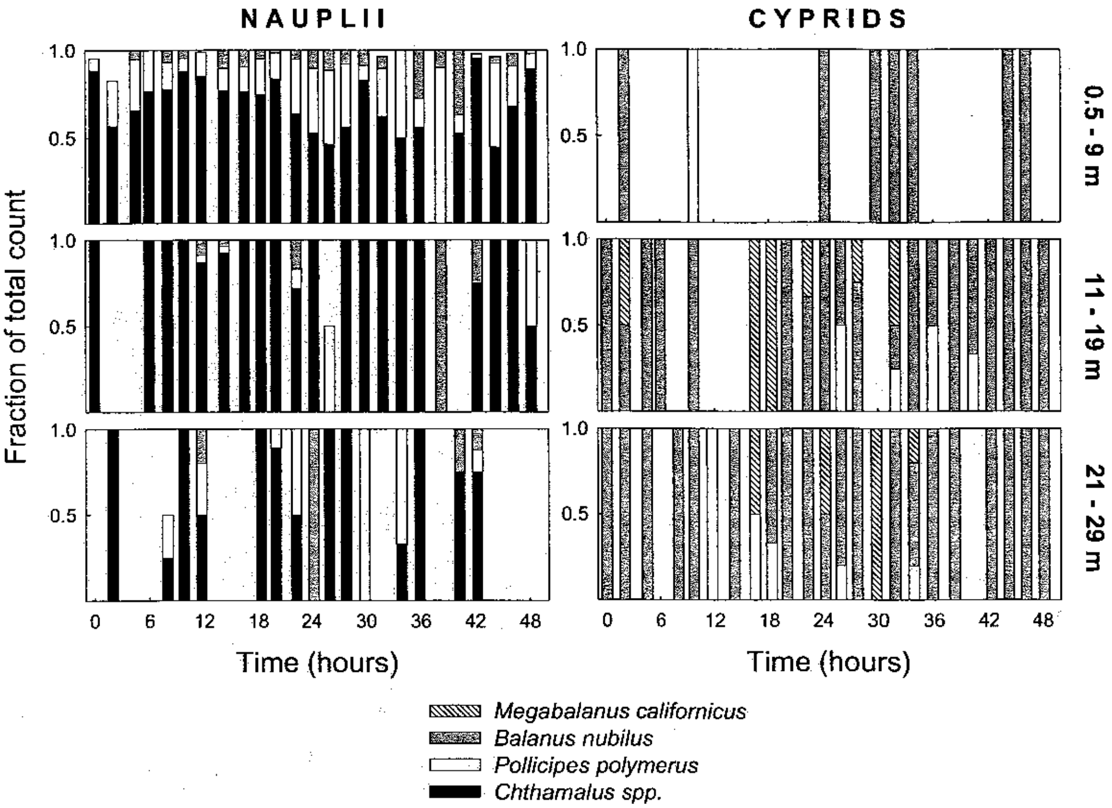

Figure 3.3

Species composition of total counts for nauplii (left panels) and cyprids (right panels) at three depth intervals. The four most abundant species are shown.

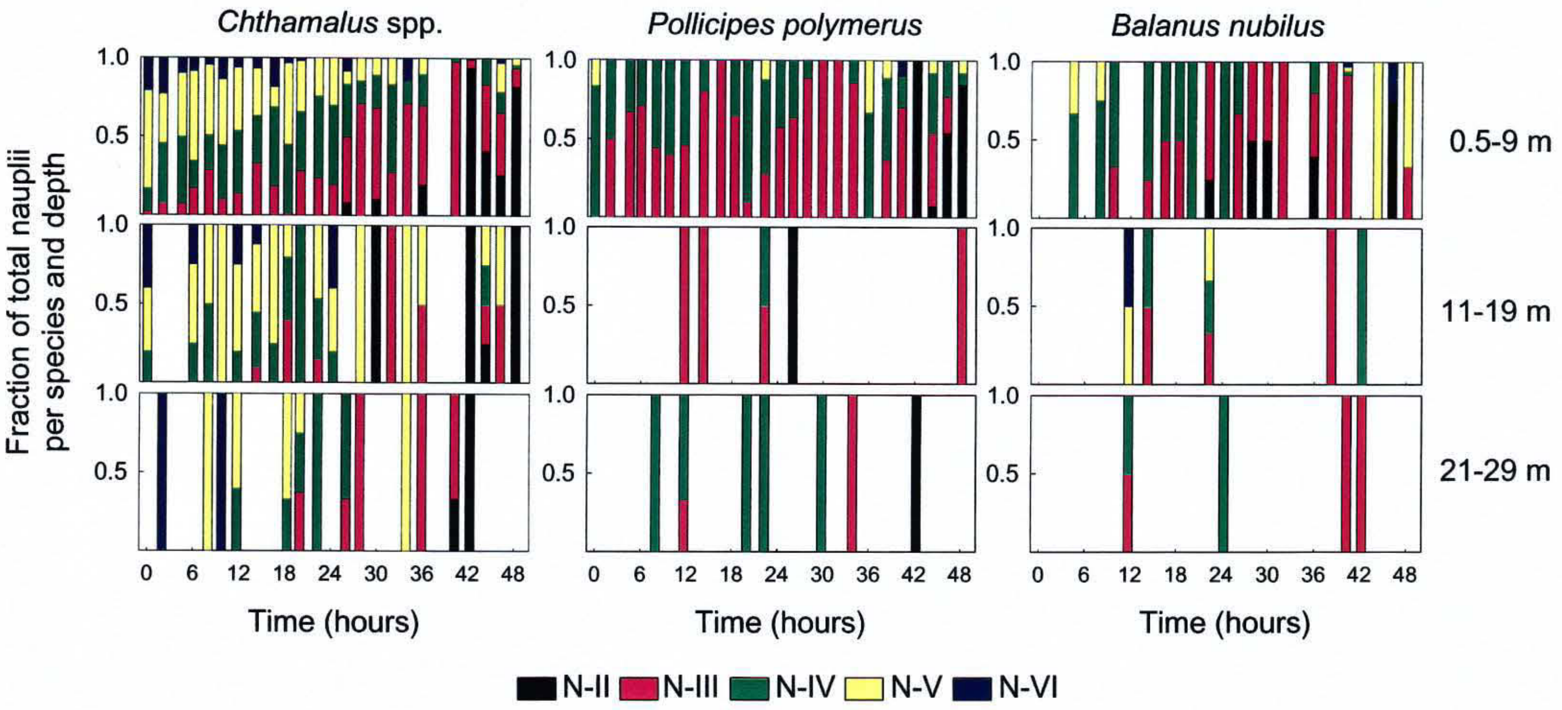

Figure 3.4

Temporal variability in the stage composition of *Chthamalus* spp., *Pollicipes polymerus*, and *Balanus nubilus* nauplii at the three depth intervals sampled in this study.

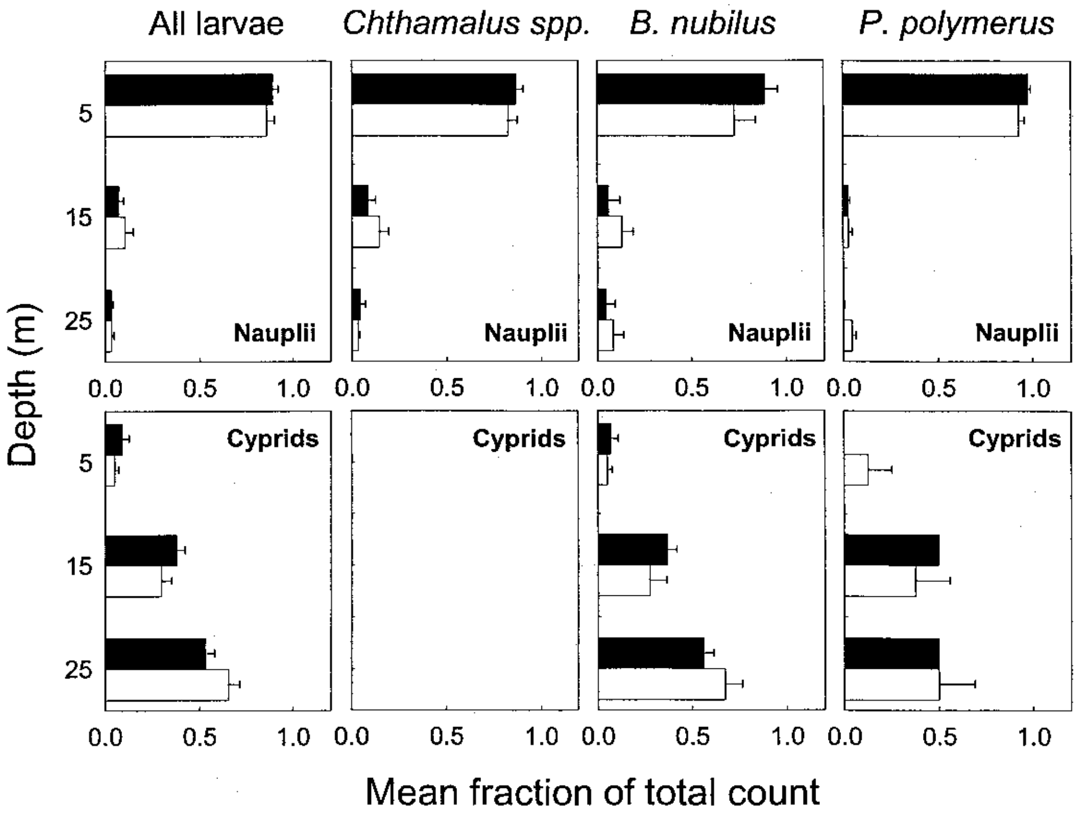

Figure 3.5

Mean vertical distributions of barnacle nauplii and cyprids during the day (white bars) and night (black bars) at a coastal station in Southern California (32°55.91'N, 117°16.79'W). Fractions of total counts were computed separately for nauplii and cyprids in each plankton profile, and averaged for each depth interval across daytime and nighttime samples. Error bars are standard errors.

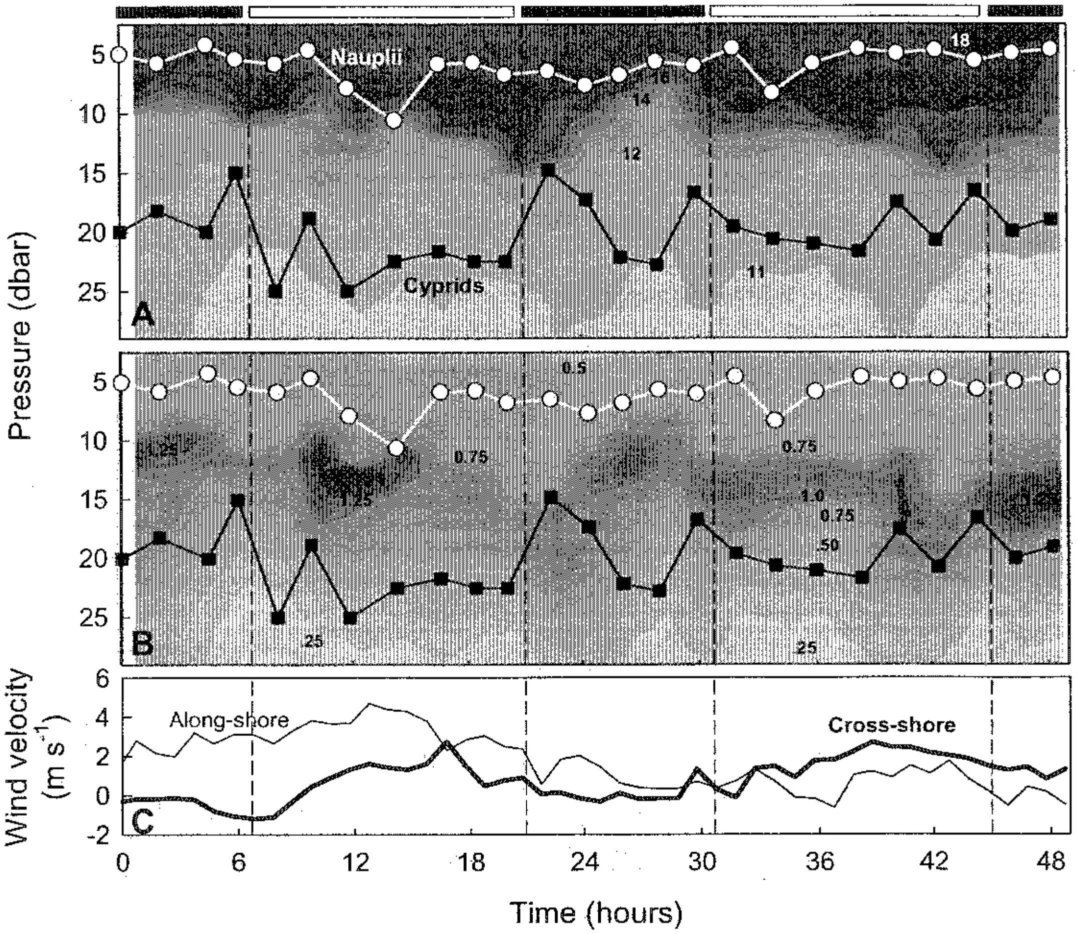

Figure 3.6

Mean Depths of Distribution (MDD) of barnacle larvae and environmental variability. MDDs are superimposed on temperature (A) and chlorophyll (B) contours from CTD data collected after each plankton station. Hourly winds (C) were measured at a site ca. 8 km SE of the sampling station. Horizontal black and white bars indicate nighttime and daytime. Dashed vertical lines correspond to sunrise and sunset time.

4. CHAPTER 4

SPATIAL PATTERNS IN LIFE HISTORY TRAITS OF INTERTIDAL BARNACLES: IMPLICATIONS FOR GEOGRAPHIC RANGES

4.1. ABSTRACT

Regional changes in demography of the intertidal barnacle *Balanus glandula* were studied over 400 km of shoreline in Southern California and Baja California. Significant spatial differences were found in the size distribution, growth, and survival rates of adult individuals along the study region. Size-specific fertility did not significantly change over the same geographic range. Field observations were used to parameterize a stage-structured matrix population model for sites at the extremes and at the middle of the region. Estimates of growth rate and net reproductive rate were greater than one throughout the region, although values calculated for the southernmost site, Punta Baja, were substantially smaller and closer to a demographic threshold that separates persistence from local extinction. Sensitivity calculations indicated that larval survival had the largest effect on population growth and net reproductive rate. Robustness of the three local models to environmental stochasticity was assessed by simulating different regimes of interannual variability in the survival of larvae and juveniles. Simulation results showed large between-site differences, with the model parameterized for Punta Baja being the least robust to environmental stochasticity and more prone to local extinction. I conclude that a spatial gradient in vital rates and temporal variability in the environment would be sufficient conditions to generate a range endpoint for *Balanus glandula* near Punta Baja.

4.2. INTRODUCTION

Biogeography is concerned with the geographic distribution of species and the factors that determine their range endpoints over long periods of time. The endpoints of a species' range often correlate with physical and biological factors that prevent or limit dispersal of individuals (for a review see Gaston 2003, Chapter 2). Mountains, lakes, or an ocean can be effective barriers for the dispersal of terrestrial species. In the marine environment, barriers for dispersal are more difficult to characterize. In the absence of physical, topographic barriers, the exchange of individuals between two areas is constrained by hydrodynamic features and discontinuities in physical-chemical conditions that often change in their intensity and spatial extent. Thus, the geographic limits of distribution for marine species are intrinsically more flexible than those of terrestrial species.

Many coastal species, particularly benthic invertebrates, have complex life cycles (Thorson 1950). Sedentary adults produce planktonic larvae that can disperse over potentially long distances during their development (Scheltema 1986). Surviving larvae settle as adults on habitats that are often far from their parental populations. Larval stages are thus the "vector" by which many benthic species can colonize new habitats, and the potential limits of a species range are determined by physical and biological processes that affect the horizontal distribution of larvae. The factors that ultimately determine the geographic range of a species, however, are those that affect post-settlement survival and the subsequent recruitment of settlers into reproductive adults (see Gosselin and Qian 1997). Regional differences in these factors must affect the spatial variability of a population's demography (i.e. its structure and vital rates) and, by extension, the position and variability of its range endpoints.

Range endpoints have been traditionally attributed to discontinuities in the environment and to physiological limitations of a species (e.g. Hutchins 1947; Cox and Moore 2000; Gaston 2003). Regional differences in survival, growth, and fertility of benthic invertebrates have been correlated with changes in environmental factors such as the availability of food and temperature (e.g. Sanford and Menge 2001; Phillips 2005), availability of substrate (e.g. Wethey 1984), physiological stress and inter-specific competition (Wethey 2002), as well as regional differences in larval supply (e.g. Connolly and Roughgarden 1998). Recent analyses of metapopulation models, however, have shown that range endpoints could arise from smooth spatial gradients in demographic rates, in the absence of environmental discontinuities (Lennon et al. 1997; Holt and Keitt 2000). Other modeling studies have suggested that dynamic physical boundaries such as coastal currents could set and maintain limits in the distribution of coastal species (Gaylord and Gaines 2000) in the absence of demographic gradients or physiological limitations.

In this paper I combine field observations and a stage-structured matrix population model to submit that the southern range endpoint of *Balanus glandula*, an intertidal barnacle from the west coast of North America, could be explained by spatial changes in demographic rates that make local populations less robust to environmental stochasticity. Matrix models have been extensively applied to terrestrial and marine populations (Caswell et al. 1997). Age-structured and size-structured models have been previously formulated for sedentary benthic species with complex life cycles (Roughgarden et al. 1985; Pascual and Caswell 1991; Hyder et al. 2001; Svensson et al. 2004). I use a simple two-stage model to explore the effects of environmental stochasticity and spatial changes in vital rates on the persistence of local populations. Parameters for this model were estimated from field observations on size structure, growth, survival, and reproductive activity of adult *B. glandula* over 1.5 years in a 400-kilometer region of Southern California and Baja California. I conclude that a spatial gradient in vital rates and temporal variability in the environment would be sufficient conditions to generate a range endpoint for *B. glandula* near the southern limit of our study region.

4.3. MATERIALS AND METHODS

4.3.1. Species, study sites and sampling procedure

The acorn barnacle *Balanus glandula* Darwin, 1854 is a widespread and abundant intertidal species that occurs in the middle to high intertidal zone along the west coast of North America, from the Aleutian Islands to Punta Baja, Baja California (Newman and Abbott 1980 and author's personal observations). Recent reports indicate its occurrence as an invasive species of intertidal habitats in Japanese (Kado 2003) and Argentinean shores (Orensanz et al. 2002). The reproduction of *B. glandula* is seasonal in Southern California and Baja California. Larvae are released by adults from early winter to late spring (Barnes and Barnes 1956; Hines 1979; Newman and Abbott 1980), and settlement takes place between late winter and early summer (Hines 1979; Pineda and López 2002).

The study region encompassed ~400 kilometers of shoreline, from Dana Point (33°27.78'N, 117°42.92'W) in Southern California, USA, to Punta Baja (29°57.25'N, 115°48.64'W) in Baja California, Mexico (Fig. 4.1). Seven sites were visited approximately monthly over 16-month period (Table 4.1). On each visit, ca. 100 adult *Balanus glandula* were collected haphazardly from an area that spanned ~ 100 m of coastline and the entire vertical range of distribution. Individuals were preserved in 95% ethanol for further analysis in the laboratory.

Pictures of four 5 x 5 cm quadrats were taken on each visit using a 4 megapixel digital camera (Nikon Coolpix 4500, Nikon Inc.). Low magnification pictures of whole quadrats were taken, as well as high-magnification shots of smaller portions that resolved the smallest settlers (~300 μm). Thermistors (Tidbit loggers, Onset Computer) that recorded temperature at hourly intervals were deployed in the lower intertidal at each site.

4.3.2. Measurements and data analysis

Up to 100 individuals from each site and sampling month were measured and inspected for reproductive status. They were classified into three different stages: immature (no apparent egg masses or gonad development), mature with no egg masses (yolk accumulation, no distinct egg mass), and mature with egg masses (egg masses distinct, with individual eggs clearly visible). Egg masses that appeared intact were removed from gravid individuals and preserved in 95% ethanol for subsequent fertility analysis (see below).

The following measurements were taken to the nearest 0.01 mm from each individual: basal length (longest axis of base), basal width (perpendicular to longest axis), opercular length, opercular width (perpendicular to opercular length), and height. We investigated the existence of spatial trends in morphometry with a Principal Component Analysis (PCA) of measurements collected at all sites and sampling times (N = 6,957 individuals). In a PCA, new variables (i.e. components) are computed as linear combinations of the variables originally measured (Morrison 1976). The sets of coefficients that defined those linear combinations in our case corresponded to the eigenvectors of the correlation matrix for all five sets of measurements. We used the principal component that explained the largest percentage of total variance (i.e. eigenvector corresponding to the largest eigenvalue) to summarize size information along the study region, and to conduct between-site comparisons of mean size for each season. Mean sizes within each season were compared with a one-way Analysis of Variance (ANOVA) that used sites as treatments. Homogeneity of variances was tested prior to this analysis using the Hartley test of largest to smallest variance ratio (Sokal and Rohlf 1995).

4.3.3. Estimation of growth and survival rates

Photographs collected over 16 months were used to estimate a growth function for *B. glandula* at the extremes of the study region, Dana Point and Punta Baja. Individuals that had been photographed repeatedly at those sites for 1-14 months were tracked and measured. Lack of individuals that survived for sufficiently long periods after settlement precluded the estimation of growth parameters at other sites. Assignments of age to recently settled individuals were based on a set of daily measurements of settlers in La Jolla, Southern California. Individuals with opercular lengths of 440 – 530 μm were assigned age 0 months with an error assumed to be no greater than a few days.

Size-at-age data were used to estimate the parameters of a von Bertalanffy growth function:

$$L_t = L_\infty\left(1 - e^{-k(t-t_0)}\right), \tag{4.1}$$

where t is time, L_∞ is the asymptotic maximum size, k is a parameter proportional to the rate at which L_t approaches L_∞, and t_0 corresponds to the age expected for an individual of size zero. Estimates of L_∞, k and t_0 were obtained for each site with a non-linear ordinary least squares regression. The two sets of parameters were compared using a randomization algorithm devised by Weinberg and Helser (1996), which is briefly outlined below.

Under the null hypothesis of no difference in growth parameters between sites, age-size pairs are all drawn from the same population. If that is the case, a growth curve fitted to the combined dataset of size $N_C = N_1 + N_2$, where 1 and 2 are site indices, should not differ from curves fitted separately for each site using N_1 and N_2 observations. Thus, the sum of squared residuals obtained from a curved fitted to the combined dataset (SSR_C) should not be greater than the sums of squared residuals obtained from fitting two separate curves (SSR_1+SSR_2), hence the test statistic

$$D_0 = SSR_E - \left(SSR_1 + SSR_2\right) \tag{4.2}$$

should be small. A large value of D_0 indicates that one curve fitted to the combined dataset cannot explain part of the variability that two separate site-specific fits do explain, hence there is a small chance that the null hypothesis is true.

Prior to the calculation of D_0, a von Bertalanffy growth curve was fitted to the combined set of size-age observations gathered from Dana Point (N_1=28) and Punta Baja (N_2=57). The significance of D_0 was evaluated by comparing it with a probability distribution obtained from the repeated computation of

$$D_x = SSR_E - \left(SSR_1^* + SSR_2^*\right), \tag{4.3}$$

where the asterisks indicate sums of squared residuals from growth curves fitted to groups of N_1 and N_2 observations that are randomly allocated to each group from the pooled dataset. This random allocation of data pairs and computation of D_x was repeated N_T= 10,000 times, and a *p*-value was computed as $P(D_x > D_0) = (x+1)/(N_T+1)$, where x is the number of iterations in which $D_x > D_0$ (Edgington 1986).

Survival probabilities were estimated separately for adults and juveniles from frequency distributions of minimum longevity, which was measured as the number of months an individual was photographed alive. Lack of sufficient data precluded the estimation of survival rates at all sites. Only Dana Point and Punta Baja, together with pooled observations from La Jolla and San Antonio (hereby referred to as LJ-SA), provided sufficient data to estimate survival rates of adults and juveniles. The assignment of juvenile or adult status to each individual in the photographs was done by comparing their size with the average minimum opercular length of gravid individuals found in the field samples (2.03 mm, SD = 0.33 mm). Because photographs were taken monthly, many juveniles were only photographed once. Minimum ages for these specimens were estimated from their opercular length and the above mentioned growth curves.

The probability of surviving until time t was computed as

$$P(l \leq t) = 1 - \frac{1}{N}\sum_{i=1}^{t} n_i , \tag{4.4}$$

where n_i is the number of individuals with longevity i and N is the total number of individuals tracked in the photographs. Temporal changes in survival probability were modeled for t = 1-12 months using a negative exponential function, which was fitted to probabilities computed as in Eq. 4.4 by least-squares regression.

4.3.4. Fertility analysis

A subset of gravid individuals collected during the 2002-2003 winter was used to conduct an analysis of fertility at size, i.e. number of eggs per brood as a function of individual size. Individuals spanning the range of sizes found at each site were chosen among those with intact egg masses. A volumetric method was used to estimate the total number of eggs per brood. The egg masses extracted from an individual barnacle were suspended in water and separated mechanically using a combination of vortexing and manual brushing, after which they were placed in a suspension of 80 ml of water. Ten 1-ml aliquots were examined under the microscope, and the numbers of eggs were recorded, averaged, and used to estimate total number of eggs. Aliquots were taken with an automatic pipette in sets of five at a time, so as to minimize the effect of sampling without replacement. Extra sets of aliquots were taken whenever the coefficient of variation of egg counts was greater than 20%. Comparisons of volumetric estimates and the total number of eggs counted in a subset of individuals indicated that the method was accurate within 6-15%.

A Principal Component Analysis (PCA) was performed on the morphometric data of individuals used for egg counting, in order to find the best predictor variable for the analysis of fertility at size, as well as to compare the size structure of gravid individuals between sites. The first principal component (PC1) was used as predictor variable in a reduced major axis regression of log-transformed fertility versus size data. This type of model II regression is recommended for cases in which both the predictor and response variable are observed with error (Rayner 1985). Prior to the analysis, an upper cutoff was chosen for the predictor variable, so that comparisons would be made among regression lines fitted within similar size ranges. A threshold of 20 mm was chosen for PC1, which resulted in a total of 11 observations removed from the original dataset (2, 1, 1, and 7 from DP, LJ, SA and ST, respectively).

4.3.5. Stage-structured matrix population model

Observations were modeled with a seasonal two-stage matrix model for the population of *Balanus glandula* (Fig. 4.2). The model relates the abundance of juvenile and adult individuals with transition probabilities at two different times of the year: a settlement season centered on March, and a reproductive season centered on December. The choice of these periods was based on the available literature (e.g. Hines 1979) as well as on the author's field observations. The separation of a yearly cycle into two different transition matrices with different projection intervals is warranted by the difference in time scales at which such transitions take place (Caswell 2001). On average, the transition between settlement and reproduction takes place over a period of nine months, whereas the transition between larval production and settlement as juveniles occurs within 3 months (Fig. 4.2). For the first transition, the number of adults (n_2) that will be alive to reproduce in December is a function of the survival probabilities for individuals that were juveniles (a) and adults (b) in March:

$$n_2 = \begin{pmatrix} a & b \end{pmatrix} \begin{pmatrix} n_1 \\ n_2 \end{pmatrix} \tag{4.5}$$

In the second transition (December to March), the numbers of juvenile and adult individuals are given by

$$\begin{pmatrix} n_1 \\ n_2 \end{pmatrix} = \begin{pmatrix} fs \\ d \end{pmatrix} n_2 \tag{4.6}$$

where d is the probability of adult survival from December to March, and the reproductive term fs (Fig. 4.2) is a product of the per capita fertility of adults (f) and the survival of larvae in the plankton (s).

Both transitions can be combined to obtain one matrix equation that projects the number of individuals from one yearly census to the next. However, different equations are obtained depending on the time of year for which projections are made. For example, if a census is conducted every December, there will be no juveniles in the population, and the abundance of adults will be given by the juveniles that survived after settlement plus adults that survived from the previous year. The equation that projects the population from year to year is found by substituting Eq. (4.6) into Eq. (4.5):

$$n_2(t+1) = (afs + bd)\, n_2(t) \tag{4.7}$$

where $afs + bd = \lambda$ is the population growth rate (i.e. rate at which the population will increase from year to year).

For a March-March projection interval, both juveniles and adults are encountered on each census, and a projection matrix is found by substituting Eq. (4.5) into Eq. (4.6):

$$\begin{pmatrix} n_1 \\ n_2 \end{pmatrix}_{t+1} = \begin{bmatrix} afs & bfs \\ ad & bd \end{bmatrix} \begin{pmatrix} n_1 \\ n_2 \end{pmatrix}_{t}, \tag{4.8}$$

where afs amounts to a recruitment probability (i.e. production and survival of larvae times post-settlement survival), ad is the probability of surviving the first year of benthic life, bfs is the reproductive output of surviving adults, and bd is the year-round probability of adult survival (Fig. 4.2).

If the projection matrix in Eq. (4.8) is separated into a transition matrix (**T**) and a reproduction matrix (**F**),

$$\mathbf{T}+\mathbf{F}=\begin{bmatrix} 0 & 0 \\ ad & bd \end{bmatrix}+\begin{bmatrix} afs & bfs \\ 0 & 0 \end{bmatrix}, \tag{4.9}$$

formulas to compute life expectancies and net reproductive rates can be obtained from the fundamental matrix (**N**)

$$\mathbf{N}=(\mathbf{I}-\mathbf{T})^{-1}=\begin{bmatrix} 1 & 0 \\ ad/_{1-bd} & 1/_{1-bd} \end{bmatrix}, \tag{4.10}$$

where **I** is the identity matrix. Life expectancies (i.e. number of years an individual is expected to live) for juveniles and adults in the population were calculated as the sum of the first and second column of this matrix, respectively. Finally, the largest eigenvalue of the matrix that results from pre-multiplying the fundamental matrix (Eq. 4.10) by the reproductive matrix (**F** in Eq. 4.9) corresponds to the Net Reproductive Rate (R_0)

$$R_0=\frac{afs}{1-bd}, \tag{4.11}$$

which is the mean number of individuals a juvenile will produce by the end of its life, hence the rate by which the population will increase from one generation to the next (Caswell 2001).

I studied the asymptotic and transient behavior of the model when parameterized for three different localities along the study region: Punta Baja, La Jolla – San Antonio, and Dana Point. The original goal was to estimate model parameters for at least three sites, at the extremes and middle of the study region. Insufficient data precluded the satisfactory parameterization of the model for any single locality other than Punta Baja and Dana Point. Observations taken at La Jolla and San Antonio were pooled in order to obtain a third case study. For each site, population growth rate ($\lambda = afs+bd$) and net reproductive rate (Eq. 4.11) were computed, as well as their sensitivity to changes in the model parameters. Sensitivities were calculated as partial derivatives of the respective rate with respect to each parameter. Life expectancies were calculated for juveniles and adults at each site.

To analyze the effect that interactions between parameters could have on population persistence, I first defined persistence as a population state where the growth rate $\lambda > 1$. A condition for persistence in terms of the model parameters can be found by substituting the definition of λ (Eq. 4.7) into this inequality and solving for the reproductive term *fs*:

$$fs > \frac{1-bd}{a} \tag{4.12}$$

where the ratio on the right hand side is proportional to mortality in the benthic part of the life cycle. Thus, the population will persist if the reproductive term *fs* – which would be proportional to larval supply – balances the combined effect of juvenile and adult mortality. Dividing both sides of Eq. 4.12 by $(1\text{-}bd)/a$, the left hand side of the inequality is equivalent to the Net Reproductive Rate (Eq. 4.11) and the condition for persistence is reduced to $R_0 > 1$. Thus, R_0 could also be interpreted as the ratio by which larval supply exceeds mortality in a population, or as how far a population is from crossing the line between persistence and local extinction. Assuming that per capita fertility (*f*) is constant at any given site – owing to a characteristic size distribution of reproductive individuals and a space invariant fertility function – I calculated the minimum per capita fertility required to attain persistence given a combination of survival probabilities.

To explore the effects of environmental stochasticity on the persistence of each population, I simulated random interannual fluctuations in the parameters to which growth and net reproductive rates were most sensitive. Two scenarios were used. In one of them, larval survival varied from year to year while all other parameters were kept constant. In the second scenario, the stochastic parameter was juvenile survival. Values for larval survival (s) and juvenile survival (a) were drawn at random from uniform probability distributions. Parameters for these distributions were chosen such that the range of possible values would encompass, and go beyond, those estimated from our field observations. For example, ranges used for the lower and upper limits of the larval survival distribution were $s_{\min} = .00005 - .0025$ and $s_{\max} = .0025 - .01$, which assuming a constant mortality rate and a 21-day larval period would correspond to instantaneous mortality rates of ca. 0.5 – 0.3 and ca. 0.3 – 0.2 d^{-1}, respectively. Recent estimates of instantaneous mortality rates for *B. glandula* larvae ranged from 0.2 to 0.4 d^{-1} (see Chapter 2).

For each site and simulation, the transition matrix and initial conditions n_1=1 juveniles and n_2=1 adults were used to project population size over T=40,000 time steps. On each time step, a value for the respective stochastic survival parameter was taken at random from its probability distribution. The log of the mean stochastic growth rate (λ_s) was estimated as

$$\log \lambda_s = \frac{1}{T} \sum_{t=0}^{T-1} \log\left(\frac{N_{t+1}}{N_t} \right), \tag{4.13}$$

where N_t is the total number of individuals in the population at time t. Population size $N(t)$ is lognormally distributed when the population is projected over a sufficiently long period, so that $\log \lambda_s$ is normally distributed with mean $t \log \lambda_s$ and variance $t\sigma^2$ (Caswell 2001). Survival values in the simulations were independent and identically distributed, hence it was possible to estimate σ^2 (i.e. rate of increase of the variance of log N) as

$$\sigma^2 = 2(\log \mu - \log \lambda_s) \tag{4.14}$$

where log μ is the growth rate of mean population size, computed as the log of the dominant eigenvalue of the average projection matrix. This estimate was used to compute the probability of quasi-extinction, defined as the probability that population size declines below a fraction θ of the initial population size, and calculated as

$$P_q(\theta)=\begin{cases} 1 & \text{if } \log\lambda_s \le 0 \\ \exp\left(\dfrac{2\log\lambda_s\log\theta}{\sigma^2}\right) & \text{if } \log\lambda_s > 0 \end{cases} \tag{4.15}$$

4.3.6. Estimation of model parameters

Mean per capita fertility (*f*) was estimated from the mean size of gravid individuals at each site and the corresponding fertility regression. Confidence limits for *f* were obtained from bootstrap distributions, which were computed by resampling with replacement from the size and fertility data available for each site (see Manly 1997). A reduced major axis regression of fertility (see above) was performed on each of N_{it} = 10,000 iterations per site, using bootstrap datasets sampled from the original sets of fertility-at-size observations. The same number of size datasets was generated by bootstrapping from size observations at each site, and used to compute the mean size of gravid individuals. Size and fertility observations for La Jolla and San Antonio were pooled prior to this procedure.

The mean estimate for larval survival (*s*) was based on recent estimates of the instantaneous mortality rate of larval *B. glandula* in nearshore waters off La Jolla, Southern California (see Chapter 2). I assumed that the number of surviving larvae decayed exponentially at a constant rate of 0.2 d^{-1} over a 21-day period. The choice of 21 days for larval duration was based on published observations of development time (Brown and Roughgarden 1985) at temperatures similar to those recorded at the intertidal sites during the reproductive season. Mean estimates for the survival probabilities of juveniles and adults (*a, b* and *d*) were obtained from negative exponential curves fitted to survival data from each site (see above). All of these mean estimates (*s, a, b, d*) had associated sampling errors that I attempted to include in the calculations of population growth rate, net reproductive rate, and life expectancies with a Monte Carlo procedure. Rather than using only one parameter value on each rate calculation, vectors of values were generated by random sampling from their respective probability distributions. Values of larval survival (s) were obtained from a uniform distribution with limits defined by the fraction of larvae that would survive after 14 – 28 days with a constant mortality rate of 0.2 d^{-1} ($s_{min} = 0.0037$, $s_{max} = 0.061$). Juvenile survival (a) was sampled from a uniform distribution that ranged between the minimum and maximum estimates obtained from field measurements. Adult survival after 3 and 9 months (d and b) was calculated using the exponential curves fitted to survival data from each site: $y = e^{-rx}$, where y is survival, x is time (in months) and the parameter r is a normally distributed random variable with mean and standard deviation given by its least-squares estimator and standard error. On each iteration of the Monte Carlo procedure, a different vector of parameter values was used to compute growth rate, net reproductive rate, and juvenile and adult life expectancies. I used 10,000 repetitions to obtain probability distributions from which 95% confidence limits were obtained using the bias-corrected percentile method (Manly 1997).

4.4. RESULTS

4.4.1. Size structure and timing of reproductive activity

A Principal Component Analysis of morphometric data for all sites and measured individuals (Table 4.2) produced a first principal component that explained 75.4% of the total variability in size structure. A new variable (PC1) was produced with this set of weights, and is used for the remainder of this paper to describe the size structure of *Balanus glandula*. The weights used to compute PC1 from five originally measured variables were very similar in magnitude relative to PC2 and PC3 (Table 4.2), hence the new variable approximately corresponds to the summation of all five measurements, and could be visualized as the outer line or external perimeter of each individual.

The frequency distributions of PC1 (Fig. 4.3) were similar in shape for some pairs of neighboring sites (e.g. San Quintín and Punta Baja in winter 2003-2004 and summer 2003), with a weak trend of decreasing mean size from Dana Point to Punta Baja. Significant between-site differences were found when means were compared for each season using a one-factor ANOVA ($F_{6,3005} = 62.03$ for winter 2002-03, $F_{6,2004} = 91.68$ for summer 2003, $F_{6,1927} = 40.85$ for winter 2003-04, $F_{6,1161} = 41.60$ for gravid individuals; all $P<0.001$). Bonferroni-adjusted pairwise comparisons showed consistent spatial patterns (Table 4.3). For example, differences in mean sizes recorded at the extremes of the study region were always significant (e.g. DP-LJ versus SQ-PB). San Quintín and Punta Baja were significantly different from the rest, but not from each other, on two out of three seasons and when gravid individuals were compared. Finally, differences in mean size were always significant between La Jolla and sites located south of it (Table 4.3). In addition to spatial differences in their means, size distributions recorded at the extremes of the study region differed significantly in their shapes. A comparison of standardized residuals from a two-way contingency table analysis of PC1 distributions showed that large individuals were more abundant, and smaller ones more scarce, than expected at Dana Point and La Jolla under the hypothesis of independence (Fig. 4.4). The opposite was true for San Quintín and Punta Baja: small and large individuals were more and less numerous, respectively, than expected under the hypothesis of independence between site and size frequency (Fig. 4.4).

Temporal changes in the proportion of brooding individuals occurred synchronously across the study region at the monthly sampling interval (Fig. 4.5). A small and narrow peak in brooding activity, centered on March 2003, was observed during the first winter. Brooding increased earlier in the reproductive season and remained high for a longer time during the second winter (Fig. 4.5), with maximum percentages observed between January and March 2004. It is possible that the small peak recorded during the first winter of our study corresponded to a late-season pulse of reproduction. High percentages of brooding individuals were found at San Quintín and Santo Tomás in September 2002 (author's personal observations), suggesting that reproduction started earlier on that season. The synchronous increase in brooding activity observed between November 2003 and January 2004 coincided with a downward trend in intertidal temperatures (Fig. 4.5). Differences in temperature of up to 7 °C between Dana Point and Punta Baja were observed from spring to late summer.

4.4.2. Growth and survival rates

Growth parameters estimated from size-at-age observations at each site were significantly different ($D_0 = 3.872$, $P = 0.0001$) and indicated that individuals at Punta Baja grew more slowly than at Dana Point ($k_{PB}=0.11 < k_{DP}=0.20$, Fig. 4.6). Estimated asymptotic maximum sizes (L_∞) suggest that barnacles at Punta Baja could grow to larger sizes than those at Dana Point ($L_{\infty PB}=4.20 > L_{\infty DP}=4.05$, Fig. 4.6). However, the comparatively low estimate of adult survival obtained for Punta Baja (Fig. 4.7) suggests that these individuals are unlikely to survive the time necessary to attain larger sizes. This is consistent with observed differences in size distributions at the extremes of the region (Fig. 4.4). A rapid decline in the survival of juveniles was observed at all sites during the first four months after settlement (Fig. 4.7). This decrease was less pronounced at Punta Baja, where the probability of a juvenile to survive for nine months after settlement was greater than at LJ-SA and Dana Point (Fig. 4.7).

4.4.3. Fertility at size and mean per capita fertility

A PCA of morphometric data for gravid barnacles utilized in the fertility analysis produced a first principal component that explained 81.7% of the total variability in size structure (Table 2). As with the PCA performed on the full dataset, these weights were very similar in magnitude, so the interpretation of the variable PC1 as body perimeter remained valid. The second principal component explained an additional 7.8% of the total variability (Table 2). Scores computed with these two components for all individuals used in the fertility analysis showed no apparent separation between sites when plotted on a PC1-PC2 plane (results not shown), suggesting that differences in morphometry could be ruled out as the cause of any between-site differences in size specific fertility.

With the exception of Santo Tomás, fertility regressions yielded similar relationships between number of eggs and individual size throughout the study region (Fig. 4.8). The slope of the fertility function at Santo Tomás was larger than those estimated for neighboring sites. However, there was partial overlap among bootstrap confidence intervals when a correction was made to allow for pairwise comparisons with a group significance of $\alpha = 0.05$ (Table 4.4). Similar estimates of mean per capita fertility were obtained for Dana Point and LJ-SA (ca. 6,000 eggs), whereas an average individual at Punta Baja was expected to produce less than half as many eggs (Table 4.5). Bootstrap distributions of per capita fertility were symmetrical around mean estimates for each site (Fig. 4.9) and very similar for Dana Point and LJ-SA, with ca. 70% overlap in their 95% confidence intervals (Table 4.5). There was no overlap between these two distributions and that obtained for Punta Baja (Fig. 4.9, Table 4.5).

4.4.4. Matrix population model

Results from the analyses detailed in previous sections were used to parameterize the projection matrix in Eq. (4.8) for Dana Point, LJ-SA, and Punta Baja. Median estimates of population growth rate (λ) were greater than one at all three sites (Table 4.5), with values obtained for the northern sites being three times higher than at Punta Baja (Table 4.5). Probability distributions of λ were very similar in shape and width at Dana Point and LJ-SA, with wide confidence intervals that almost completely overlapped (Table 4.5). Greater differences were found in the probability distributions of Net Reproductive Rate (R_0). Median estimates were all greater than one, but increased by a factor of two from Dana Point to LJ-SA, and decreased by a factor of thirteen between LJ-SA and Punta Baja (Table 4.5). In terms of the condition for persistence previously defined (Eq. 4.12), Punta Baja was thirteen times closer than LJ-SA to crossing the line between persistence and local extinction. A very narrow and positively skewed distribution at Punta Baja (Fig. 4.10b) yielded a 2% probability of finding values of $R_0 < 1$. The difference in R_0 between Dana Point and LJ-SA was due to differences in estimated adult survival (e.g. Table 4.5), which also generated substantial differences in the probability distributions of juvenile and adult life expectancies at these sites (Fig. 4.10c,d). Juveniles and adults at LJ-SA were expected to live 0.23 and 2.53 years longer than at Dana Point. Distributions of juvenile and adult expectancies at Punta Baja were extremely narrow and close to one (Fig. 4.10c,d and Table 4.5), indicating that barnacles at this site are not likely to be in the population for much longer than one yearly census.

Sensitivity calculations indicated that growth rates and net reproductive rates were disproportionately more sensitive to changes in the survival of early stages of the life cycle. Larval survival (s) had the largest effect at all three sites, although the importance of juvenile survival (a) appeared to increase at LJ-SA (Table 4.6). Based on these findings and the assumption that per capita fertility (f) is constant for a given site, I used the inequality in Eq. 4.12 to compute minimum fertilities required to attain persistence under different combinations of larval survival and 'benthic mortality ratios', i.e. $(1-bd)/a$.

The results showed that northern sites, given their per capita fertility, could persist with larval survival an order of magnitude lower than values that would drive Punta Baja to local extinction (Fig. 4.11). The horizontal arrows on Figure 4.11 point to survival values of 0.0029, 0.0006 and 0.0005 for Punta Baja, LJ-SA and Dana Point, respectively. Assuming an exponential decay in the number of surviving larvae and an average development time of 21 days, these values would correspond to instantaneous mortality rates of 0.28 d^{-1}, 0.35 d^{-1}, and 0.36 d^{-1}. Mortality rates that are comparable to these values have been recently estimated for the larvae of *Balanus glandula* in nearshore waters off La Jolla (see Chapter 2).

Sensitivity calculations suggested that the persistence of a local population could be greatly affected by temporal fluctuations in the survival probabilities of larvae (s) and juveniles (a). The sensitivity of R_0 to these parameters was a function of per capita fertility and adult survival (Table 4.6), which showed the largest differences between Punta Baja and the two northern sites (Table 4.5). The effects that interannual variability in these parameters would have on population persistence are summarized in Figures 4.12 and 4.13. Each panel in these figures shows the results of 900 simulations, corresponding to 900 different probability distributions from which survival values were drawn at random. Contours on Figure 4.12 correspond to the stochastic growth rate (log λ_s), which was always positive for Dana Point and LJ-SA, and negative on ca. 30% of the simulations for Punta Baja (Fig. 4.12). A similar pattern was observed for quasi-extinction probabilities (Fig. 4.13). Dana Point and LJ-SA had a zero probability of quasi-extinction throughout the parameter space used in the simulations. Quasi-extinction had a probability of one in 30% of the simulations conducted for Punta Baja (Fig. 4.13). Consistent with Figure 4.11, persistence was not possible at Punta Baja when larval survival ranged between values smaller than 0.0029 (Fig. 4.13). Persistence at Punta Baja was possible only when years with low survival (of either larvae or juveniles) were as likely to occur as years with high survival (Fig. 4.13). In other words, this population could withstand very low recruitment years only if years with very high recruitment were equally likely.

4.5. DISCUSSION

I have found spatial differences in the size distribution, growth, and survival rates of *Balanus glandula* within a 400-km range in Southern and Baja California. The results suggest that a range endpoint for this species could result from spatial changes in demography in a temporally variable environment. Previous studies based on spatially explicit models have suggested that range endpoints in coastal populations could result from the interaction between larval advection and substrate availability (Roughgarden et al. 1988), or from advective transport only (Gaylord and Gaines 2000). On the other hand, a recent field-based experimental study shows that interactions between physiological stress and inter-specific competition could limit the distribution of intertidal species (Wethey 2002). Here I used field observations and a stage-structured matrix model to show that a spatial gradient in vital rates and environmental stochasticity are sufficient conditions to generate a range endpoint for *Balanus glandula* near Punta Baja.

4.5.1. Population structure and vital rates

There were consistent spatial patterns in the size structure of *Balanus glandula*. Both the mean and shape of size distributions changed significantly from Dana Point to Punta Baja in all three seasons. Mean sizes were significantly smaller at Punta Baja because small and large individuals were, respectively, more and less abundant than expected under the hypothesis of spatial homogeneity in size distributions. Such differences may be caused by differences in the growth rate and survival of adults at Punta Baja and Dana Point.

Spatial changes in the growth rate of adult *Balanus glandula* have been ascribed to differences in temperature (Phillips 2005), food availability (Duggins et al. 1989), or both (Sanford and Menge 2001). In general, warmer temperatures and higher food availability should increase growth rates, although temperature appears to be a more important factor. Differences in *B. glandula* growth rates recently found around Point Conception (Phillips 2005) occurred in the absence of patterns in chlorophyll-*a* concentration (used as a proxy for food availability), and attributed to spatial differences in temperature. These results are consistent with the differences in growth found between Punta Baja and Dana Point. Growth at Punta Baja was significantly slower than at Dana Point, where intertidal water temperatures were up to 7°C warmer during the summer and early autumn. Although *in situ* chlorophyll concentrations were not measured, shipboard measurements conducted in the spring of 2002, 2003 and 2004 off Punta Baja and La Jolla (Pineda et al., unpublished results) showed higher chlorophyll-*a* concentrations and colder temperatures in nearshore waters off Punta Baja. Satellite-derived chlorophyll maps for the region (Espinosa-Carreon et al. 2004) suggest that such spatial differences in pigment concentration are consistent over inter-annual scales. Thus, differences in growth rate between the extremes of the sampling region could be caused by spatial differences in temperature rather than food availability. Differences in adult survival, on the other hand, could be linked to spatial changes in a number of physical and biological factors, including predation pressure, substrate availability and substrate quality. Given the low sampling frequency used in this study, at this point I could only speculate as to the role of these factors in determining survival. Experimental work at local scales and higher sampling frequencies is needed to gather a more complete picture of the interaction between physical and biological factors that determine the observed differences in vital rates.

Although size distributions were significantly different between the extremes of the study region, no spatial differences in morphometry (i.e. relative magnitudes of different body dimensions) were detected. This finding supported the use of one global variable (PC1) to describe and compare the size structure of *B. glandula* along the study region. Furthermore, it allowed the direct comparison of fertility regressions from different sites. With the exception of Santo Tomás, between-site differences in the slope of fertility regressions were small, and suggested that changes in reproductive output over regional scales are determined primarily by changes in the size structure and density of reproductive adults. Results from other comparisons of crustacean fertility conducted at similar latitudes and spatial scales are consistent with these results. For instance, Dugan et al. (1991) found no significant differences in the slopes of their fertility regressions for sand crabs *Emerita analoga* from six sites along 400 kilometers of the Southern California coast.

4.5.2. Stage structured matrix model

The analysis of a stage-structured matrix model indicated that an imbalance between the reproductive term *fs* and the mortality of adults and juveniles (Eq. 4.12) is a necessary condition for population persistence. Field observations verified that such condition holds at all three sites for which the model was parameterized. However, the factor by which population renewal was larger than the benthic mortality ratio – equivalent to the net reproductive rate (Table 4.5) – decreased more than ten times between La Jolla – San Antonio and Punta Baja, a site that is near the southern limit of distribution of *Balanus glandula*. This latitudinal change in net reproductive rate suggests that, as barnacle populations get closer to Punta Baja, they get closer to crossing a threshold between persistence and local extinction.

Sensitivity calculations showed that larval survival and juvenile survival had the largest proportional effects on growth rate (λ) and net reproductive rate (R_0), and by extension on population persistence. The simulations confirmed these results and suggested that inter-annual fluctuations in the survival of larvae and juveniles could generate between-site differences in susceptibility to quasi-extinction, defined here as the event of population size falling below a fraction θ=0.1 of the initial population size. Dana Point and LJ-SA, the two northern sites, appeared robust to large changes in the survival of larvae and juveniles. These sites yielded positive estimates of the log mean stochastic growth rate, and zero probability of quasi-extinction, for the entire range of parameter values used in the simulations. Results were dramatically different for Punta Baja, which was susceptible to quasi-extinction under ca. 30% of the simulated regimes of stochasticity in larval survival and juvenile survival.

The stage-structured matrix model was formulated in a non-spatial context, where larval numbers decrease due to natural mortality (e.g. predation and starvation) as well as by advection and diffusion. Thus, stochasticity in the larval survival parameter (s) must reflect the combined variability of biological and physical processes that affect mortality and advection-diffusion of larvae in the nearshore. It follows that spatial differences in physical forcing should generate spatial differences in larval supply. In the context of the model, this amounts to saying that different local populations may experience degrees of stochasticity found at different regions of the parameter space shown on Figures 4.12 and 4.13 (left panels), which could increase between-site differences in susceptibility to local extinction.

Physical observations conducted in recent years show more intense advective forcing at Punta Baja than at La Jolla. Coastal upwelling is more prevalent at Punta Baja, and can be detected as net offshore flows down to depths of ca. 40 m (López and Pineda 2004). Such conditions might increase the offshore transport of larvae (e.g. Roughgarden et al. 1988; but see Garland and Zimmer 2002) and the interannual variability in larval supply at Punta Baja. Low per capita fertilities at San Quintín and Punta Baja could further contribute to a reduction of larval abundance in the nearshore.

4.5.3. Caveats and limitations of this study

The spatial coverage that allowed to show geographic patterns in the demography of *Balanus glandula* was attained at the expense of sampling frequency. Therefore, it was not possible to simultaneously investigate processes that could generate some of these patterns. Settlement rate, i.e. number of larvae settling per unit time per unit area of available substrate, has been traditionally used as a proxy for larval supply (e.g. Gaines et al. 1985; Miron et al. 1995), although small scale hydrodynamics, behavioral factors and space availability may decouple these two processes (Pineda 2000). Information on settlement rates at the sampling sites could have provided valuable insight on inter-site differences in larval supply and susceptibility to extinction. Sampling intervals, however, would have had to be much shorter (e.g. 1 day), as inter-site differences due to larval supply can be obscured by differences due to post-settlement mortality.

Another limitation imposed by a low sampling frequency was the lack of temporal resolution in the observation of reproductive timing. Although spatial differences in the timing or duration of the brooding season were not apparent in the data, the frequency of field observations was probably insufficient to resolve differences of days to weeks in the timing of reproduction across the study region. Laboratory and field observations indicate that warm water may shorten the brooding season of *Balanus glandula* and that, to some extent, cold water would have the opposite effect (Hines 1976, 1979). Temperature differences between Dana Point and Punta Baja fluctuated around 7°C in spring-summer and approached zero in late fall to early winter. The effect of such spatial differences in temperature regime on the timing and duration of a brooding season, and potentially on the number of broods produced per individual, remains to be investigated. Spatial differences in the number of broods produced per individual in one season could change the latitudinal gradient observed in mean per capita fertility and perhaps affect the model's predictions.

Finally, the simplicity of this matrix model made it possible to obtain simple linear expressions for growth rate (λ) and net reproductive rate (R_0), which made it possible to calculate sensitivities of these rates to individual parameters. However, leaving density-dependent effects out of the model might have been an over simplification that could potentially affect this work's conclusions. It has been shown that sharp boundaries in spatial distribution could be generated by smooth gradients in intra-specific interactions (Wilson et al. 1996), many of which could be attributed to density dependence. For example, survival rates of juveniles and adults are likely to depend on local density (Svensson et al. 2004). Per capita fertility could decrease at low densities due to an Allee effect (Wethey 1984), as adult barnacles must be within a minimum distance of their neighbors in order for fertilization to take place (Barnes and Crisp 1956). Settlement, whether gregarious (Knight-Jones and Stevenson 1950; Kent et al. 2003) or proportional to free space (Gaines and Roughgarden 1985; Hyder et al. 2001, but see Pineda and Caswell 1997), could also be a function of local adult density.

Thus, the possibility that a range endpoint for *Balanus glandula* at Punta Baja is the manifestation of one or more density dependent effects on local demography cannot be ruled out. I can only argue that, in the framework of these field observations and model results, spatial differences in adult survival and mean per capita fertility alone can largely affect the susceptibility of a population to local extinction, and possibly the geographic limits of a species' distribution.

4.6. ACKNOWLEDGEMENTS

This work was supported by a National Science Foundation grant to Jesús Pineda (WHOI). I thank J. Leichter (SIO) and L. Ladah (CICESE) for their support while conducting field work in Southern California and Baja California. The matrix model analysis greatly benefited from comments provided by H. Caswell. Statistical advice from V. Starczak was fundamental. This manuscript is part of FT's doctoral dissertation at the MIT/WHOI Joint Program in Biological Oceanography.

4.7. REFERENCES

Barnes H, Barnes M (1956) The general biology of *Balanus glandula* Darwin. Pacific Science 10: 415-422

Barnes H, Crisp DJ (1956) Evidence of self-fertilization in certain species of barnacles. Journal of the Marine Biological Association of the United Kingdom 35: 631-639

Brown SK, Roughgarden J (1985) Growth, morphology, and laboratory culture of larvae of *Balanus glandula* (Cirripedia: Thoracica). Journal of Crustacean Biology 5: 574-590

Caswell H (2001) Matrix Population Models: Construction, Analysis, and Interpretation. Sinauer, Sunderland, MA

Caswell H, Nisbet RM, de Roos AM, Tuljapurkar S (1997) Structured-population models: Many methods, a few basic concepts. In: Tuljapurkar S, Caswell H (eds) Structured-population Models in Marine, Terrestrial and Freshwater Systems. Chapman and Hall, New York, pp 3-17

Connolly SR, Roughgarden J (1998) A latitudinal gradient in northeast Pacific intertidal community structure: evidence for an oceanographically based synthesis of marine community theory. American Naturalist 151: 311-326

Cox CB, Moore PD (2000) Biogeography. An ecological and evolutionary approach. Blackwell Science, Malden, MA

Dugan JE, Wenner AM, Hubbard DM (1991) Geographic variation in the reproductive biology of the sand crab *Emerita analoga* (Stimpson) on the California coast. Journal of Experimental Marine Biology and Ecology 150: 63-81

Duggins DO, Simenstad CA, Estes JA (1989) Magnification of secondary production by kelp detritus in coastal marine ecosystems. Science 245: 170-173

Edgington ES (1986) Randomization tests. In: Kotz S, Johnson N (eds) Encyclopedia of Statistical Sciences. Wiley, New York, pp 530-583

Espinosa-Carreon TL, Strub PT, Beier E, Ocampo-Torres F, Gaxiola-Castro G (2004) Seasonal and interannual variability of satellite-derived chlorophyll pigment, surface height, and temperature off Baja California. Journal of Geophysical Research 109: doi:10.1029/2003JC002105

Gaines S, Brown S, Roughgarden J (1985) Spatial variation in larval concentrations as a cause of spatial variation in settlement for the barnacle, *Balanus glandula*. Oecologia 67: 267-272

Gaines S, Roughgarden J (1985) Larval settlement rate: a leading determinant of structure in an ecological community of the marine intertidal zone. Proceedings of the National Academy of Sciences USA 82: 3707-3711

Garland ED, Zimmer CA (2002) Hourly variations in planktonic larval concentrations on the inner shelf: emerging patterns and processes. Journal of Marine Research 60: 311-325

Gaston KJ (2003) The Structure and Dynamics of Geographic Ranges. Oxford University Press, Oxford

Gaylord B, Gaines SD (2000) Temperature or transport? Range limits in marine species mediated solely by flow. American Naturalist 155: 769-789

Gosselin LA, Qian P-Y (1997) Juvenile mortality in benthic marine invertebrates. Marine Ecology Progress Series 146: 265-282

Hines AH (1976) Comparative reproductive ecology of three species of intertidal barnacles. Ph.D. Zoology Department, Berkeley

Hines AH (1979) The comparative reproduction ecology of three species of intertidal barnacles. In: Stancyk SE (ed) Reproductive Ecology of Marine Invertebrates. University of South Carolina Press, Columbia, pp 213-234

Holt RD, Keitt TH (2000) Alternative causes for range limits: a metapopulation perspective. Ecology Letters 3: 41-47

Hutchins LW (1947) The bases for temperature zonation in geographical distribution. Ecological Monographs 17: 325-335

Hyder K, Åberg P, Johnson MP, Hawkins SJ (2001) Models of open populations with space-limited recruitment: extension of theory and application to the barnacle *Chthamalus montagui*. Journal of Animal Ecology 70: 853-863

Kado R (2003) Invasion of Japanese shores by the NE Pacific barnacle *Balanus glandula* and its ecological and biogeographical impact. Marine Ecology Progress Series 149: 199-206

Kent A, Hawkins SJ, Doncaster CP (2003) Population consequences of mutual attraction between settling and adult barnacles. Journal of Animal Ecology 72: 941-952

Knight-Jones EW, Stevenson JP (1950) Gregariousness during settlement in the barnacle *Elminius modestus* (Darwin). Journal of the Marine Biological Association of the United Kingdom 29: 281-297

Lennon JJ, Turner JRG, Connell D (1997) A metapopulation model of species boundaries. Oikos 78: 486-502

López M, Pineda J (2004) Coastal winds and pressure signals along the Baja California and Southern California coasts Ocean Sciences Meeting. EOS Transactions 84, Portland, OR

Manly BF (1997) Randomization, Bootstrap and Monte Carlo Methods in Biology. Chapman & Hall / CRC, New York

Miron G, Boudreau B, Bourget E (1995) Use of larval supply in benthic ecology - Testing correlations between larval supply and larval settlement. Marine Ecology Progress Series 124: 301-305

Morrison DF (1976) Multivariate Statistical Methods. McGraw-Hill, New York

Newman WA, Abbott DP (1980) Cirripedia: the barnacles. In: Morris RH, Abbott DP, Haderlie EG (eds) Intertidal Invertebrates of California. Stanford University Press, Stanford, pp 502-535

Orensanz JM, Schwindt E, Pastorino G, Bortolus A, Casas G, Darrigran G, Elias R, Lopez Gappa JJ, Obenat S, Pascual M, Penchaszadeh P, Piriz ML, Scarabino F, Spivak ED, Vallarino EA (2002) No longer the pristine confines of the world ocean: A survey of exotic marine species in the Southwestern Atlantic. Biological Invasions 4: 115-143

Pascual M, Caswell H (1991) The dynamics of a size-classified benthic population with reproductive subsidy. Theoretical Population Biology 39: 129-147

Phillips NE (2005) Growth of filter-feeding benthic invertebrates from a region with variable upwelling intensity. Marine Ecology Progress Series 295: 79-89

Pineda J (2000) Linking larval settlement to larval transport: assumptions, potentials, and pitfalls. In: Färber-Lorda J (ed) Oceanography of the Eastern Pacific. CICESE, Ensenada, pp 84-105

Pineda J, Caswell H (1997) Dependence of settlement rate on suitable substrate area. Marine Biology 129: 541-548

Pineda J, López M (2002) Temperature, stratification and barnacle larval settlement in two Californian sites. Continental Shelf Research 22: 1183-1198

Rayner JMV (1985) Linear relations in biomechanics: the statistics of scaling functions. Journal of Zoology 206: 415-439

Roughgarden J, Gaines SD, Possingham H (1988) Recruitment dynamics in complex life cycles. Science 241: 1460-1466

Roughgarden J, Iwasa Y, Baxter C (1985) Demographic theory for an open marine population with space-limited recruitment. Ecology 66: 54-67

Sanford E, Menge BA (2001) Spatial and temporal variation in barnacle growth in a coastal upwelling system. Marine Ecology Progress Series 209: 143-157

Scheltema R (1986) On dispersal and planktonic larvae of benthic invertebrates: An eclectic overview and summary of problems. Bulletin of Marine Science 39: 290-322

Sokal RR, Rohlf FJ (1995) Biometry: The principles and practice of statistics in biological research. W.H. Freeman & Co., New York

Svensson CJ, Jenkins SR, Hawkins SJ, Myers AA, Range P, Paula J, O'Riordan RM, Åberg P (2004) Models of open populations with space-limited recruitment in stochastic environments: relative importance of recruitment and survival in populations of *Semibalanus balanoides*. Marine Ecology Progress Series 275: 185-197

Thorson G (1950) Reproductive and larval ecology of marine bottom invertebrates. Biological Reviews 25: 1-45

Weinberg JR, Helser TE (1996) Growth of the Atlantic surfclam, *Spisula solidissima*, from Georges Bank to the Delmarva Peninsula, USA. Marine Biology 126: 663-674

Wethey DS (1984) Effects of crowding on fecundity in barnacles: *Semibalanus* (*Balanus*) *balanoides*, *Balanus glandula*, and *Chthamalus dalli*. Canadian Journal of Zoology 62: 1788-1795

Wethey DS (2002) Biogeography, competition, and microclimate: The barnacle *Chthamalus fragilis* in New England. Integrative and Comparative Biology 42: 872-880

Wilson WG, Nisbet RM, Ross AH, Robles C, Desharnais RA (1996) Abrupt population changes along smooth environmental gradients. Bulletin of Mathematical Biology 58: 907-922

4.8. TABLES

Table 4.1

Sampling effort for each site and month, showing the numbers of individuals sampled, measured and inspected for reproductive condition. Sampling sites from north to south (see Fig. 1), are Dana Point (DP), La Jolla (LJ), San Antonio (SA), Santo Tomás (ST), Eréndira (ER), San Quintín (SQ), and Punta Baja (PB).

Sampling Date	**SITE**						
	DP	**LJ**	**SA**	**ST**	**ER**	**SQ**	**PB**
Winter 2002 - 2003							
November 2002	117	102	96	93	94	100	92
December 2002	100	97	100	-	94	100	68
January 2003	99	98	100	96	93	100	-
February 2003	85	54	97	53	95	101	40
March 2003	100	98	91	105	75	92	87
Summer 2003							
April 2003	98	79	75	43	57	37	40
May 2003	92	65	99	-	-	89	100
July 2003	62	86	60	76	72	47	64
September 2003	100	96	99	99	94	94	88
Winter 2003 - 2004							
November 03	100	69	96	73	96	100	60
December 03	99	95	95	99	96	100	44
January 04	69	56	-	69	-	-	66
March 04	78	64	-	79	59	64	108
Total	**1199**	**1059**	**1008**	**885**	**925**	**1024**	**857**

Table 4.2

Principal Component Analysis performed on morphometric data collected for *Balanus glandula* at all localities. Columns show the weights assigned to originally measured variables. Weights were computed as eigenvectors corresponding to the three largest eigenvalues of the correlation matrix for each dataset. Only the components that explained more than 5% of the total variance are reported.

Variable	**Global data (*N* = 6,957)**			**Fertility subset (*N* = 202 gravid indiv.)**		
	PC1	**PC2**	**PC3**	**PC1**	**PC2**	**PC3**
Basal length	0.459	0.020	-0.491	0.456	0.279	-0.363
Basal width	0.452	0.011	-0.588	0.448	0.247	-0.576
Opercular length	0.458	-0.426	0.377	0.460	-0.448	0.114
Opercular width	0.466	-0.332	0.376	0.447	-0.596	0.159
Height	0.398	0.841	0.359	0.425	0.552	0.706
% Total var.	75.408	9.816	8.357	81.732	7.786	5.718

Table 4.3

Pairwise comparisons of mean size (PC1) between sites. Black bars connect sites with no significant differences in their mean size (i.e. Bonferroni-adjusted $P > 0.05$). Means are sorted in decreasing order from left to right on each set of comparisons. Site labels correspond to Dana Point (DP), La Jolla (LJ), San Antonio (SA), Santo Tomás (ST), Eréndira (ER), San Quintín (SQ), and Punta Baja (PB).

Season / Category	**SITE** ——— **Decreasing means** ———→						
	LJ	**DP**	**ER**	**ST**	**SA**	**PB**	**SQ**
Winter 2002-2003	■	■					
			■	■	■		
						■	■
	LJ	**DP**	**SA**	**ST**	**ER**	**SQ**	**PB**
Summer 2003		■	■	■			
						■	■
			■	■	■		
	LJ	**DP**	**ST**	**SA**	**ER**	**PB**	**SQ**
Winter 2003-2004		■	■	■			
				■	■	■	
	LJ	**DP**	**ER**	**ST**	**SA**	**PB**	**SQ**
Gravid individuals		■	■	■			
						■	■
			■	■	■		

Table 4.4

Mean slope estimates from the reduced major axis regression of fertility at size. Confidence intervals were obtained by bootstrapping. The 99.6% confidence limits ($\alpha = 0.004$) were used for pairwise comparisons with a group significance of $\alpha = 0.05$.

Site	Mean estimate	95% Conf. Limits		99.6% Conf. Limits	
		Lower	Upper	Lower	Upper
Dana Point	2.949	2.404	3.549	2.159	3.888
La Jolla	3.327	2.855	3.788	2.529	4.115
San Antonio	2.833	2.223	3.299	1.910	3.623
Santo Tomás	4.388	3.857	4.962	3.548	5.398
San Quintín	3.640	2.729	5.261	1.618	7.159
Punta Baja	3.095	2.621	3.552	2.368	3.801

Table 4.5

Parameterization and asymptotic analysis of projection matrices for Punta Baja (PB), La Jolla – San Antonio (LJ-SA) and Dana Point (DP). Numbers in brackets correspond to 95% confidence limits computed from bootstrap ($^{\#}$) and Monte Carlo ($^{+}$) distributions (see Materials and Methods).

			SITE	
Parameter	**Symbol/Formula**	**PB**	**LJ-SA**	**DP**
Per capita fertility	f	2436	6625	6232
		[2032 - 2998]$^{\#}$	[5844 - 7530]$^{\#}$	[5513 - 7025]$^{\#}$
Larval survival	s*	0.015	0.015	0.015
Juvenile survival	a	0.135	0.044	0.110
Mar-Dec Adult survival	b	0.154	0.860	0.736
Dec-Mar Adult survival	d	0.535	0.951	0.903
Growth rate	$afs + bd$	6.5	18.1	17.2
(λ)		[1.1 – 17.1]$^{+}$	[3.5 – 46.5]$^{+}$	[3.2 – 44.2]$^{+}$
Net Reproductive Rate	$afs/(1\text{-}bd)$	7.0	95.2	49.0
(R_0)		[1.1 - 18.6]$^{+}$	[14.8 - 255.1]$^{+}$	[7.7 - 130.6]$^{+}$
Juvenile life expectancy	$1+[ad/(1\text{-}bd)]$	1.05	1.47	1.24
(*JLE*)		[1.03 – 1.08]$^{+}$	[1.24 – 1.72]$^{+}$	[1.12 - 1.37]$^{+}$
Adult life expectancy	$1/(1\text{-}bd)$	1.09	5.50	2.97
(*ALE*)		[1.06 - 1.13]$^{+}$	[4.93 - 6.28]$^{+}$	[2.69 - 3.35]$^{+}$

* : Based on a 21-day larval duration and a constant mortality rate of 0.2 d^{-1}

Table 4.6

Sensitivity (S) of the population growth rate (λ) and net reproductive rate (R_0) to each of the model parameters. Parameter estimates obtained for each site (Table 5) were used in the computations.

Model parameter	Sensitivity formula	Punta Baja		La Jolla San Antonio		Dana Point	
		S	%	S	%	S	%
Population growth rate (λ)							
f	as	0.002	0.00	0.001	0.00	0.002	0.00
s	af	328.86	89.83	291.50	74.23	685.52	87.82
a	fs	36.54	9.98	99.38	25.31	93.48	11.97
b	d	0.54	0.15	0.95	0.24	0.90	0.12
d	b	0.15	0.04	0.86	0.22	0.74	0.09
Net reproductive rate (R_0)							
f	$as/(1-bd)$	0.002	0.00	0.004	0.00	0.005	0.00
s	$af/(1-bd)$	358.39	89.10	1600.42	67.11	2043.94	82.67
a	$fs/(1-bd)$	39.82	9.90	545.60	22.88	278.72	11.27
b	$afsd/(1-bd)^2$	3.13	0.78	125.34	5.26	82.55	3.34
d	$afsb/(1-bd)^2$	0.90	0.22	113.35	4.75	67.28	2.72

4.9. FIGURES

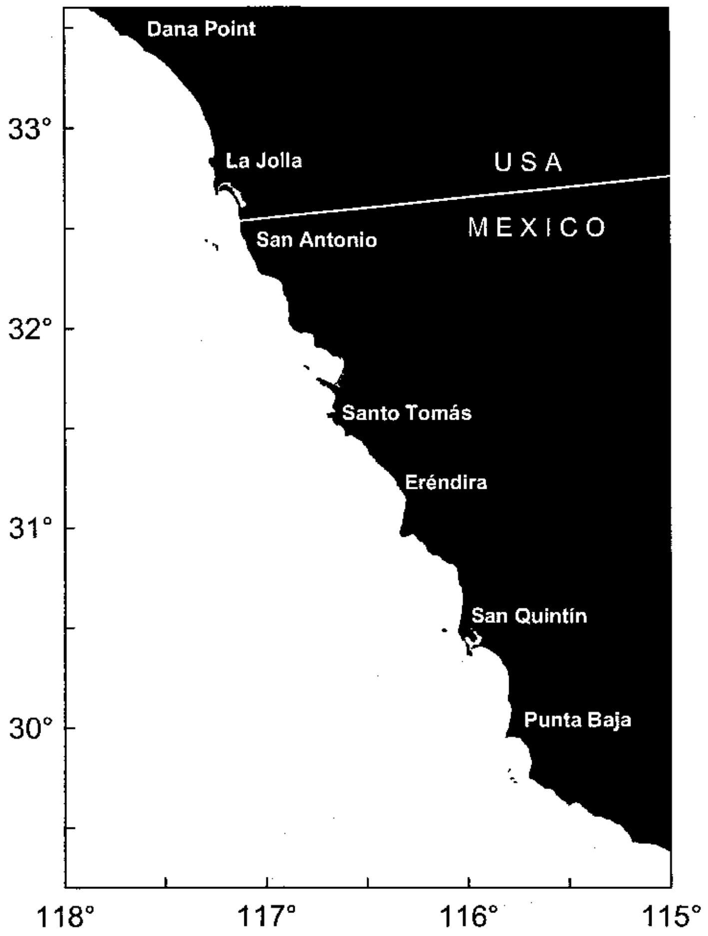

Figure 4.1

Map of the Southern California and Baja California region where this study was conducted. Labels correspond to intertidal sampling sites.

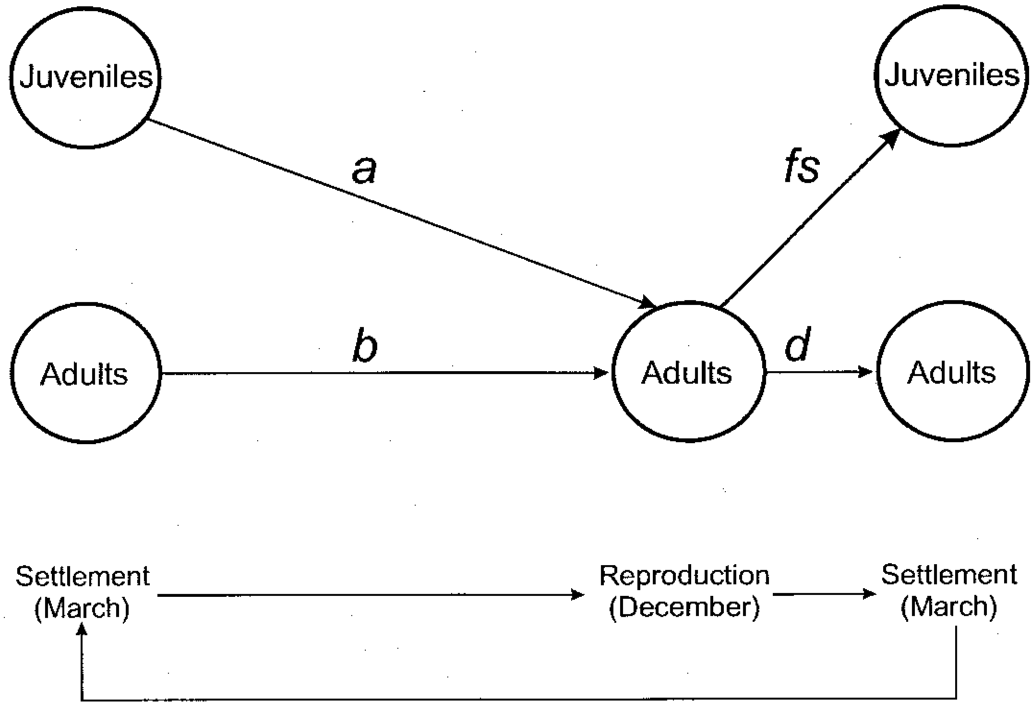

Figure 4.2

Life cycle diagram of the stage-structured matrix model for the intertidal barnacle *Balanus glandula*. Arrows correspond to transitions in the model. Survival probabilities are indicated by *a*, *b*, and *d*. The product *fs* is a reproductive term, proportional to per capita fertility (*f*) and the survival probability for larvae (*s*).

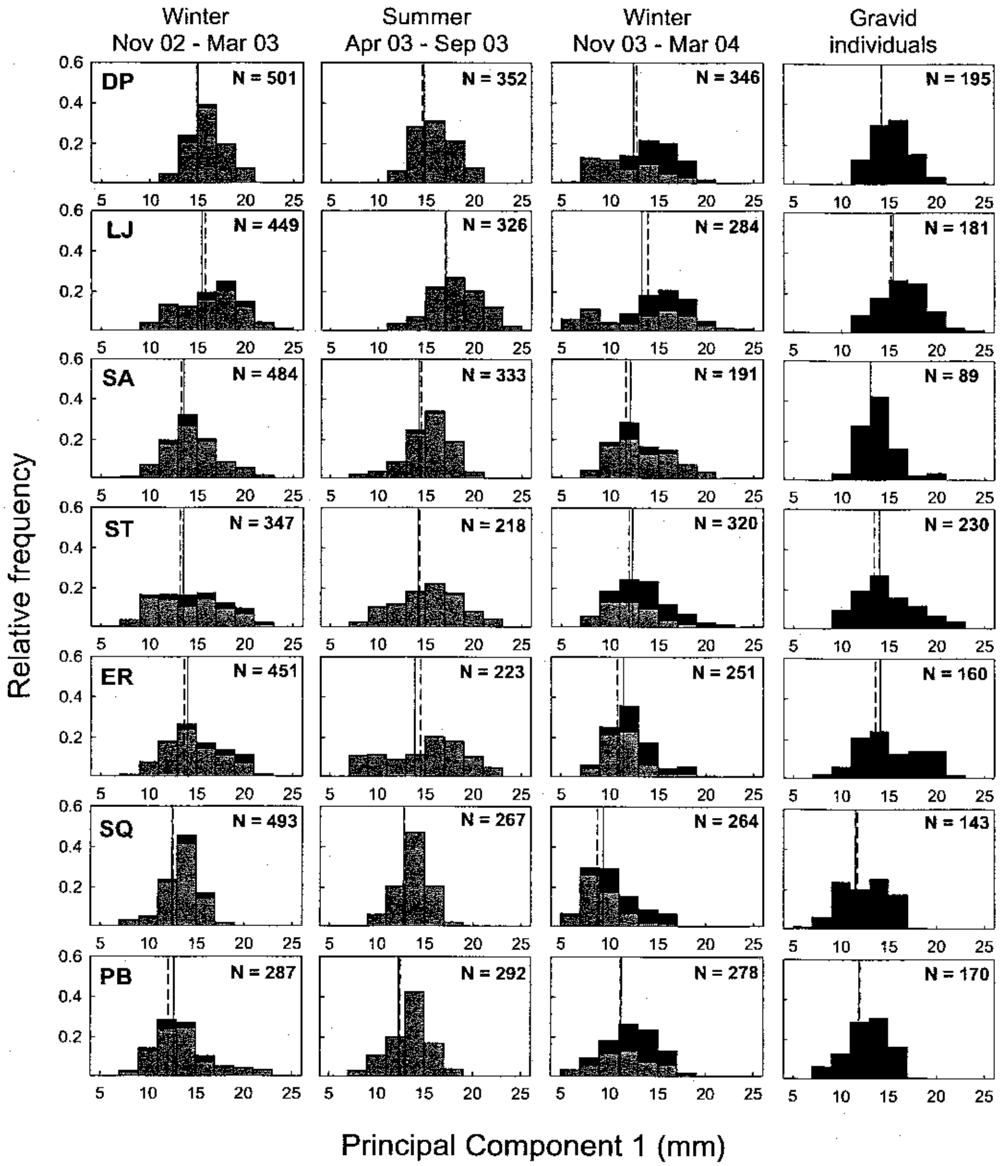

Figure 4.3

Size distribution of *Balanus glandula* per season, site and reproductive state in Southern and Baja California. Size is the first principal component of a PCA performed on the global set of size measurements (Table 2). Vertical solid and dashed lines are the mean and median size for each distribution. Black bars correspond to gravid individuals. Two-letter codes for site names (see Figure 1) correspond to Dana Point (DP), La Jolla (LJ), San Antonio (SA), Santo Tomás (ST), Eréndira (ER), San Quintín (SQ), and Punta Baja (PB).

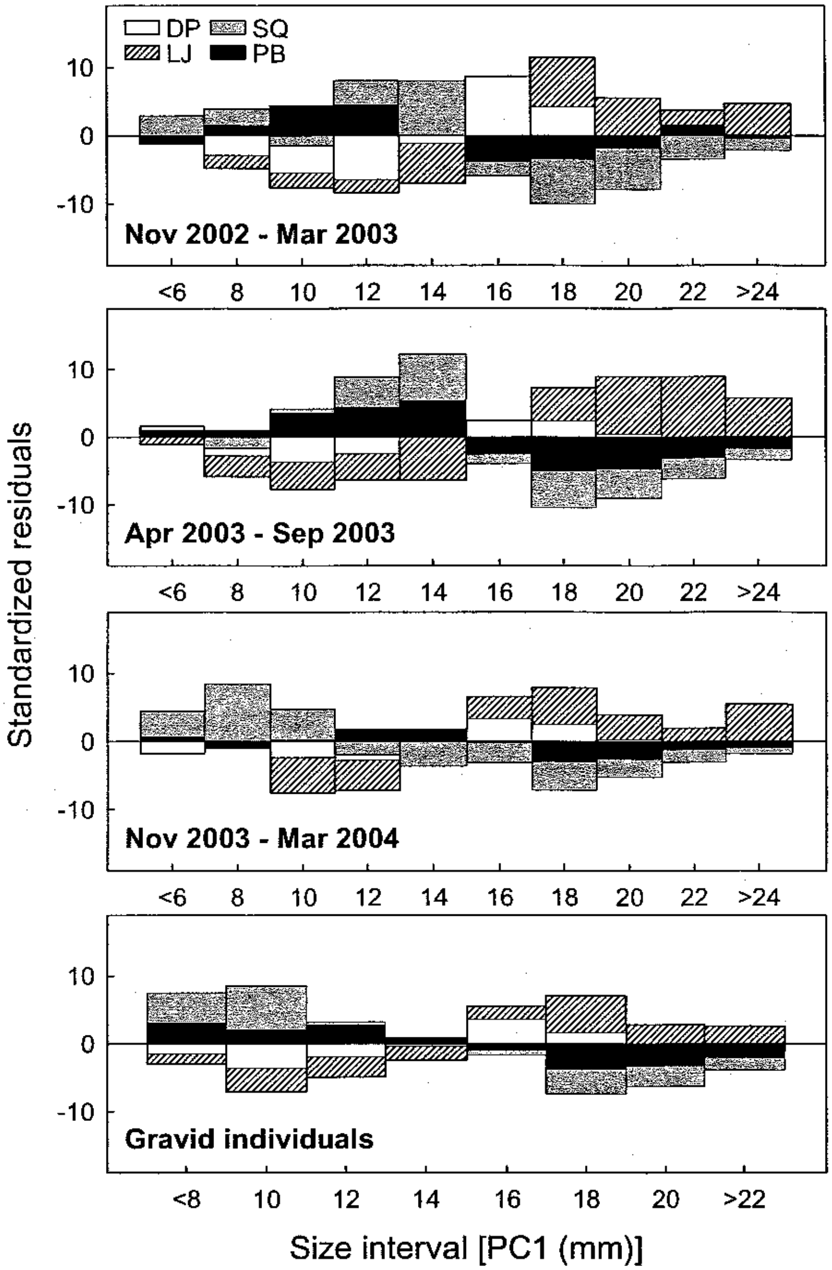

Figure 4.4

Distribution of residuals from a two-way contingency table analysis of size frequency distributions at the extremes of the sampling region. Standardized residuals were computed as $(O_{ij}-E_{ij})/\sqrt{E_{ij}}$, where O_{ij} corresponds to the frequency of size interval j observed at site i, and E_{ij} is the frequency expected for that site and size interval under the hypothesis of independence.

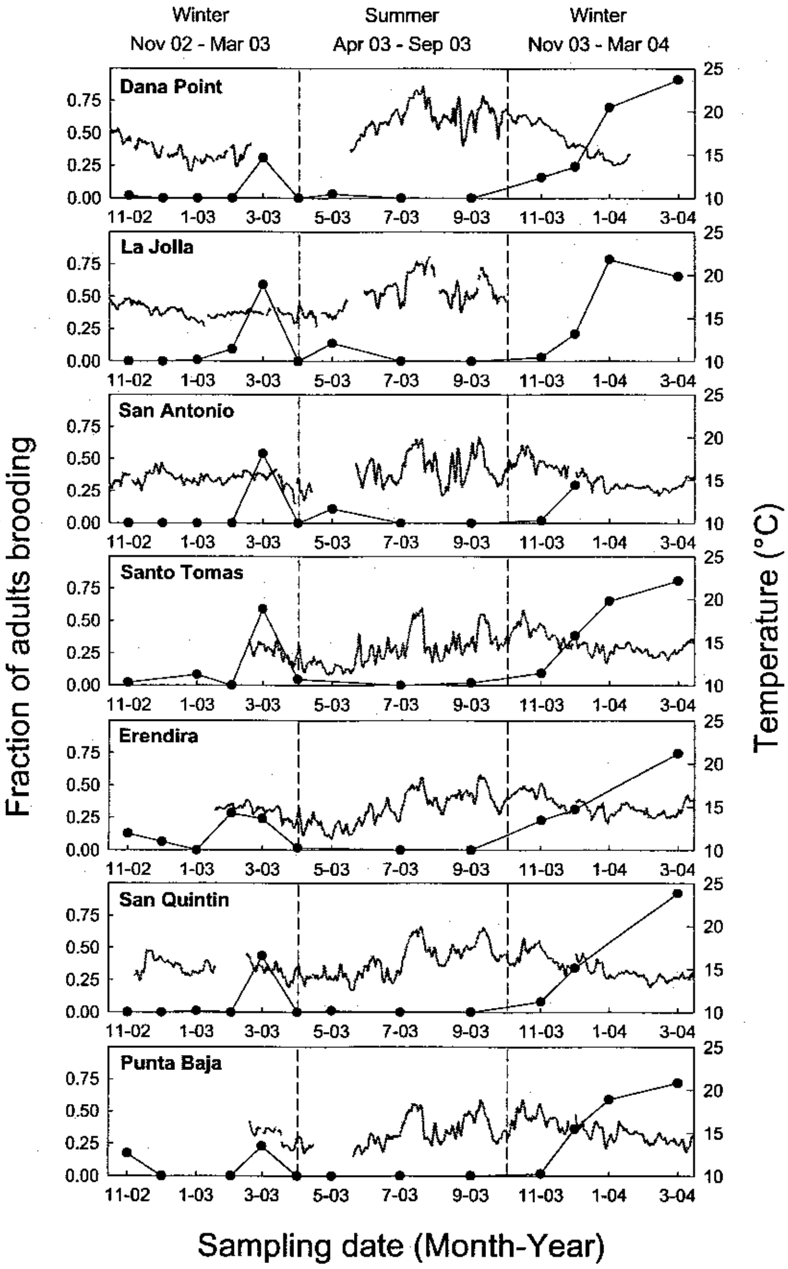

Figure 4.5

Time series of the proportion of gravid individuals at each site and sampling date. Gray lines correspond to water temperatures measured in the lower intertidal at each site. Data for La Jolla were obtained from the Network of Environmental Observations of the Coastal Ocean database (http://www.es.ucsc.edu/~neoco/). Dashed vertical lines separate the seasons used in the analysis of size data.

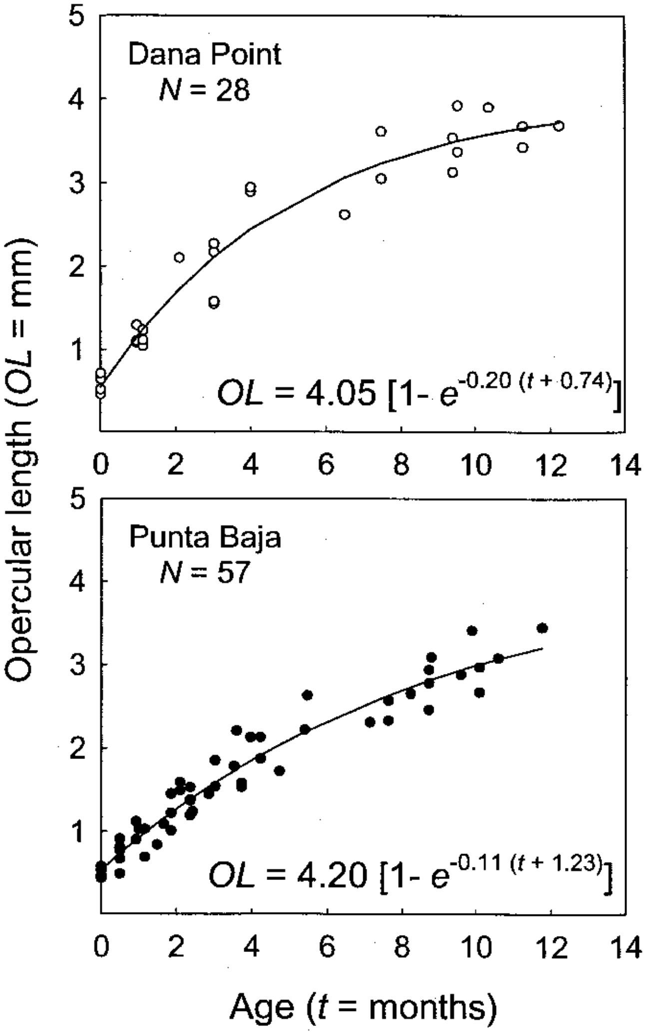

Figure 4.6

Growth parameters for *Balanus glandula* at Dana Point and Punta Baja. Lines are von Bertalanffy growth curves fitted to age-size observations. Equations with the corresponding estimates of von Bertalanffy parameters are shown on the lower right corner of each panel.

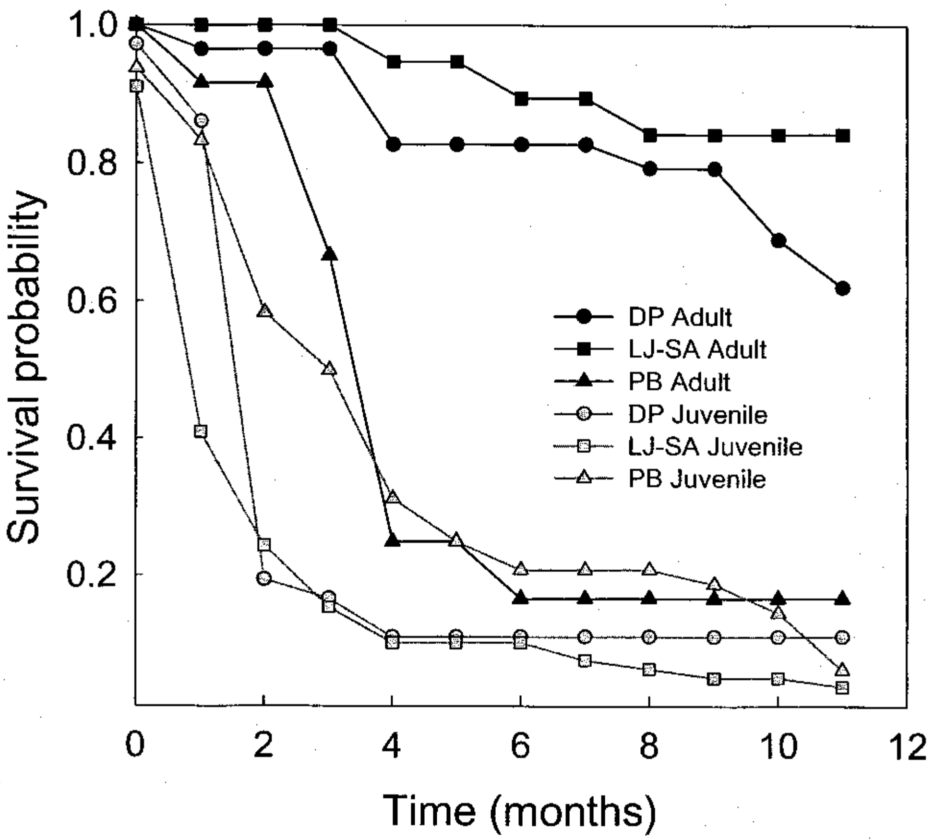

Figure 4.7

Survival curves estimated for juveniles (gray lines and symbols) and adults (black lines and symbols) from Dana Point (circles), La Jolla – San Antonio (squares), and Punta Baja (triangles).

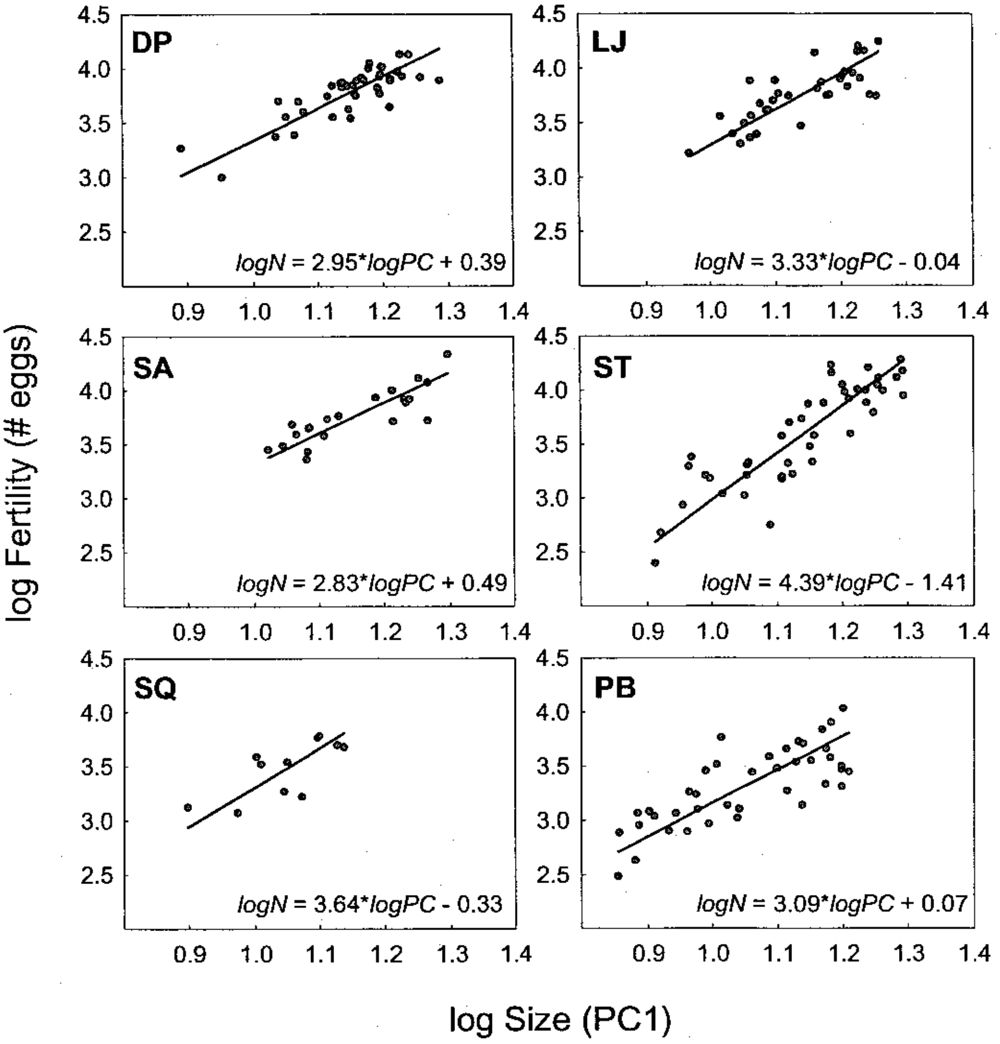

Figure 4.8

Regressions of fertility versus size in adult *Balanus glandula* from Dana Point (DP), La Jolla (LJ), San Antonio (SA), Santo Tomás (ST), San Quintín (SQ), and Punta Baja (PB). Parameter estimates for the linear equations shown on each panel were obtained by reduced major axis regression (see Materials and Methods). Size data used in the regression correspond to the first principal component of a PCA performed using morphometric measurements on the 202 individuals analyzed for fertility (see Table 4.2).

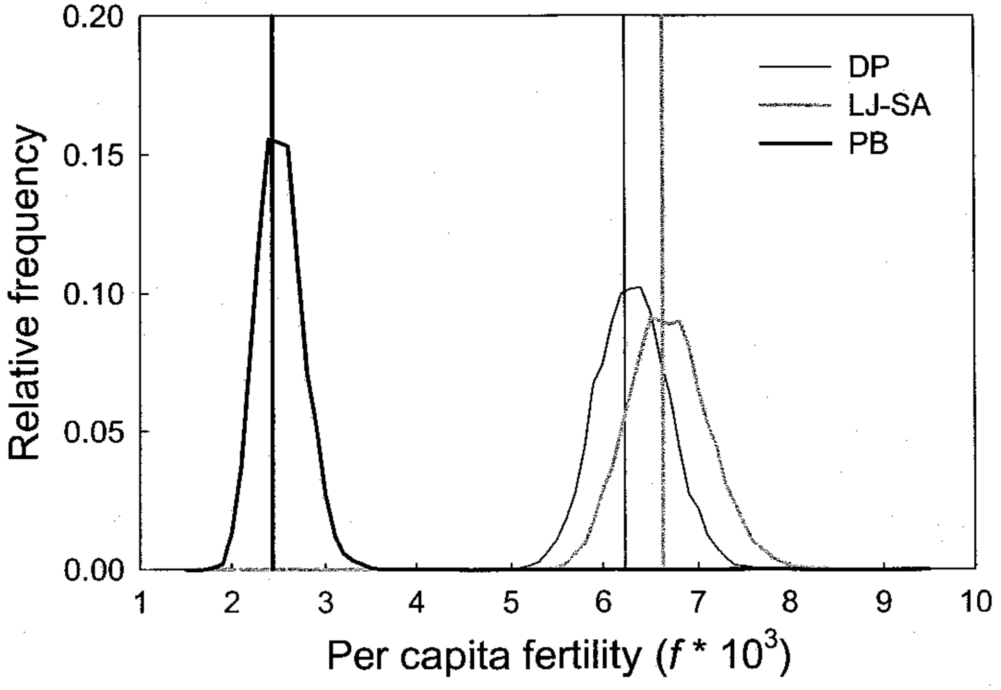

Figure 4.9

Bootstrap distributions (10,000 repetitions each) of per capita fertility computed for Dana Point (DP), La Jolla – San Antonio (LJ-SA), and Punta Baja (PB). Vertical lines correspond to mean estimates obtained for each site from their mean size of gravid individuals (Fig. 4.3) and size specific fertility (Fig. 4.8). Confidence limits computed with the bias-corrected percentile method (Manly 1997) are given on Table 4.5.

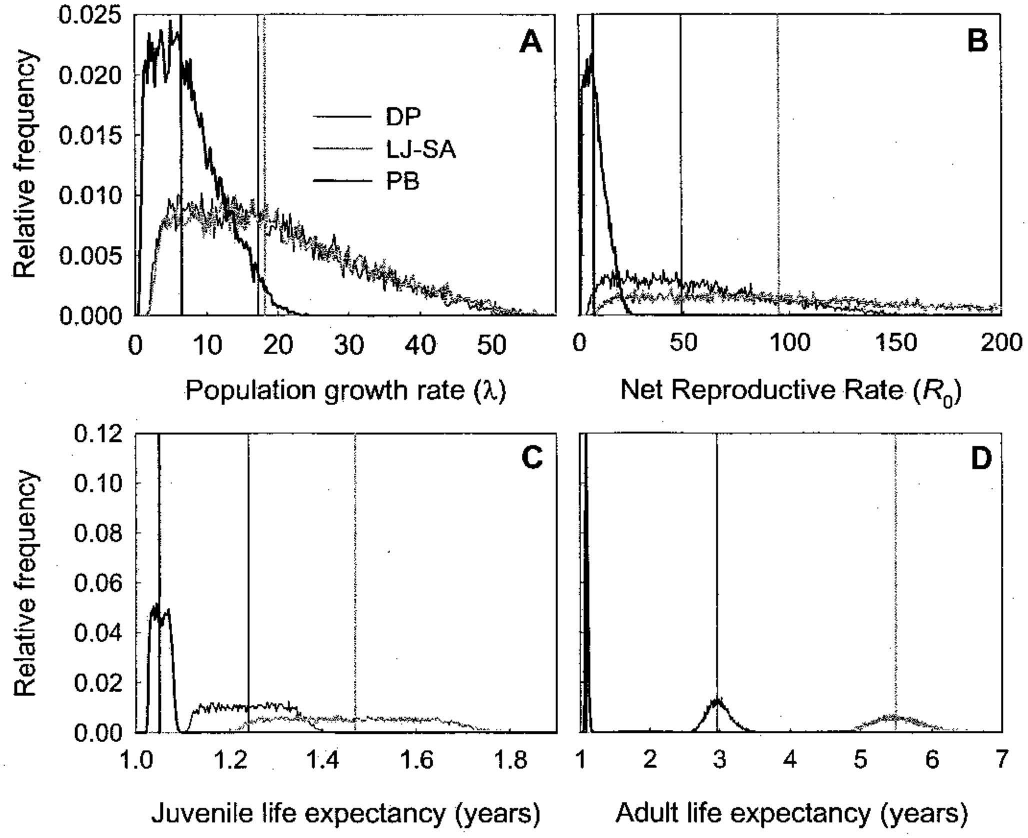

Figure 4.10

Probability distributions of population growth rate (A), net reproductive rate (B), and juvenile and adult life expectancies (C, D) computed for Dana Point (DP), La Jolla – San Antonio (LJ-SA), and Punta Baja (PB). Vertical lines correspond to the median of each distribution. The probability of finding a net reproductive rate smaller than one (B) were calculated as the number of cases with $R_0<1$ divided by the total number of repetitions. Confidence limits computed with the bias-corrected percentile method (Manly 1997) are given on Table 4.5.

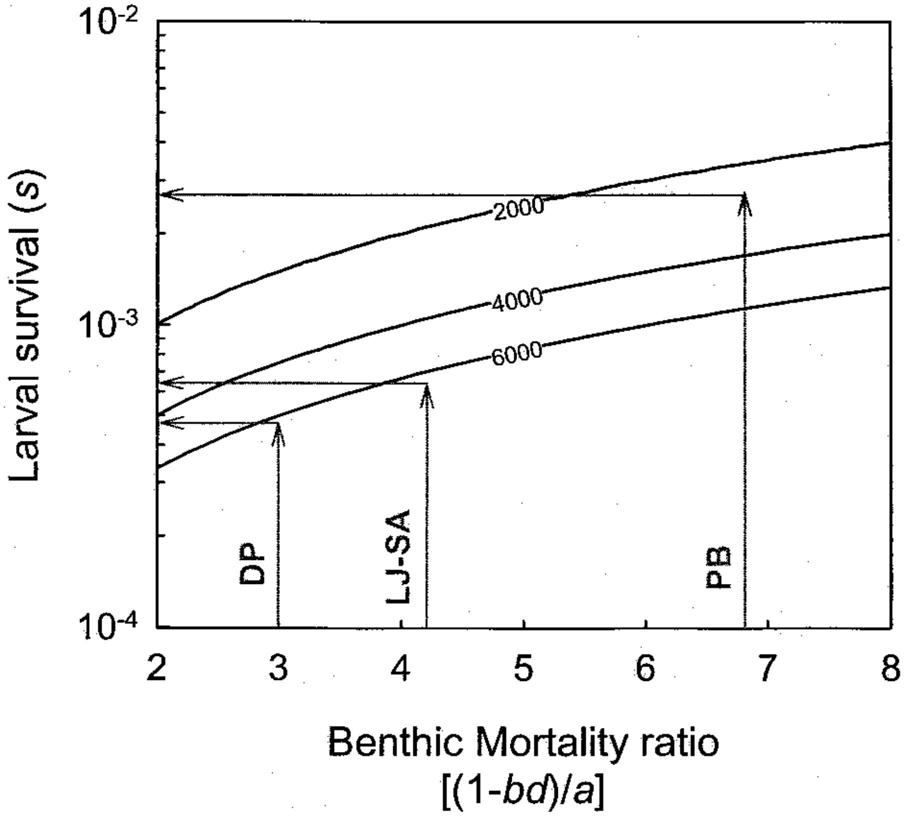

Figure 4.11

Fertility thresholds for *Balanus glandula* at Dana Point (DP), La Jolla – San Antonio (LJ-SA), and Punta Baja (PB). Contours correspond to the minimum per capita fertility required to attain population persistence given the benthic mortality ratio and larval survival shown on the x and y axes. Gray arrows originate from the x-axis value computed for each site (see Table 4.5), intersect their corresponding contour of mean per capita fertility, and point to the minimum larval survival (y–axis) that would allow them to persist ($\lambda > 1$).

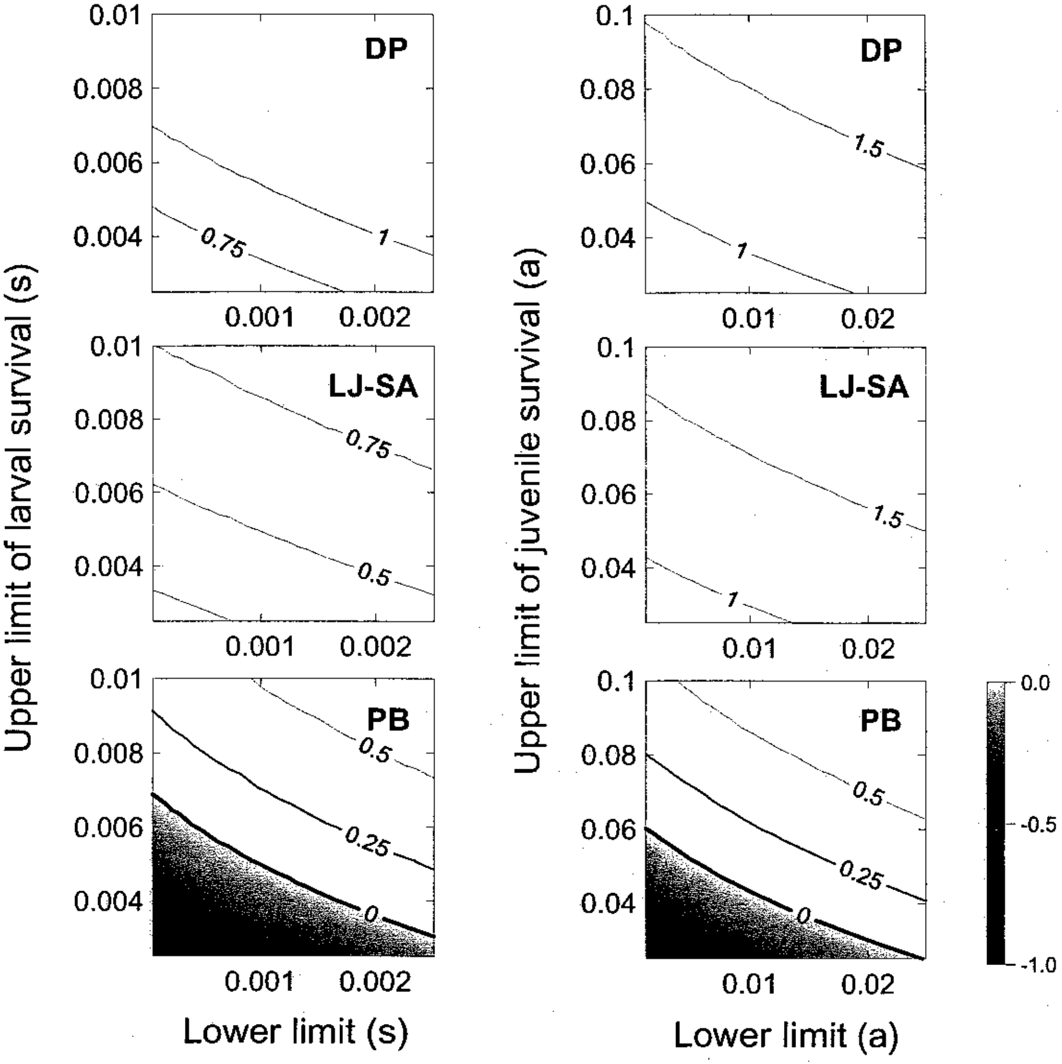

Figure 4.12

Stochastic growth rate log λ_s computed for Dana Point (DP), La Jolla – San Antonio (LJ-SA) and Punta Baja (PB) under different regimes of environmental stochasticity. Axes correspond to lower and upper limits of the uniform probability distributions used to simulate interannual fluctuations in larval survival (left panels) and juvenile survival (right panels). The thick contour indicates combinations of parameters for which log $\lambda_s = 0$.

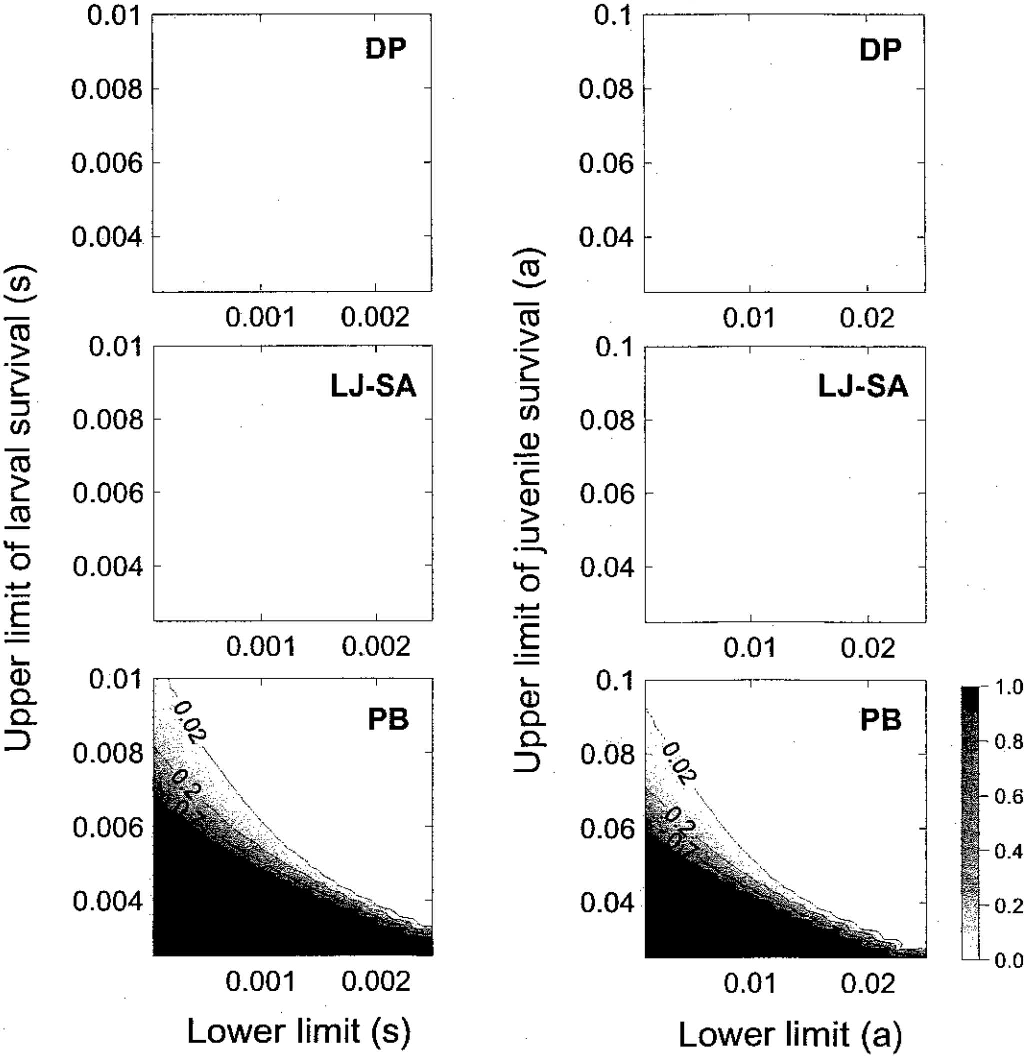

Figure 4.13

Quasi-extinction probabilities $P_q(\theta=0.1)$ computed for Dana Point (DP), La Jolla – San Antonio (LJ-SA) and Punta Baja (PB) under different regimes of environmental stochasticity. Axes correspond to lower and upper limits of the uniform probability distributions used to simulate interannual fluctuations in larval survival (left panels) and juvenile survival (right panels). Regions of the parameter space for which $P_q(\theta)=1$ are shown in black.

5. CHAPTER 5

GENERAL CONCLUSIONS

The results of this dissertation emphasize the importance of a small-scale, high-frequency approach to study nearshore phenomena, especially in relation with the dispersal of invertebrate larvae. The importance of choosing right temporal and spatial scales cannot be overstated. In recent years it has become clear that often there is not a unique right scale of observation, and that small-scale physical and biological processes in the nearshore may be modulated by large-scale phenomena (e.g. Pineda and López 2002). The question of whether a population functions as an open or closed system is also dependent on the spatial and temporal scales of observation. For example, populations separated by 100 kilometers may not exchange individuals at demographically relevant temporal scales (i.e. years), but still be genetically connected by larval dispersal occurring at scales of decades to thousands of years.

Observed patterns of nearshore larval distribution (Chapter 2) agree with recent suggestions that long distance dispersal of larvae in the nearshore may not be as pervasive as traditionally thought (e.g. Jones et al. 1999; Swearer et al. 1999). Consistent small-scale (0.1-1 km) patterns in the stage-specific horizontal distribution of *Balanus glandula* and *Chthamalus* spp. larvae suggest that larvae may be retained within short distances to shore over the duration of their planktonic life. Horizontal segregation of nauplii and cyprids in both species, with the latter being substantially more abundant at the inshore station, suggests that ontogenetic changes in behavior may impact the expected horizontal distribution and dispersal distances for the larvae of coastal invertebrates.

The mortality estimates obtained for barnacle nauplii in nearshore waters fluctuated around 20-40% per day (Chapter 2). These are substantially higher than a 5% d^{-1} previously assumed for *B. glandula* and *Chthamalus* spp. (Connolly and Roughgarden 1998, p. 323), but within the range of mortality estimates found in the literature for other benthic invertebrate larvae (Rumrill 1990; Morgan 1995; Lamare and Barker 1999). Although more studies are needed to verify these estimates, a four- to six-fold increase in mortality should reduce the number of larvae that complete their planktonic development and, by extension, shorten mean travel distances and scales of connectivity among populations. The shape of a dispersal kernel – the distribution of dispersal distances from a point source – depends on larval duration relative to local hydrodynamics (e.g. Siegel et al. 2003). For example, dispersal kernels with long tails may be observed when strong residual currents disperse larvae with a short development time. Increasing larval mortality could truncate the tails of such distributions and cause a reduction in the mean distance of dispersal. A recent modeling study (Ellien et al. 2004) has shown that losses due to mortality can be more important than those due to hydrodynamics when larval duration is short relative to the intensity of residual currents. Increasing mortality rates from 5% to 9% d^{-1} greatly reduced effective dispersal distances for larvae of the polychaete *Pectinaria koreni*. Thus, depending on the species and local hydrodynamics, changes in larval mortality rates may shift our view as to whether a population is open or closed.

Results presented in Chapter 2 suggest that coastal invertebrate populations separated by distances as short as tens of kilometers might be demographically disconnected. Such disconnection would reduce the spatial scales of coherence in population dynamics, affect the robustness of local populations to environmental perturbations, and ultimately impact the persistence of a species within its geographic limits of distribution.

The observation of distinct and consistent patterns of vertical distribution in the nauplii and cyprids of two barnacle species at a nearshore site (Chapter 3) suggested that horizontal segregation of larval stages might result from the interaction of ontogenetic changes in behavior and vertical shear of horizontal currents in the nearshore. The absence of *Chthamalus* spp. cyprids from the sampling station, located ca. 2 km offshore and approximately 10 km NW of La Jolla – where high concentrations of *Chthamalus* spp. cyprids have been observed (Pineda 1999 and Chapter 2) – is intriguing because *Chthamalus* spp. nauplii were numerically dominant and present at all stages of development. This absence did not allow testing whether *Chthamalus* spp. nauplii and cyprids occur at different depths. Thus, a connection between the horizontal segregation observed between nauplii and cyprids of *Chthamalus* spp. at La Jolla and differences in the vertical distribution of these stages must be tested. More field observations are needed in a future attempt to verify the biological-physical mechanisms that generate the observed patterns of larval distribution. Future efforts to model the relationship between local population dynamics and hydrodynamics must shift from an emphasis on mesoscale processes to a better description of nearshore processes and spatial changes in dispersal and self-recruitment. Also, the variability in nearshore hydrodynamics must be better resolved, perhaps with high-frequency observations of horizontal flows collected simultaneously at several points over a larger area. Estimates of dispersal trajectories and distances would benefit from an assessment of the spatial variability in mean horizontal flows in the nearshore.

Finally, the analysis of adult demography over scales of hundreds of kilometers yielded valuable insights on the interaction between spatial changes in vital rates, robustness to environmental stochasticity, susceptibility to local extinction, and geographic ranges of distribution. The combination of extensive field observations on population structure, growth, and reproductive rates with a simple mathematical model proved to be a fruitful approach to the assessment of factors that might determine the geographic distribution of coastal benthic populations. Future studies should include the actual geographic limit of distribution of this species, and monitor the regional variability in recruitment and larval supply, as well as the variability in physical-chemical factors that are likely to affect rates of growth and reproduction and ultimately generate spatial patterns in population demography.

REFERENCES

Connolly SR, Roughgarden J (1998) A latitudinal gradient in northeast Pacific intertidal community structure: evidence for an oceanographically based synthesis of marine community theory. American Naturalist 151: 311-326

Ellien C, Thiebaut E, Dumas F, Salomon J-C, Nival P (2004) A modelling study of the respective role of hydrodynamic processes and larval mortality on larval dispersal and recruitment of benthic invertebrates: example of *Pectinaria koreni* (Annelida: Polychaeta) in the Bay of Seine (English Channel). Journal of Plankton Research 26: 117-132

Lamare MD, Barker MF (1999) *In situ* estimates of larval development and mortality in the New Zealand sea urchin *Evechinus chloroticus* (Echonodermata: Echinoidea). Marine Ecology Progress Series 180: 197-211

Jones GP, Milicich MJ, Emslie MJ, Lunow C (1999) Self-recruitment in a coral reef fish population. Nature 402: 802-804

Morgan SG (1995) Life and death in the plankton: larval mortality and adaptation. In: McEdward L (ed) Ecology of Marine Invertebrate Larvae. CRC Press, Boca Raton, FL, pp 279-321

Pineda J (1999) Circulation and larval distribution in internal tidal bore warm fronts. Limnology and Oceanography 44: 1400-1414

Pineda J, López M (2002) Temperature, stratification and barnacle larval settlement in two Californian sites. Continental Shelf Research 22: 1183-1198

Rumrill SS (1990) Natural mortality of marine invertebrate larvae. Ophelia 32: 163-198

Siegel DA, Kinlan BP, Gaylord B, Gaines SD (2003) Lagrangian descriptions of marine larval dispersion. Marine Ecology Progress Series 260: 83-96

Swearer SE, Caselle JE, Lea DW, Warner RR (1999) Larval retention and recruitment in an island population of a coral-reef fish. Nature 402: 799-802

6. APPENDIX A

High-frequency observations of wind-forced onshore transport
at a coastal site in Baja California.

Tapia FJ, Pineda J, Ocampo-Torres FJ, Fuchs HL, Parnell PE, Montero P, Ramos S

Continental Shelf Research 24: 1573-1585. 2004.

Reprinted with permission of Elsevier Ltd.

Available online at www.sciencedirect.com

SCIENCE DIRECT

Continental Shelf Research 24 (2004) 1573–1585

CONTINENTAL SHELF RESEARCH

www.elsevier.com/locate/csr

High-frequency observations of wind-forced onshore transport at a coastal site in Baja California

Fabián J. Tapia[a,*], Jesús Pineda[a], Francisco J. Ocampo-Torres[b], Heidi L. Fuchs[a], P. Edward Parnell[c], Paulina Montero[d], Sergio Ramos[b]

[a] *Biology Department MS-34, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA*
[b] *Departamento de Oceanografía Física, Centro de Investigación Científica y de Educación Superior de Ensenada, Km 107 Carretera Tijuana-Ensenada, Ensenada, BC 22860, Mexico*
[c] *Scripps Institution of Oceanography, Integrative Oceanography Division, 9500 Gilman Drive 0227, La Jolla, CA 92093-0227, USA*
[d] *Centro de Ciencias y Ecología Aplicada, Universidad del Mar, Carmen 446 - Cerro Placeres, Valparaíso, Chile*

Received 26 August 2003; received in revised form 27 February 2004; accepted 26 March 2004

Abstract

We investigated the effect of the daily sea breeze on the surface flow at Bahia Salsipuedes, Baja California, Mexico. Drifter-tracking experiments were conducted over a 2-week period in July, 1999. Surface drifters were deployed daily and their trajectories tracked from a small boat for 3–7 h. Wind speed and direction, as well as the vertical distribution of temperature and current velocities were measured throughout the observation period. Our results indicate that strong winds associated with the daily sea breeze at the study area can produce onshore surface currents with velocities of up to $10\,\mathrm{cm\,s^{-1}}$ (net transport of up to 2 km in a diurnal cycle). There was a hyperbolic relationship between onshore wind stress and net onshore transport of the drifters. A decrease in stratification and more consistent pattern of onshore transport were associated with sustained winds $>6\,\mathrm{m\,s^{-1}}$ towards the end of the study. Progressive vector diagrams computed from near-surface currents failed to predict the trajectory of drifters, especially on days where wind forcing was more consistent in terms of direction and magnitude. We discuss the implications of these results regarding the collection of settlement data and their interpretation in terms of larval supply to coastal populations.

Keywords: Sea breeze; Onshore transport; Drifters; Neuston; Baja California

1. Introduction

The dynamics of coastal populations is highly dependent on the mechanisms and processes affecting the spatial distribution and the fate of larvae prior to settlement. Research efforts during the past decades have been focused on the physical processes that are likely to affect the distribution of larvae relative to adult populations (e.g. Johnson, 1939; Scheltema, 1968; Butman, 1987; Pineda, 1994b; Epifanio and Garvine, 2001), and on the importance of substrate availability (e.g. Bertness et al., 1992; Pineda, 1994a). Such a

---

*Corresponding author.
E-mail address: ftapia@whoi.edu (F.J. Tapia).

0278-4343/$ - see front matter © 2004 Elsevier Ltd. All rights reserved.
doi:10.1016/j.csr.2004.03.013

'supply side' approach (see Underwood and Fairweather, 1989) has yielded valuable insights on the relevance of physical processes as predictors of the local and regional dynamics of adult populations. In order to characterize the variability of larval supply to coastal populations, however, it is necessary to assess patterns of larval distribution at spatial and temporal scales that are relevant to a species' life cycle and ecology. Plankton patchiness and logistic constraints preclude the use of such sampling strategy in most cases, thus forcing the use of proxies for larval supply that are more feasible to monitor over extended periods of time (e.g. settlement—see Pineda, 2000).

Settlement has been the proxy of choice in a number of studies focused on the supply of larvae to adult populations of coastal invertebrates, such as crabs (Wing et al., 1995b; Reyns and Sponaugle, 1999), sea urchins (Ebert et al., 1994; Wing et al., 1995a), and barnacles (Gaines et al., 1985; Pineda, 1994a). Artificial and/or natural surfaces are provided for the larvae to settle on, and monitored at intervals of days to weeks. Settlement time series data are then analyzed in conjunction with environmental data series to identify temporal correlations between larval supply and physical variability (e.g. Farrel et al., 1991; Wing et al., 1995a; Pineda and López, 2002). A number of published studies have documented correlations between larval settlement and physical processes occurring at a range of temporal scales: from intraseasonal changes in wind forcing (Bertness et al., 1996), upwelling intensity (Wing et al., 1995a), and the stratification of the water column (Pineda and López, 2002), to interannual changes in river discharge (Gaines and Bertness, 1992). The importance of higher-frequency physical variability for settlement, however, has not been extensively studied and cannot be resolved at the sampling frequencies typically used in settlement surveys. Therefore, inferences made so far about larval transport are probably biased towards lower-frequency mechanisms if based only on settlement data (Pineda, 2000).

Few high-frequency mechanisms with a potential effect on the onshore transport of larvae have been documented so far. Internal tidal bores, a seasonal and somewhat predictable phenomenon that occurs in coastal environments at scales of hours to days, are an example of high-frequency forcing likely to affect the onshore transport of both planktonic and neustonic larvae (Pineda, 1994b, 1999).

The diurnal sea breeze, which is also seasonal and locally predictable in its occurrence, represents another highly episodic phenomenon that could potentially affect larval settlement (Kaplan et al., 2003; but see Epifanio and Garvine, 2001, p. 54). The sea breeze is characterized by a daily regime of variability, generated by oscillations in the land-sea temperature gradient, which in some regions can explain fluctuations of up to $7\,\mathrm{m\,s^{-1}}$ in onshore wind speed (Simpson, 1994). Such daily surges in onshore winds may affect the cross-shore distribution of material suspended in the upper centimeters of the water column (i.e. neuston), including the larvae of a number of coastal invertebrates. Thus, by modulating the onshore flow of surface waters, the sea breeze could have an effect on the timing and variability of recruitment in coastal populations with neustonic larvae.

In this contribution we investigate the effect of the sea breeze on cross-shore surface currents by means of drifter-tracking experiments, which were conducted over a period of 2 weeks at Bahia Salsipuedes in northern Baja California. Our results demonstrate the potential for the diurnal sea breeze to substantially affect onshore transport of neustonic material. We discuss the implications of these results regarding the collection of settlement data and their interpretation in terms of larval supply to coastal populations.

2. Materials and methods

The experiments were conducted on 13–22 July, 1999 (Table 1), at Bahia Salsipuedes (31° 56′ N, 116° 46′ W) in northern Baja California (Fig. 1). Every morning at about 7:30–9:30 AM (PDT), we deployed a set of 5–6 drifters, which were circular pieces of soft and flexible, Scootguard™ non-slip surface (30 cm in diameter, 1 mm thickness) with six small lead "split-shot" lead weights (2.5 g each) attached to the edges (Fig. 2). When deployed, the drifters remained at the air–sea interface, with less

Table 1
Details on the time (PDT), number of observations, and wind conditions during the drifter deployments at Bahia Salsipuedes, Baja California

Date	Drifter deployments				Wind speed		Wind direction		PVD-drifter discrepancy		
	Number drifters	Time start	Time end	Number observ.	Mean ($m\,s^{-1}$)	S.D. ($m\,s^{-1}$)	Mean (deg)	S.D. (deg)	PO dist (km)	LD dist (km)	(PO/LD)
13-Jul-99	5	10:40	13:15	9	2.45	0.42	125.4	49.2	1.04	1.03	1.01
15-Jul-99	5	10:00	14:50	12	2.11	0.50	100.9	31.5	1.04	1.60	0.65
16-Jul-99	6	8:15	15:30	18	2.80	1.03	104.3	66.4	2.36	1.68	1.40
19-Jul-99	5	8:50	15:00	19	3.88	2.26	96.5	74.8	0.94	2.08	0.45
20-Jul-99	5	7:15	12:15	17	3.13	3.00	92.6	79.1	0.97	2.00	0.49
21-Jul-99	5	7:30	11:50	14	3.01	2.01	109.0	69.4	1.40	1.77	0.79
22-Jul-99[a]	5	7:45	13:40	21	3.18	3.05	102.1	71.4	—	1.63	—

The magnitude and variability of wind forcing is presented in relation to an index of discrepancy between observed drifter displacements and those predicted from Progressive Vector Diagrams (PVDs). PO dist: Distance between the end points of the actual drifter path and a PVD; LD dist: Linear distance between the initial and final positions recorded for drifters on each day.

[a] No current meter data available on this day.

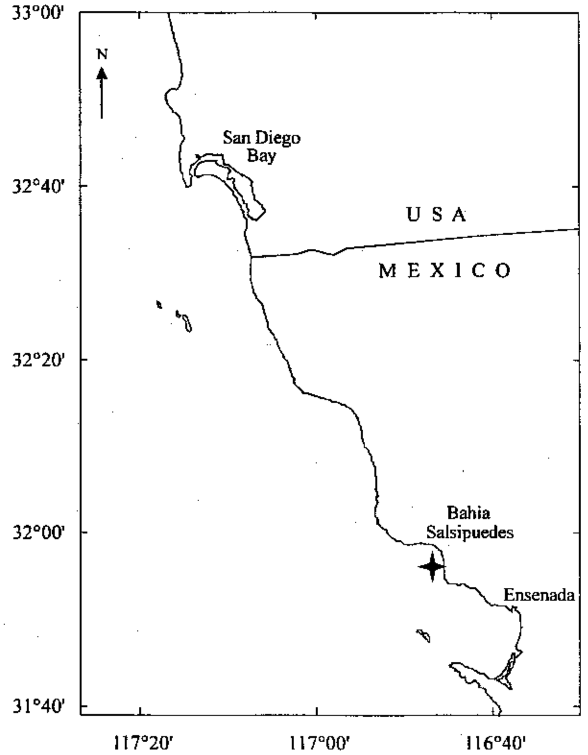

Fig. 1. Geographic location of Bahia Salsipuedes. The star indicates the study site.

than 50% of their surface area exposed to direct wind forcing (Fig. 2). Drifters were deployed at the onset of the sea breeze events (i.e. a sudden increase in onshore winds that occurred at 8:00–12:00 each day), at approximately the same location every day (31° 56.31′ N; 116° 46.72′ W), and tracked from a small motor boat for 3–7 h, depending on the weather conditions and on the boat's proximity to the surf zone. The location of each drifter was recorded about every 20 min using a differential GPS.

We assumed that the drifters were tracking the motion of the uppermost layers of the water column, rather than their own response to wind forcing. Our assumption was based on the drifter design (Fig. 2), and on the statistical similarity between the drifter paths and those followed by pieces of kelp that were found at the air–sea interface, collected in situ, and deployed

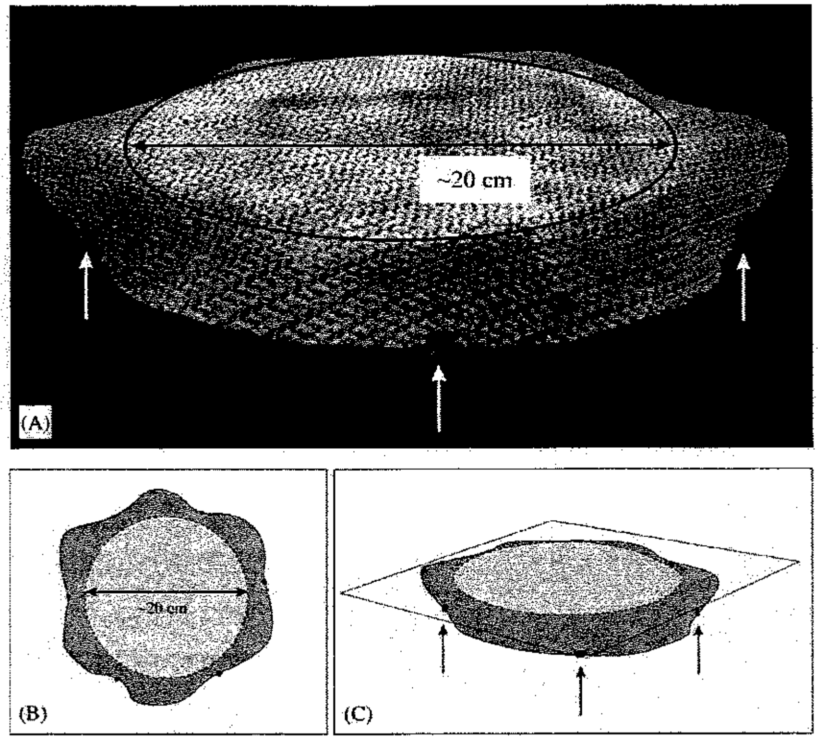

Fig. 2. Side view picture (A), and top and side view schematics (B and C) of the drifters used in this study. The arrows (and black circles in B and C) indicate the position of the six small lead weights attached to the drifter's edge. The edge areas (dark shading in B and C) correspond to the fraction of the drifter's surface that remained underwater. The central area (light shade in B and C) corresponds to the portion that was exposed to the wind during a deployment.

concurrently with the drifters (Solow, WHOI, pers. comm.).

Throughout the observation period we monitored the thermal structure of the water column using a string of Onset StowAway XTI loggers (response time <15 s), programmed with a sampling interval of 40 s and located at 2, 5, 8, and 11 meters above the bottom (mab), plus one logger at the surface. We also monitored the vertical structure of nearshore currents with a bottom-mounted, upward looking 1200 kHz Doppler current meter (RD Instruments, San Diego, CA), which measured at intervals of 40 s (100 pings per ensemble) and in bins of 0.4 m within a depth range of 0.95–14.55 mab. Both the temperature mooring and the current meter were located at a depth of 16 m (31° 56.28′ N; 116° 45.68′ W). Average wind velocity and direction were recorded over 5 min intervals using a CMB3280 Aanderaa Coastal Monitoring Buoy, anchored at a nearby location (31° 55.28′ N; 116° 45.39′ W, ca. 2 km south of the current meter mooring). Prior to the analysis, wind directions were rotated and aligned to the average shoreline orientation (355°), and then decomposed into alongshore and cross-shore components.

We studied the effect of wind forcing on the water column using two different approaches. First, on a time-domain approach, we studied the effect of wind forcing on stratification by computing wind stress at the surface as

$$|\tau_0| = \rho u^{*2}, \tag{1}$$

where ρ is air density and u^* is the friction velocity, which was computed from wind speed data as in Large et al. (1995, Eq. 8). We calculated stratification as the square of the Brunt–Väisälä frequency (N^2) for each one of the four pairs of temperature series (i.e. 2–5 mab, 5–8 mab, 8–11 mab, and 11 mab -surface) as

$$N^2 = -\frac{g}{\rho_0}\frac{\partial \rho}{\partial z}, \tag{2}$$

where g is gravity (9.8 m s^{-2}), ρ_0 is the mean density of the water column, and z is depth. We then obtained depth-averaged values for N^2 by vertically averaging the four series mentioned above. The temperature and wind time series were low-pass filtered prior to the computations (cutoff frequency of 6 cycles h^{-1}), and a constant salinity value of 34 psu was assumed. Second, on a frequency-domain approach, we performed spectral analyses on the time series for wind (~5,000 observations) and temperature (~42,000 observations) collected at the study site between 7–23 July and 4–23 July, respectively. Raw data were linearly detrended prior to the computation of an average Welch periodogram. The wind and temperature series were divided into non-overlapping segments of 2^{10} (3.6 d) and 2^{13} points (3.8 d), respectively.

To understand the contribution of wind to onshore transport, we analyzed the effect of wind stress on the motion and trajectory of the drifters. We computed net onshore displacements for each drifter/day, and then performed a nonlinear regression of net onshore displacement versus the onshore wind stress integrated over the duration of each deployment. We also analyzed changes in the correlation between drifter trajectories and wind direction as a function of wind speed for each deployment. For n average drifter positions recorded during a deployment, we computed $n-1$ velocity vectors. Velocity vectors were decomposed into cross-shore and alongshore components of the drifter trajectories, which were linearly regressed against the respective components of wind forcing. We chose a 10 min lag between wind measurements and the drifter observations to which they were paired (i.e. midpoint between drifter observations). We tested whether drifter trajectories can be predicted from current-meter data by comparing the observed trajectories with progressive vector diagrams (PVDs) from our measurements of horizontal velocities near the surface. The predicted (x, y) positions were computed as

$$x(t_n) = \Delta t \sum_{i=1}^{n} u(t_i), y(t_n) = \Delta t \sum_{i=1}^{n} v(t_i), \tag{3}$$

where $u(t)$ and $v(t)$ are the east and north current speeds measured by the current meter at time t, and Δt is the sampling interval (Emery and Thomson, 1998, p. 165). Due to large errors introduced by tidal fluctuations in water depth, surface wave action, and side lobbing, data collected from the surface bins by the Doppler current meter had to be discarded. Thus, our uppermost bin with reliable data was located at 13 mab, on average 2 m below the surface.

Finally, we observed settlement of invertebrate larvae on the drifters. Although these observations were not quantitative, we use the taxonomic composition of the settlers and the time scales over which settlement was observed to conjecture on the potential effects of sea breeze events on the distribution and onshore transport of neustonic larvae.

3. Results

We completed 7 days of drifter observations during which a total of 36 drifters were deployed and tracked for an average of 5 h (Table 1). Wind speeds measured during the study were highly variable, with most of the variability explained by changes in the cross-shore component (Figs. 3a and 4a). Onshore winds dominated during the second half of the study, with daily oscillations of up to 8 m s^{-1} which extended for about 8 h (Fig. 3a). The dominance of a diurnal frequency in the variability of cross-shore winds was confirmed by the computed power spectra (Fig. 4a). Coincident with these daily surges in onshore winds, we observed short-term increases in the temperature of surface waters (Fig. 3b). Towards the end of the observation period, these rapid increases in temperature could be detected throughout the water column (Fig. 3b), which is consistent with the observed decrease in the depth-averaged stratification (Fig. 3c). A diurnal frequency dominated the variability of temperature between the surface and

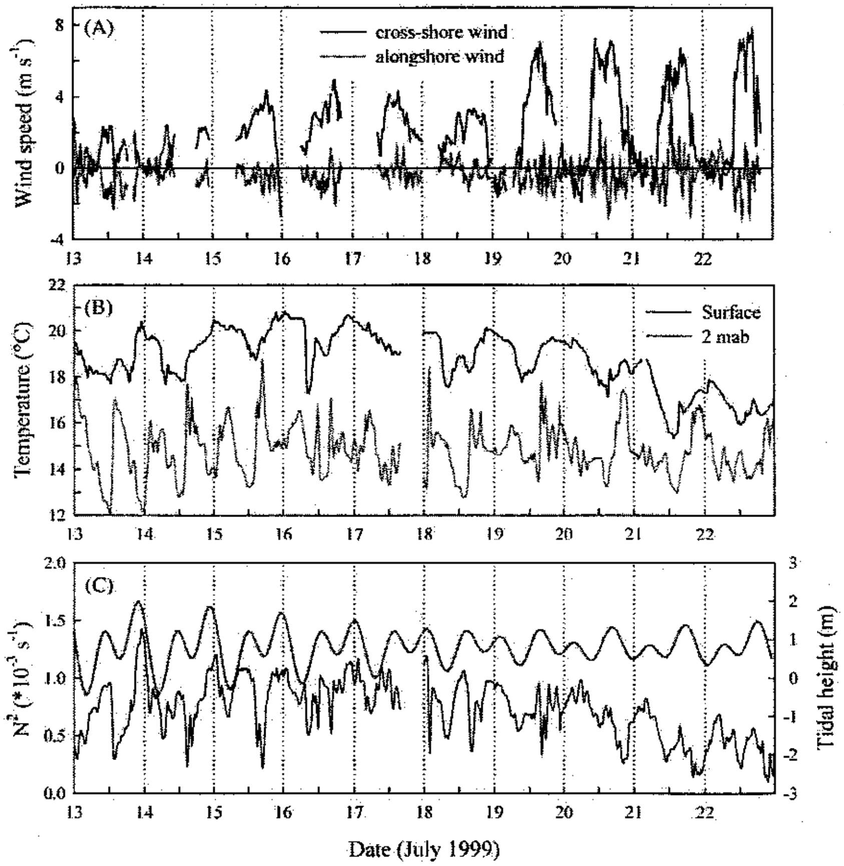

Fig. 3. Wind speed (A), water temperature (B) and mean stratification of the water column (C) during the drifter deployments at Bahia Salsipuedes in July 1999. Tidal heights predicted for the port of Ensenada, Baja California, are also shown in C (gray line).

11 mab (Fig. 4b–c), and could be detected at depth to 2 mab (Fig. 4f). A second peak in the power spectra was found at the semi-diurnal frequency (i.e. about 2 cycles day^{-1}, Fig. 4c–f), which dominated the variability of temperature near the bottom, but nonetheless could be detected up to 11 mab (Fig. 4c–f). Large fluctuations in stratification observed at the beginning of our study (Fig. 3c) appeared to be driven by the semi-diurnal internal tides rather than wind forcing.

Persistent wind forcing towards the end of the study caused a net onshore transport of the drifters (Fig. 5a), which increased as a function of wind stress integrated over the duration of the deployments (Fig. 5b). Drifters were transported onshore at speeds of up to 10 cm s^{-1}. The intensity of wind forcing during the experiments determined the degree of correlation between drifter paths and wind direction (Fig. 6). A better alignment of drifter paths and wind on the cross-shore direction is consistent with the higher wind speeds recorded along this axis (Fig. 3a). The response of surface waters (and therefore drifter paths) to the temporal variability in wind forcing can be clearly seen in Fig. 7, in which the wind vectors have been superimposed on the drifter trajectories for July 20 and July 22.

The temporal variability in the horizontal velocities of near-surface currents (Fig. 8b) was consistent with the timing and intensity of wind forcing (Fig. 8a). Near-surface currents showed a tendency to be decoupled from currents measured

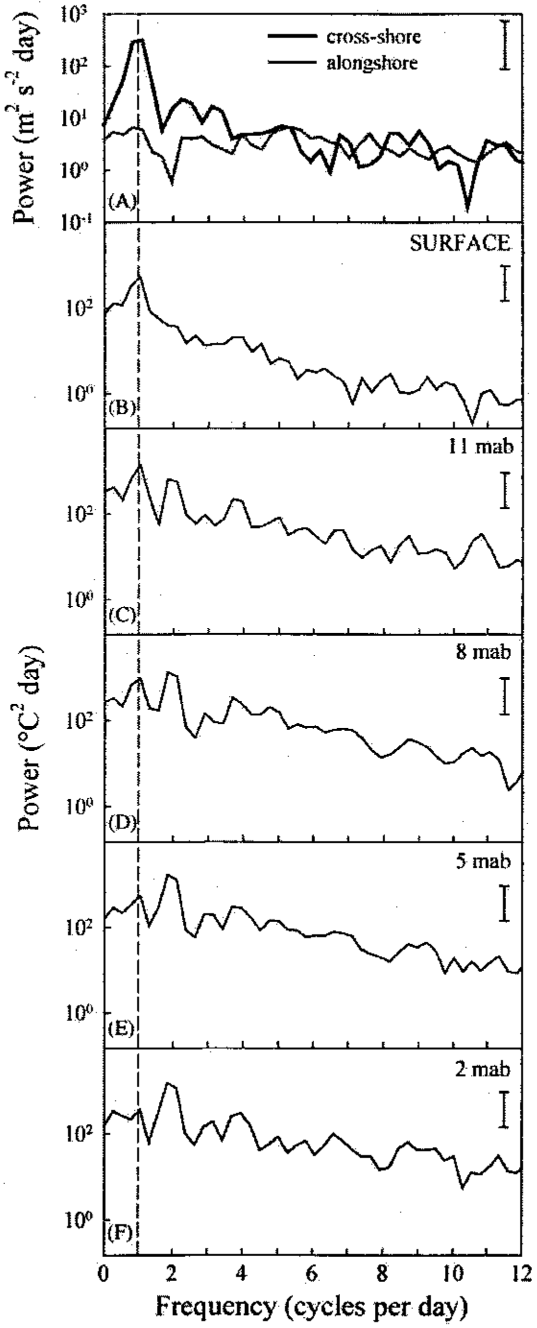

Fig. 4. Power spectra computed for the wind (A) and temperature time series (B–F) recorded at Bahia Salsipuedes in July 1999. Bars on the right-hand side of each panel correspond to 95% confidence intervals. The dashed lines indicate diurnal variability; mab: meters above the bottom.

deeper in the water column (Fig. 8b). PVDs computed from horizontal velocities measured at 13 mab (Fig. 9) showed a poor performance as predictors of drifter trajectories. The observed trajectories seemed to be the result of an interaction between wind and tidal forcing, which explained most of the variability in the PVDs (Fig. 9). The discrepancy between predicted and observed drifter displacement varied as a function of the magnitude and variability of wind forcing during the deployments. The largest discrepancies were observed on days with strong and persistent winds, whereas smaller values tended to occur on days with more variable wind forcing, both in terms of speed and direction (Table 1). A closer inspection of Fig. 9 and the wind data series (Fig. 3a) suggests that not only the magnitude and variability of wind forcing, but also its timing relative to the tidal cycle (Fig. 3c) ultimately determined drifter trajectories.

We incidentally observed settlement of neustonic zooplankton on the drifters. The most abundant taxa corresponded to flatworms (0.5–52.8 indiv h^{-1}), brachyuran and anomuran megalopae (0.4–3.0 indiv h^{-1}), isopods (0.2–2.0 indiv h^{-1}), amphipods (0.2–1.7 indiv h^{-1}), and lepadid barnacle larvae (0.4–1.0 indiv h^{-1}). The highest settlement rates for these taxa were observed during the last four days of the study (19–22 July), which exhibited the strongest onshore winds (Fig. 3a).

4. Discussion

Our results indicate that neustonic material has the potential to be transported onshore by the daily sea breeze at Bahia Salsipuedes (Fig. 5). A causal relationship is supported by the observed drifter trajectories (Figs. 5 and 6) and their response to short-term fluctuations in wind direction (Fig. 7), as well as by the discrepancies between actual drifter trajectories and those predicted by progressive vector diagrams (PVDs) computed from the horizontal velocities of near-surface currents (Fig. 9). These results are relevant because currents in the coastal ocean are generally more energetic on the alongshore axis (Winant,

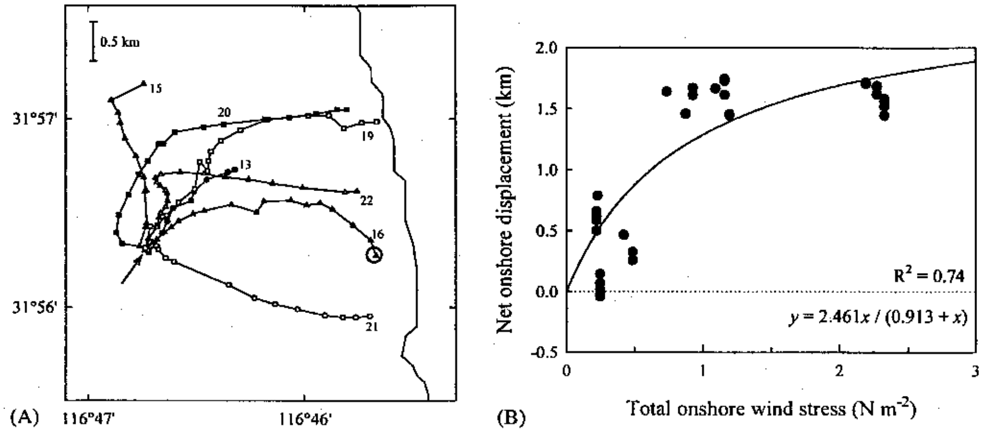

Fig. 5. (A) Average paths followed by drifters on different days; the numbers are the July date corresponding to each trajectory, whereas the arrow indicates the point of deployment. (B) Net onshore displacement of drifters as a function of onshore wind stress integrated over the duration of each deployment. The large open circle in (A) indicates the position of the Doppler current meter and temperature moorings.

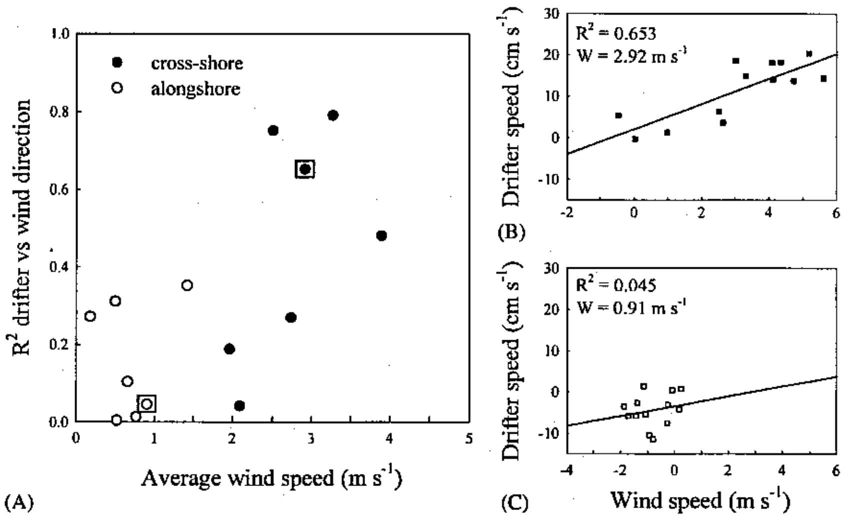

Fig. 6. (A) Changes in the correlation between average drifter and wind direction as a function of the average wind speed during each deployment. Linear regression analyses were performed separately for alongshore (closed symbols) and cross-shore (open symbols) components of wind and drifter direction, and for each day with drifter deployments (July 13, 15, 16, 19, 20, 21, 22). (B and C) Example of how the values indicated with squares (in A) were obtained for July 21; *W* is average wind speed for the deployment.

1980), with few mechanisms acting on the cross-shore dimension with sufficient energy to generate onshore transport at the temporal and spatial scales observed here (e.g. internal tidal bores—see Pineda, 1994b).

The surface drifters used in this study are an effective means to investigate the short-term response of the surface layer (i.e. first few centimeters) to local wind forcing. Water movement at this biologically relevant layer—where a suite of particles including neustonic plankton can be accumulated (see LeFevre, 1986)—is left unresolved by most instruments, including acoustic current meters and other drifter designs that

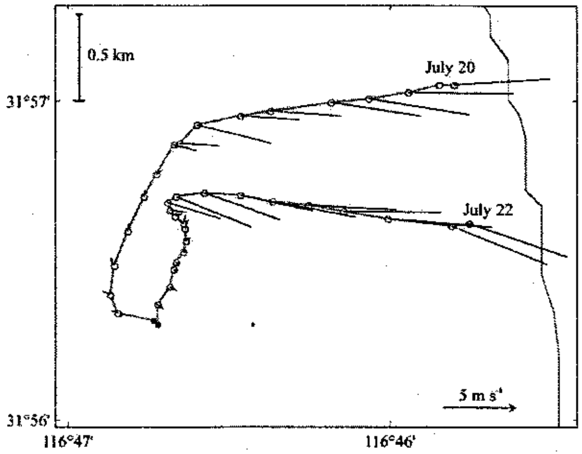

Fig. 7. Example of drifter trajectories in relation to the temporal variability of wind forcing on July 20 and July 22, 1999. Open circles correspond to drifter positions, whereas the thin lines are a vectorial representation of the average wind speed and direction measured during the interval prior to each drifter observation. Closed circles indicate the point of drifter deployment.

can go deeper into the water column and/or be directly affected by wind forcing. One disadvantage of our approach, however, is the need to visually and continuously track the drifters from a boat. Currently available technology should make it feasible to address such problem by attaching a small positioning/tracking device to each surface drifter, so that their position can be recorded without compromising their ability to track the surface layer.

The discrepancies we observed between actual drifter paths and those predicted by PVDs should be taken into account before any conclusions about larval transport are drawn from Eulerian current data. Our data suggest that the observed discrepancies between the PVDs and drifter trajectories may be due to an interaction between the magnitude and variability of wind forcing and tidal currents. However, one source of error that could explain part of the discrepancy is the varying distance between our top bin with reliable current meter data (13 mab) and the surface of the water column. Given that our main objective was to study the effect of the daily sea breeze on the onshore transport of surface currents, the experiments were conducted at roughly the same time of the day. This means that on some days the observations took place at high tide (July 13, 15), at low tide (July 20, 21), or during the transition from low to high (July 16, 19). Unfortunately, a pressure sensor was not available and therefore we lack accurate data on the sea level at our study site during drifter deployments. Tidal predictions for Ensenada (ca. 20 km south of Bahia Salsipuedes), indicate sea-level fluctuations of up to 2.4 m during the course of the deployments, which would have increased the distance from the top ADCP bin to the surface from 2 to 4.4 m. Such a change could certainly increase the discrepancy between the trajectories predicted from a PVD and those actually followed by the drifters, especially on a highly stratified water column (Figs. 8 and 9).

Our observations were focused on drifter paths and on the physical variables associated with the water column's response to wind forcing, and did not include an assessment of the spatial distribution and/or settlement of neustonic larvae in the area. Therefore, a connection between this transport mechanism and the recruitment of coastal species with neustonic larvae is yet to be demonstrated. If there is a connection, however, and larvae of coastal invertebrates are in fact transported onshore by the sea breeze, it would be possible to predict the spatial-temporal distribution of larval settlement in some populations based on local wind patterns and shore orientation. An assessment of the effect of sea breeze events on the spatial distribution and timing of settlement is thus warranted.

A follow up of our study should include a survey of neustonic meroplankton in the area with concurrent drifter deployments and settlement observations. Given the diurnal frequency of sea breeze events, any attempt to link such events to local settlement patterns will have to consider observations taken at shorter intervals than it is customary (i.e. at least semi-diurnally). Lack of temporal resolution could result in a misinterpretation of the mechanisms that determine the timing and intensity of settlement in populations with neustonic larvae.

Wind-driven onshore transport of neustonic invertebrates has been suggested as a cause of

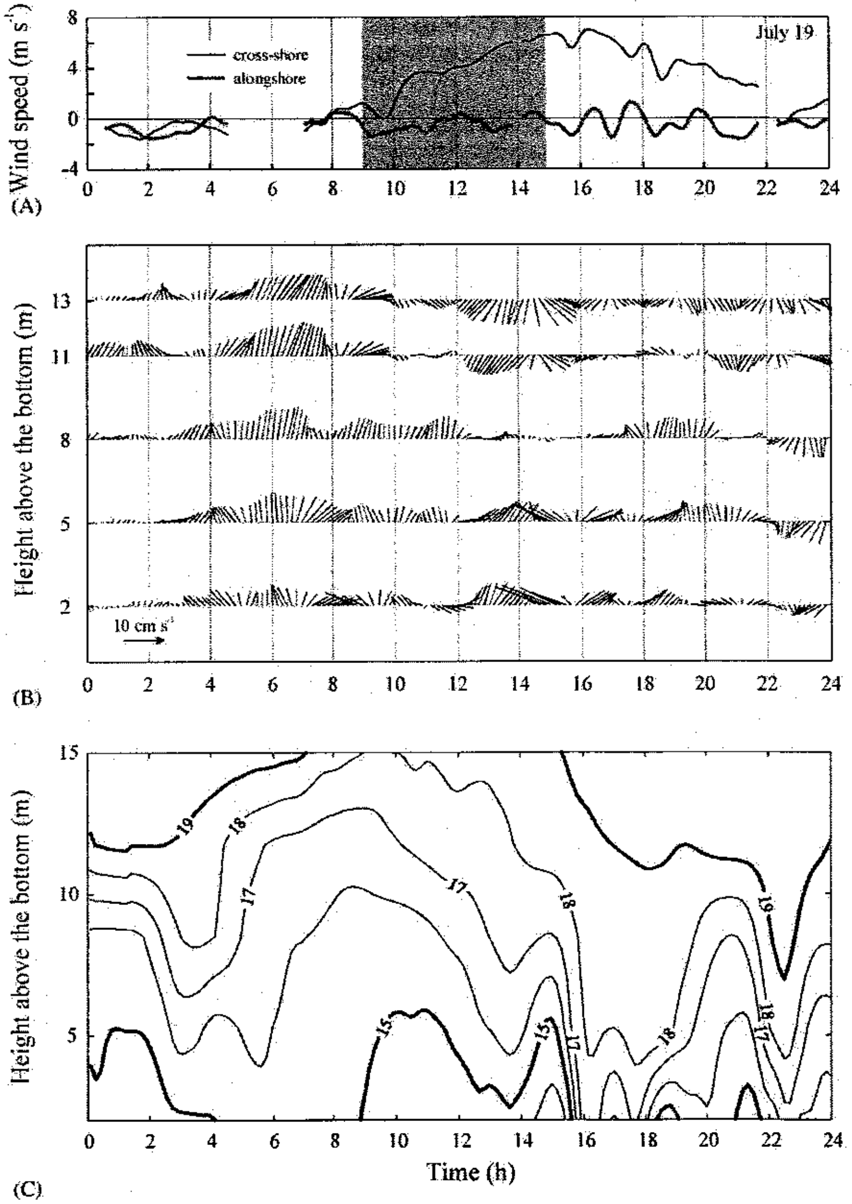

Fig. 8. Example of the effect of wind forcing (A) on the circulation (B) and thermal structure (C) of the water column in Bahia Salsipuedes on July 19, 1999. The shaded area in A corresponds to the duration of the drifter deployment. The stickplots in B show the variability in direction and magnitude (see scale bar at lower left corner) of horizontal currents at the same depths at which temperature was recorded. The vectors indicate the direction currents are flowing towards (up is north).

the spatial patterns observed in barnacle settlement (Kendall et al., 1982; Bertness et al., 1996), and in the spatial distribution of neustonic isopods (Locke and Corey, 1989), post-larval crabs (Shanks, 1986; Eggleston et al., 1998) and lobster megalopae (Hudon and Fradette, 1993). If such wind events are persistent and consistent enough over demographically relevant time scales, they

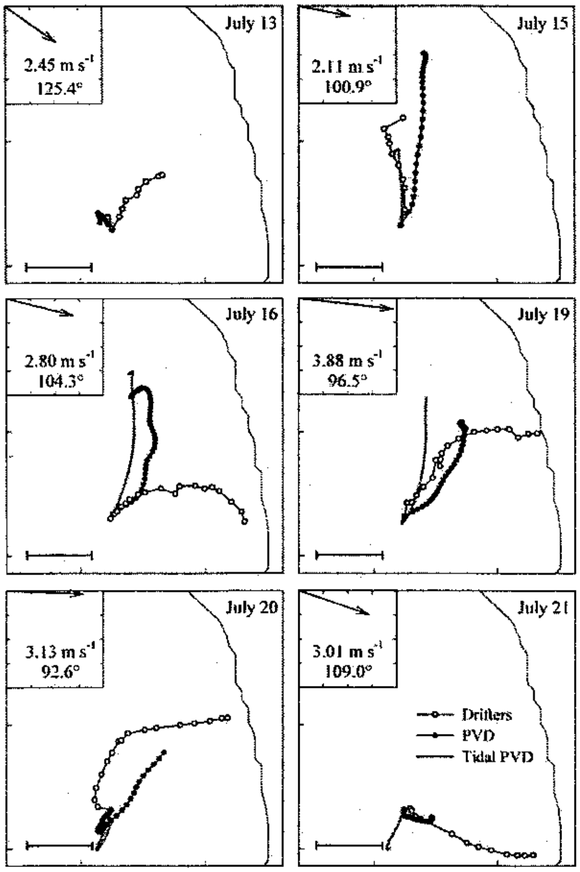

Fig. 9. Comparison of observed versus predicted trajectories of drifters at Bahia Salsipuedes, Baja California, in July 1999. Open circles indicate the observed drifter trajectories. Predicted trajectories (closed circles) correspond to a PVD, computed from horizontal current velocity data collected at 13 mab. The gray line is a PVD computed using only those frequencies of the current data that correspond to the barotropic tide. The insets show average wind speed and direction (0° = N) over the duration of each deployment. The scale bar at the lower left corner of each panel corresponds to a distance of 1 km.

could have an impact on the connectivity and/or demographic isolation among adjacent coastal populations. At sea level, the sea breeze is highly asymmetrical, with a marked predominance of onshore over offshore winds (Fig. 3a). Hence, the sea breeze can have a cumulative effect (i.e. over more than one diurnal cycle) on the cross-shore distribution of neustonic larvae. A persistent sea breeze-mediated onshore transport could allow neustonic larvae to either remain close to the shoreline throughout their development, or to repeatedly reach it, hence increasing their probability of being close to adult habitats when competent to settle. Thus, the sea breeze could constitute an effective transport and/or retention mechanism in areas with a configuration of shoreline and wind forcing such as that observed at Bahia Salsipuedes.

The effect of wind forcing on larval retention and demographic isolation could be intensified if larval behavior is invoked, such as the reverse vertical migration hypothesized by Poulin et al. (2002) for neustonic larvae of the subtidal gastropod *Concholepas concholepas*. Even under conditions of strong upwelling (i.e. strong offshore Ekman transport), the larvae of *C. concholepas* are consistently found between the shoreline and the upwelling front. Such observation, along with data on the temporal variability of larval distribution, suggests that a reverse vertical migration behavior might be allowing these larvae to stay close to subtidal habitats (see Fig. 6 in Poulin et al., 2002). The interaction between physical processes like the sea breeze and behavioral mechanisms such as vertical migrations could increase the local retention of neustonic larvae and the demographic isolation of adjacent populations.

Finally, these results might also be relevant for understanding the onshore transport of pollutants, often discharged a few kilometers from shore near coastal cities (e.g. Boehm et al., 2002). Such discharges are likely to contain buoyant particles than can reach surface waters. Our observations suggest that such particles could be rapidly transported onshore by the sea breeze.

Acknowledgements

Supported by US NSF grant to JP and Mexican CONACYT grant DAJ J002/750/00 C-834/00 to FJO-T. FT was supported by the Chilean MIDEPLAN, and PM by WHOI and CIPO-IAI. M. Hendershott (SIO) first suggested to one of us (JP) the use of low profile, flexible floating objects for measuring surface circulation. We thank J. Leichter (SIO), M. López (CICESE), and two anonymous reviewers for their comments on an earlier version of this manuscript, and S. Ortegon and A. Bravo for their assistance in the field. This is WHOI contribution number 11,098.

References

Bertness, M.D., Gaines, S.D., Stephens, E.G., Yund, P.O., 1992. Components of recruitment in populations of the acorn barnacle *Semibalanus balanoides* (Linnaeus). Journal of Experimental Marine Biology and Ecology 156, 199–215.

Bertness, M.D., Gaines, S.D., Wahle, R.A., 1996. Wind-driven settlement patterns in the acorn barnacle *Semibalanus balanoides*. Marine Ecology Progress Series 137, 103–110.

Boehm, A.B., Sanders, B.F., Winant, C.D., 2002. Cross-shelf transport at Huntington Beach. Implications for the fate of sewage discharged through an offshore ocean outfall. Environmental Science and Technology 36, 1899–1906.

Butman, C.A., 1987. Larval settlement of soft-sediment invertebrates: The spatial scales of pattern explained by active habitat selection and the emerging role of hydrodynamical processes. Oceanography and Marine Biology Annual Review 25, 113–165.

Ebert, T.A., Schroeter, S.C., Dixon, J.D., Kalvass, P., 1994. Settlement patterns of red and purple sea urchins (*Strongylocentrotus franciscanus* and *S. purpuratus*) in California, USA. Marine Ecology Progress Series, 111, 41–52.

Eggleston, D.B., Armstrong, D.A., Elis, W.E., Patton, W.S., 1998. Estuarine fronts as conduits for larval transport: Hydrodynamics and spatial distribution of Dungeness crab postlarvae. Marine Ecology Progress Series 164, 73–82.

Emery, W.J., Thomson, R.E., 1998. Data Analysis Methods in Physical Oceanography. Pergamon Press, New York.

Epifanio, C.E., Garvine, R.W., 2001. Larval transport on the Atlantic continental shelf of North America: A review. Estuarine Coastal and Shelf Science 52, 51–77.

Farrel, T.M., Bracher, D., Roughgarden, J., 1991. Cross-shelf transport causes recruitment to intertidal populations in central California. Limnology and Oceanography 36, 279–288.

Gaines, S., Brown, S., Roughgarden, J., 1985. Spatial variation in larval concentrations as a cause of spatial variation in settlement for the barnacle, *Balanus glandula*. Oecologia 67, 267–272.

Gaines, S.D., Bertness, M.D., 1992. Dispersal of juveniles and variable recruitment in sessile marine species. Nature 360, 579–580.

Hudon, C., Fradette, P., 1993. Wind-induced advection of larval decapods into Baie de Plaisance (Îles de la Madeleine, Québec). Canadian Journal of Fisheries and Aquatic Sciences 50, 1422–1434.

Johnson, M.W., 1939. The correlation of water movements and dispersal of pelagic larval stages of certain littoral animals, especially the sand crab *Emerita*. Journal of Marine Research 2, 236–245.

Kaplan, D.M., Largier, J.L., Navarrete, S., Guiñez, R., Castilla, J.C., 2003. Large diurnal temperature fluctuations in the nearshore water column. Estuarine Coastal and Shelf Science 57, 385–398.

Kendall, M.A., Bowman, R.S., Williamson, P., Lewis, J.R., 1982. Settlement patterns, density and stability in the barnacle *Balanus balanoides*. Netherlands Journal of Sea Research 16, 119–126.

Large, W.G., Morzel, J., Crawford, G.B., 1995. Accounting for surface wave distortion of the marine wind profile in low-level ocean storms wind measurements. Journal of Physical Oceanography 25, 2959–2971.

LeFevre, J., 1986. Aspects of the biology of frontal systems. Advances in Marine Biology 23, 163–299.

Locke, A., Corey, S., 1989. Amphipods, isopods and surface currents: A case for passive dispersal in the Bay of Fundy, Canada. Journal of Plankton Research 11, 419–430.

Pineda, J., 1994a. Spatial and temporal patterns in barnacle settlement rate along a southern California rocky shore. Marine Ecology Progress Series 107, 125–138.

Pineda, J., 1994b. Internal tidal bores in the nearshore: Warm-water fronts, seaward gravity currents and the onshore transport of neustonic larvae. Journal of Marine Research 52, 427–458.

Pineda, J., 1999. Circulation and larval distribution in internal tidal bore warm fronts. Limnology and Oceanography 44, 1400–1414.

Pineda, J., 2000. Linking larval settlement to larval transport: assumptions, potentials, and pitfalls. In: Färber-Lorda, J. (Ed.), Oceanography of the Eastern Pacific, Vol. 1. CICESE, Ensenada, pp. 84–105.

Pineda, J., López, M., 2002. Temperature, stratification and barnacle larval settlement in two Californian sites. Continental Shelf Research 22, 1183–1198.

Poulin, E., Palma, A.T., Leiva, G., Narvaez, D., Pacheco, R., Navarrete, S.A., Castilla, J.C., 2002. Avoiding offshore transport of competent larvae during upwelling events: The case of the gastropod *Concholepas concholepas* in Central Chile. Limnology and Oceanography 47, 1248–1255.

Reyns, N., Sponaugle, S., 1999. Patterns and processes of brachyuran crab settlement to Caribbean coral reefs. Marine Ecology Progress Series 185, 155–170.

Scheltema, R.S., 1968. Dispersal of larvae by Equatorial ocean currents and its importance to the zoogeography of shoal-water tropical species. Nature 217, 1159–1162.

Shanks, A.L., 1986. Vertical migration and cross-shelf dispersal of larval *Cancer* spp. and *Randallia ornata* (Crustacea: Brachyura) off the coast of southern california. Marine Biology 92, 189–199.

Simpson, J.E., 1994. Sea Breeze and Local Winds. Cambridge University Press, Cambridge.

Underwood, A.J., Fairweather, P.G., 1989. Supply side ecology and benthic marine ecology. Trends in Ecology and Evolution 4, 16–20.

Winant, C.D., 1980. Coastal circulation and wind-induced currents. Annual Review of Fluid Mechanics 12, 271–301.

Wing, S.E., Largier, J.L., Botsford, L.W., Quinn, J.F., 1995a. Settlement and transport of benthic invertebrates in an intermittent upwelling region. Limnology and Oceanography 40, 316–329.

Wing, S.R., Botsford, L.W., Largier, J.L., Morgan, L.E., 1995b. Spatial structure of relaxation events and crab settlement in the northern California upwelling system. Marine Ecology Progress Series 128, 199–211.