AN ABSTRACT OF THE DISSERTATION OF

Douglas C. Reese for the degree of Doctor of Philosophy in Oceanography presented on October 21, 2005.

Title: Distribution, Structure, and Function of Marine Ecological Communities in the Northern California Current Upwelling Ecosystem

Abstract approved:

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Within systems characterized by substantial spatial and temporal variability, abundances of organisms tend to be higher in localized areas. Within the northern California Current system, the identification of such marine, biological hotspots would be of great importance to resource managers, conservationists, and research planners, and is consequently a growing area of research. Furthermore, in order to understand how ecosystems function and persist, it is necessary to know how ecological communities are distributed. The overall goal of this study is to provide further understanding regarding the functioning of marine ecosystems in such highly variable environments and to provide information about the distribution and structure of marine communities. Sampling was conducted during June and August of 2000 and 2002 as part of the U.S. GLOBEC mesoscale surveys from Newport, Oregon in the north to Crescent City, California in the south. A geostatistical approach was used to create surfaces used in a GIS to determine the distribution of various community characteristics. Two biological hotspots were identified and determined to persist in space and time, yet differed with respect to biological and physical features and in the amount of area covered. Various community analyses, including nonmetric multidimensional scaling, indicator species analysis, and cluster analysis were used to determine various community properties associated with the hotspots and non-hotspot regions. Results indicate that nekton biological hotspots in the northern California Current persist across differing environmental and biological conditions, although upwelling-based hotspots may be more susceptible to climatic conditions than retention-based hotspots. Analyses of the distribution of the functional groups within the region indicate that the predominant biological activity is spatially nonrandom and occurs within persistent, localized areas. Analyses of species associations suggest a moderate degree of redundancy. The presence of such complementary species within functional groups may confer the stability observed within these systems. The finding that large regional areas are composed of smaller, localized hotspots where a predominant amount of biological activity is occurring, suggests that the evaluation of large marine ecosystems may lead to erroneous or misleading results if they do not consider the more persistent, localized biological hotspots.

Distribution, Structure, and Function of Marine Ecological Communities in the Northern California Current Upwelling Ecosystem

by

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

Douglas C. Reese, Author

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CONTRIBUTION OF AUTHORS

Dr. Richard Brodeur contributed to the collection of the data and editing of all chapters of this dissertation. Todd Miller assisted in data collection, surface zooplankton identification, and analyses for Chapter 2 of this dissertation. Dr. Cynthia Suchman provided her expertise on jellyfish by editing and supplying diet information on jellyfish used in Chapter 4. Suzan Pool managed the U.S. GLOBEC database and provided data assistance.

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INTRODUCTION

Background

Ecosystems are complex systems composed of the biotic community and its abiotic environment (Krebs, 1985). In order to understand how ecosystems function and persist, it is necessary to know how ecological communities are distributed. The complexity associated with communities is due, in part, to the interaction of many species at various trophic levels, making ecosystem-based studies difficult. Traditionally, studies of fish in the marine environment have been performed and analyzed by examining the taxonomy, life history, and population dynamics of single species, which tend to be the most economically valuable species (Beamish and Mahnken, 1999). Understanding how systems function, however, requires a broader approach such that communities are examined rather than individual species. This involves examining the distributions of these communities and how species composition changes over time in relation to the biotic and abiotic environment.

One of the most frequently described attributes of communities used in ecosystem-based studies is its biodiversity. Central issues in ecological and environmental sciences over the past decade have been to understand the spatial patterns of biodiversity and to identify relationships between biodiversity and ecosystem function (Loreau et al., 2001). Biodiversity is distributed heterogeneously across the Earth (Gaston, 2000). In terrestrial systems, a large number of endemic, small-range specialists are distributed such that their distributions form biodiversity hotspots (Stevens, 1989; Pagal et al., 1991; Smith et al., 1994; Blackburn and Gaston, 1996). Environmental predictability and stability in tropical terrestrial hotspots select for specialized traits within species which results in the more localized distributions of high species diversity (Stevens, 1989). Our understanding of the spatial patterns of diversity and community dynamics within marine ecosystems, however, tends to decrease with distance from shore (Cailliet, 1997). This is due to the increased cost of sampling in the ocean compared to that of terrestrial systems. Nevertheless, our understanding is beginning to expand. For instance, the tropical Central Indo-Pacific coral reef system has been identified as one of the most distinctive regional hotspots on earth and is formed primarily from the combined contributions of numerous widespread species (Hughes et al., 2002).

Many studies have shown that increased biodiversity leads to enhanced ecosystem stability and function (e.g., Tilman, 1996; McGrady-Steed et al., 1997; Naeem and Li, 1997; Petchey et al., 1999; Cardinale et al., 2002; Zavaleta and Hulvey, 2004). The enhancement is primarily due to the increased diversity associated within each functional group, suggesting that redundancy (multiple species per functional group) is a valuable trait (Naeem and Li, 1997). Changes in species composition have the potential to affect an entire ecosystem. In fact, the exclusion of certain species from communities often results in changes in community structure due to the rearrangement of the dominance structure within the system which leads to further changes in diversity (McGowan, 1992). On the other hand, increasing species richness is thought to result in more efficient use of resources and a greater capacity to ensure ecosystem stability under disturbance or ecosystem change (Tilman, 1996; Naeem and Li, 1997; Patrick, 1997; Duarte, 2000; Loreau et al., 2001). In effect, the ability of ecosystems to endure extreme conditions is a vital test of ecosystem function and is a measure of the fundamental ecosystem properties of resistance and resilience (Woodward, 1993).

An important consideration necessary in an approach where the goal is to conserve biodiversity is to identify which portions of a region maximize the biodiversity (Walker, 1992). Changing the focus of ecosystem-based studies from individual species to functional groups, and combining this with identifying potentially redundant species within those functional groups that are important determinants, or indicators, of the ecosystems, should allow for a better understanding of how best to preserve ecosystems and maintain ecosystem processes (Walker, 1992).

Associations among species are known factors that limit the local distributions and abundances of species. It is important to evaluate biodiversity, community structure, and the associations of species to assess the status of marine communities since they are vulnerable to impacts related to environmental change. Biodiversity has become a popular topic, stimulated in part by the need to assess the health of communities and the amount of damage caused by human activities (Lubchenco et al., 1991; Peterson, 1992; Schulze and Mooney, 1994; Heywood, 1995; Cailliet, 1997). In addition to understanding how biodiversity is distributed within a system, it is necessary to understand how those species are associated. Evaluating the interactions among species is one means to help explain the patterns, distributions, and changes in communities we observe. Changes in diversity and species assemblages could potentially be indicators of large-scale changes in the environment; therefore, knowledge about the spatial and temporal distribution of diversity and how diversity is affected by both natural and anthropogenic processes are essential to our understanding of ecological communities and will allow for wiser management decisions.

Marine Systems

Within the major ocean basins of the world, eastern boundary currents create four large coastal upwelling regions along the west coasts of Africa, North America, and South America, all of which are characterized by the presence of cool surface waters and high biological productivity. One of these boundary currents, the California Current, flows southward along the west coast of the United States, forming as the eastward flowing North Pacific Current bifurcates between 45° and 50° N, becoming the California Current to the south and the Alaska Current to the north (Hickey, 1998). The California Current is responsible for transporting relatively cold, fresh water from the Subarctic Pacific along the coast. Between about 35° and 50° N, wind forcing is determined by the positions and intensities of the North Pacific High and Aleutian Low pressure systems which result in equatorward winds during the spring and summer within the region (Batchelder et al., 2002). This alongshore equatorward wind stress results in a divergence of surface water away from the coastal boundaries due to Ekman transport. Water that is transported offshore is then replaced by deeper, upwelled, nutrient-rich water. Therefore, there is a persistent supply of nutrients to the well-lit surface waters resulting in increased levels of primary production. The high levels of primary production then support higher trophic levels. The effect of coastal upwelling is the replenishment of nutrients to the photic zone within the region and leads to enhanced and sustained productivity in the California Current during the spring and summer months (Batchelder et al., 2002).

The California Current, a highly productive ecosystem, is characterized by substantial spatial and temporal variability. Strong seasonal variability within the California Current is the result of the seasonal reversal in the alongshore winds north of 37° N, which are poleward in winter and equatorward in summer (Huyer, 2003). During the summer with the equatorward winds, the northern California Current experiences substantial wind-forced upwelling resulting in high levels of primary production that are able to support higher trophic levels (Barth et al., 2005). A substantial amount of fresh water enters the system during the spring when the discharge from the Columbia River is at maximum (Hickey and Banas, 2003). During the summer, a plume of low salinity water is typically found equatorward of the mouth of the river and offshore, whereas during winter, the plume is directed poleward and over the shelf and slope.

Interannual variability within the California Current is typically associated with El Niño events (Chelton et al., 1982). Coastally trapped Kelvin waves propagate northward along the continental margin from the eastern equatorial Pacific, which results in the depression of isopycnals, raising sea-level, and the intensification of poleward currents along the coast (Huyer, 2003). El Niño events are associated with increased temperatures, as well as changes in sea level and currents, and consequently less production within the California Current region.

Decadal variability within the California Current appears to be related to large-scale regime shifts that change ocean characteristics over periods of decades (Mantua et al., 1997; Chavez et al., 2003). The regime shifts result in basin-wide changes in the environment, affecting wind patterns, ocean temperatures, and biological productivity, and are due to the position and intensification of the Aleutian Low pressure system. Recently, another form of variability was reported caused by the anomalous intrusion of cold, Subarctic Pacific waters into the California Current which greatly affected the entire ecosystem and led to anoxic events in the bottom water (Huyer, 2003; Wheeler et al., 2003).

In the past, the California Current system has experienced dramatic shifts in both abundance and species composition at both lower and higher trophic levels (Roemmich and McGowan, 1995; Emmett and Brodeur, 2000; Brodeur et al., 2003a; Rebstock, 2003). Interannual and interdecadal climate variability are known to significantly affect the biological productivity, abundance, distribution, growth, and survival of marine species within the California Current, however, the specific mechanisms responsible for this variability are not well understood (Batchelder et al., 2002). Brodeur and Pearcy (1992) examined the effects of environmental variability on trophic interactions within the northern California Current system and reported that dietary overlap and food web structure varied and depended on prevailing oceanographic conditions. Moreover, they found that during years of low to moderate upwelling, there was generally higher overall trophic diversity and a low level of dietary overlap; however, in years with strong upwelling there was less trophic diversity and consequently higher dietary overlap.

Rebstock (2003) examined multiple long term data sets from the California Current system and found that the system is simultaneously variable and stable. Significant changes in populations of kelp, phytoplankton, zooplankton, intertidal invertebrates, fishes, and seabirds were related to increases in water temperature, thermocline depth and stratification. In spite of the physical and biological variability, some populations and assemblages were found to persist for long periods of time, implying some form of stability within the system. Although there are large fluctuations in abundances of individual species, there appears to be evidence for stability at the assemblage or community level (Rebstock, 2003). For instance, many populations of species within the California Current system were found to undergo large fluctuations in abundance on interannual and interdecadal time scales, however, these species showed long-term persistence. It has been suggested that this type of stability, for at least small pelagic fishes, is the result of these pelagic populations or communities shifting location in response to changing environmental conditions (Rebstock, 2003). Stability was also apparent for assemblages of larval fish, calanoid copepods, and radiolarians.

The pelagic fauna within the northern California Current is composed of a relatively small number of endemic coastal and offshore species within a larger mixture of subarctic, transitional, and subtropical species (Brodeur et al., 2003b). Pelagic nekton abundance and biomass are known to fluctuate dramatically through time within upwelling systems. Brodeur et al. (2003b) noted that fluctuating abundances of pelagic nekton within the northern California Current system were related to large-scale changes in the ecosystem accompanying regime shifts. Given the short time periods associated with the changes in species composition, they suggest that the responses were due to shifts in migration or distribution patterns and not to recruitment. Interannual changes were attributed to strong El Niño events which led to changes in the distribution of many species.

In a similar upwelling system to the California Current, the Benguela system on the west coast of South Africa seems to be highly influenced by environmental stability (Gibbons and Hutchings, 1996). The relatively short-term, dynamic and pulsed nature of upwelling resulted in lower species diversity of zooplankton closer to shore with a general increase in species richness offshore to the oceanic front and beyond. Diversity and abundance were reduced during active upwelling when the surface water was moved offshore and was replaced by newly upwelled water characterized by low species richness. The newly upwelled water was low in temperature and chlorophyll and was generally low in zooplankton diversity. As the water mass moved offshore to the front it began to stabilize and phytoplankton biomass and zooplankton diversity increased. They also found distinct zooplankton assemblages associated with neritic, frontal, and oceanic waters which corresponded to the shelf-break/oceanic front (Gibbons and Hutchings, 1996). The nearshore assemblages were typically comprised of few but very abundant species. In contrast, oceanic assemblages were comprised of many species at low abundance. Frontal communities contained mixtures of the nearshore and oceanic assemblages.

Even within upwelling systems where overall production is high, resources are not evenly distributed throughout the systems. The highly variable conditions within the

Benguela system affect the abundances of a broad range of species from plankton to top predators (Barange et al., 1992; Shannon et al., 1992). For instance, Brown (1992) noted significant differences in both inshore/offshore and longshore distributions of primary production due to variable upwelling processes. Similarly, the distributions of higher trophic level species tend to be spatially and temporally variable with higher aggregations in localized areas (Coetzee et al., 2001). For instance, Coetzee et al. (2001) found that the spatial distribution of schooling pelagic fish within the Benguela system tended to be variable with concentrations distributed in a few dense aggregations. In general, the diversity of fish is lower within the Benguela system than in the California Current (Sakko, 1998). The low diversity is believed to be due to the continuously changing environmental conditions, due to the unique flow dynamics within the Benguela system, that favor the persistence of relatively few, generalist species that can take advantage of the pulses of high productivity (Sakko, 1998).

In contrast to the variable upwelling systems, central gyres are large, persistent systems. Upwelling regions are more eutrophic than offshore waters and species diversity tends to be low at all trophic levels (Gibbons and Hutchings, 1996). However, within the oligotrophic waters of the central North Pacific gyre, diversity is high and numerical dominance is strong at all trophic levels (McGowan and Walker, 1979; 1985). For zooplankton, differences in species diversity and constancy of assemblage structure reflect differences in the physical environments of the two regions. The central ocean basins are characterized by stability over long periods of time. With little disturbance, biological processes are permitted such as competition and predation, which have shaped the structure of the zooplankton assemblages (McGowan and Walker, 1979; Gibbons et al., 1999). In contrast, upwelling regions are both physically dynamic and of relatively recent origin (Gibbons et al., 1999).

In order to understand how these complex systems function and persist, it is necessary to know how ecological communities are distributed. However, marine communities are dynamic systems and difficult to study, often requiring extensive sampling over time. Due to the high cost associated with studies in the sea, this type of research is rarely carried out. Rather, implications tend to be based on reported catches from fisheries. This, however, is limited in scope because often data on community structure and in situ environmental measurements are not collected.

Research Objectives

Within systems characterized by substantial spatial and temporal variability, abundances of organisms tend to be higher in localized areas. Within the northern California Current system, the identification of such marine, biological hotspots will be of great importance to resource managers, conservationists, and research planners, and is consequently a growing area of research (Malakoff, 2004). The overall goal of this study is to provide further understanding to how marine ecosystems function in such highly variable environments and to provide information about the distribution and structure of marine communities. Chapter two is dedicated to examining the environmental variables within the system and the distribution and abundances of lower trophic level groups. The objectives of this chapter were to describe the distribution, community composition, and structure of near-surface dwelling zooplankton, as well as the environmental parameters that best represent the observed patterns in species distributions. Chapters three through five are dedicated to examining the nekton communities throughout the study region in the northern California Current ecosystem. The primary goal of chapter three was to examine how nektonic community characteristics are distributed in the surface environment. The examination consisted of identifying the spatial patterns of nekton species diversity, abundance, and biomass on a seasonal and interannual basis to determine whether the patterns persist through time. This analysis led to the discovery of two persistent, marine biological hotspots within this system. The primary goal of chapter four was to identify species associations of nekton and jellyfish in relation to the biological hotspots. Since the biological hotspots were found to persist, the presence of redundant species were examined in order to provide insight into the stability of the hotspots. In chapter five, the decadal persistence of the biological hotspots was examined to see if the hotspots persist on longer temporal scales under different environmental conditions. In addition, the nekton were grouped into functional groups and their distributions examined in relation to the hotspots thus providing insight into the persistence, stability, and function of the northern California Current ecosystem.

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COMMUNITY STRUCTURE OF NEAR-SURFACE ZOOPLANKTON IN THE NORTHERN CALIFORNIA CURRENT IN RELATION TO OCEANOGRAPHIC CONDITIONS

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COMMUNITY STRUCTURE OF NEAR-SURFACE ZOOPLANKTON IN THE NORTHERN CALIFORNIA CURRENT IN RELATION TO OCEANOGRAPHIC CONDITIONS

Abstract

We analyzed how near-surface zooplankton are distributed in the northern California Current, not only in space and time but also with reference to species assemblages, habitat characteristics, and environmental factors. The community structure, spatial distribution patterns, and environmental associations of near-surface zooplankton from June and August 2000 GLOBEC cruises were examined. Crab megalopae, hyperiid amphipods, euphausiids, and chaetognaths dominated the near-surface zooplankton community during both cruises. A geostatistical approach was used to determine that near-surface zooplankton concentrations differed spatially and quantitatively between June and August. Near-surface zooplankton concentration was spatially patchy during June, with the highest levels occurring nearshore in various locations throughout the study region. In August, zooplankton concentration was more uniformly distributed, however, higher concentrations were observed north of Cape Blanco. During June, zooplankton species richness was spatially patchy, whereas in August, species richness was more uniformly distributed throughout the study area. Highest values were observed during June in localized areas along the coast with lowest values observed further offshore near the shelf-break at 200 m. During August, species richness was highest nearshore south of Cape Blanco, yet in the north, higher values extended across the shelf and further offshore. To explore patterns in community structure, we applied cluster analysis, Indicator Species Analysis, and Nonmetric

Multidimensional Scaling (NMS) ordination to both data sets. Cluster analyses differentiated taxa by inshore and offshore location in the first division and by latitude in the second division. Results from NMS confirmed the cross-shelf zonation of near-surface zooplankton, with sea surface temperature the most consistent environmental parameter explaining the distributions. An offshore assemblage of zooplankton was entrained in an eddy and transported onto the shelf in August.

Introduction

The California Current is a dynamic and highly productive ecosystem, characterized by substantial spatial and temporal variability. The macrozooplanton and ichthyoplankton of this system have been intensely studied for several decades off Central and Southern California as part of the CalCOFI sampling (Moser et al., 1987; Roemmich and McGowan, 1995) and also off central and northern Oregon by researchers at Oregon State University (Peterson and Miller, 1975, 1977; Richardson and Pearcy, 1977; Morgan et al., 2003). The biota from the area between these regions, namely the southern Oregon and northern California coast, have received considerably less attention until the recent U.S. GLOBEC Northeast Pacific Program (NEP) cruises (Peterson and Keister, 2002). The main goal of the NEP is to understand biophysical mechanisms through which zooplankton and salmon populations respond to physical forcing and biological interactions in the coastal regions of the northern California Current (Batchelder et al., 2002).

The near-surface zooplankton, those living near the surface, represent a group of organisms adapted to a unique environment. This habitat often contains concentrated food resources that are utilized by early life stages of many species of fish (Kingsford and Choat, 1986; Brodeur, 1989). A substantial number of near-surface collections have been made in the northern California Current and the geographic distributions of many taxa have been described. However, with the exception of Brodeur et al. (1987) most studies within this geographic region have concentrated on only one or two taxonomic groups in their analyses (Shenker, 1988; Doyle, 1992). What is known is that the main environmental factors affecting zooplankton assemblages include water temperature, nutrient concentrations, and salinity. Increased nutrient concentrations typically correspond with increased phytoplankton abundance, which can have an effect on zooplankton. Secondary production is dependent upon primary production, and therefore changes in primary production leads to changes in the distributions and abundances of zooplankton species (Francis et al., 1998).

During summer 2000, we collected near-surface zooplankton at multiple stations at which we also trawled for juvenile fish (Brodeur et al., 2004). We examined the composition of these near-surface samples and the distribution of dominant key taxa (those greater than 5 mm) relative to the environment. We compared our results to the study done in the mid-1980s (Brodeur et al., 1987; Brodeur, 1989) to examine changes in species abundance and distribution patterns. Finally, we compared the community structure of these taxa, particularly with respect to cross-shelf and north-south differences. Cross-shelf zonation of zooplankton between northern California and British

Columbia has been observed in Euphausiacea and Copepoda (Peterson and Keister, 2002; Morgan et al., 2003; Gómez-Guttiérrez et al., 2005). The typical pattern observed is one of a nearshore and offshore zone, with a gradual transition between. Similarly, substantial latitudinal differences in species associations were observed in this study region, particularly with respect to Cape Blanco, a prominent geographic feature of the region (Peterson and Keister, 2002). These distributions however, were established using either a full water column sampling effort (vertical net tows) or oblique tows with a large vertical component. Distributions of zooplankton in the very upper water column, the neuston, have not been investigated in this regard. Thus the objectives of this study were to 1) describe the near-surface community composition and structure off the Oregon and Northern California shelf, 2) identify species patterns associated with cross-shelf and north-south gradients, and 3) describe environmental parameters that may best correlate with patterns in species distribution.

Methods

Field sampling

Near-surface zooplankton tows were conducted at each trawling station as part of a mesoscale and fine-scale sampling study within the U.S. GLOBEC NEP program. Eighty-five collections were made from May 29 to June 11 (hereafter called the June Cruise) and 77 collections from July 29 to August 12 (August Cruise) from a chartered fishing vessel, the F/V *Sea Eagle*. The sampling area extended from Newport off central Oregon (latitude 44° 40’ N) to Crescent City in northern California (approximately

42° N). Most collections took place during daytime (June, n = 81 and August, n = 73) but occasionally tows were made during twilight or nighttime. The spatial and community analyses included in this paper however are limited to collections made during daylight hours to avoid any changes in the day/night community structure.

The neuston frame had a width of 1 m and a height of 0.3 m, and contained a 335 μm mesh net. The net was released to 60 m behind the vessel, out of the wake, and was towed at the surface for five minutes while the vessel was underway at 3 km hr^{-1}. A General Oceanics flowmeter located inside the mouth of each net was used to estimate the amount of water filtered. Samples were preserved in a 5% buffered formalin/seawater solution. Planktonic organisms collected with a neuston net include both true neuston, those species possessing unique adaptations to the surface layer, as well as some members of the zooplankton that happened to be residing near the surface and subsequently captured, but which do not only live at or near the surface. Sea surface salinity and temperature were measured at 1 m and 2 m depths from each site using a Seabird SBE 19 CTD (Conductivity, Temperature, Depth) profiler. Although 85 and 77 stations were sampled in June and August, respectively, the CTD failed to record at several stations, thus reducing the available sample sizes to 71 and 58. Water from 3 m below the surface was collected with a 1-l Niskin sampler from 84 and 75 stations during June and August, respectively. After collection, samples were filtered and analyzed fluorometrically for chlorophyll-*a*.

Laboratory processing

In the lab, samples were rinsed with freshwater, and large gelatinous plankton and quantities of seagrass and algae were rinsed to separate zooplankton and then removed from the sample. The samples were rinsed into either graduated cones or cylinders, depending on the size and number of items in the sample, and allowed to settle for at least 12 hours. Volume for samples in cones was measured to the nearest 1 ml for samples less than 40 ml, to the nearest 2 ml for samples 40-100 ml, and to the nearest 5 ml for samples larger than 100 ml. Volume for samples in graduated cylinders was measured to the nearest 1 ml for samples in 100 ml cylinders, to the nearest 2 ml for samples in 250 ml cylinders, and to the nearest 5 ml for samples measured in 500 ml cylinders.

After settled volumes were measured, samples were sorted over a light table without magnification. Zooplankton larger than 5 mm (maximum dimension) were removed for identification. If a large number of organisms was present, the sample was searched for rarer taxa and then split with a Folsom plankton splitter. Larger animals were then identified to the lowest possible taxon using a dissecting microscope and counted and these counts were converted to standardized densities.

Seasonal data analysis

Seasonal differences in temperature, salinity, and zooplankton species richness were compared with a paired t-test, following previous confirmation of normality and homoscedasticity assumptions. Normality and homoscedasticity assumptions were not met for chlorophyll concentration and zooplankton concentration therefore a Wilcoxon

Rank-Sum Test was used to evaluate seasonal differences of these variables. For all analyses, alpha was set at 0.05.

Spatial analysis

The spatial structure of sea surface temperature, salinity, chlorophyll concentration, near-surface zooplankton concentration, and zooplankton species richness was analyzed by the use of semivariograms. The semivariogram is a geostatistical technique based on the patchiness hypothesis in which environmental variables tend to be more similar in value the closer they are geographically. Each spatial process consisted of observations measured at a location x, where x is defined by latitude and longitude in a 2-dimensional space for each cruise. It was assumed that: (1) the spatial distribution of each process was stable throughout the period of each cruise (approximately 2 weeks), and (2) the observations and spatial processes are the result of random processes (Pelletier and Parma, 1994; Johnston et al., 2001). The intrinsic stationarity assumption was examined by the use of semivariance data clouds in which the variance of the difference between two locations is the same between any two points that are at similar distances and direction (Johnston et al., 2001). In addition, directional influences were examined. There are two types of directional components that can affect the output surface predictions: global trends and anisotropy (Johnston et al., 2001). Global trends are dominant processes that affect all measurements in a deterministic manner and may be the result of such things as prevailing winds or currents. Global trends, once identified, can be removed from the analysis by detrending (Johnston et al., 2001). This is accomplished by representing the global trend with a mathematical formula and removing it from the analysis of the measured points, but then adding it back in before predictions are made. The second form of directional influence, anisotropy, can also influence predictions. Anisotropy differs from global trends in that the global trend can be described by a physical process (e.g., prevailing winds and currents) and modeled by a mathematical formula. However, the cause of the anisotropy in the semivariogram is not usually known, so it is modeled as random error (Johnston et al., 2001). Anisotropy is simply a characteristic of a random process that shows higher autocorrelation in one direction than in another. Directional influences were examined for each variable and where present were incorporated into the analyses.

Observations were normalized with a log transformation when necessary to prevent violations of normality and homoscedasticity. In rare cases, influential outliers were removed from the analyses. Empirical semivariograms $\{\gamma(h)\}$ were estimated by pooling pairs of observations using the following equation given by Matheron (1971):

$$\gamma(h) = \frac{\sum_{i=1}^{N_h} \{Z(x_i + h) - Z(x_i)\}^2}{2N(h)}$$

where $Z(x_i)$ is the value of the variable at location x_i, $Z(x_i + h)$ is the value separated from x_i by distance h (measured in meters), and $N(h)$ is the number of pairs of observations separated by distance h. Although a small number of stations were sampled more than once, only the first sampling was used in the spatial analyses whereas all stations were used in the community analyses. The selection of lag size has important consequences on the empirical semivariogram. If, for instance, the lag size is too large, then the short-range autocorrelation may be masked. However, if the lag size is too small, there may be many empty bins, and sample sizes within bins will be too small to get representative averages for bins. Consequently, we followed the general rule of thumb for determining the appropriate lag size by choosing a lag size such that the lag size multiplied by the number of lags was less than or equal to half the largest distance among all points (Johnston et al., 2001). Spherical and exponential theoretical models were fitted to the empirical semivariograms to estimate the semivariogram values for each distance within the range of observations (Cressie, 1993). The following parameters were estimated based on the resulting models: (1) the nugget effect (C_0), which represents independent error, measurement error, and/or variation at distances less than the sample spacing in the dataset; (2) the sill ($C_0 + C$), which represents the asymptotic value of semivariance; and (3) the range, which indicates the maximum distance over which autocorrelation exists. When anisotropy was encountered, the range consisted of a major range (the length of the longer axis to reach the sill) and a minor range (the length of the shorter axis to reach the sill). With anisotropy, the angle of rotation from north of the line that forms the major range was a fourth parameter estimated.

The expected values of the variables were estimated for each cruise by kriging, which forms weights from surrounding measured values to predict values at unmeasured locations (Johnston et al., 2001). The closest measured values have the most influence. The weights of each measured value are derived from the modeled semivariogram that characterizes the spatial structure of the data. The predictor is formed as the weighted sum of the data:

$$\hat{Z}(X_0) = \sum_{i=1}^{n} \lambda_i Z(X_i)$$

where, $Z(X_i)$ is the measured value at the ith location; λ_i is an unknown weight for the measured value at the ith location that minimizes prediction error (Cressie, 1993), and X_0 is the prediction location. The weight, λ_i, depends on the semivariogram, the distance to the prediction location, and the spatial relationships among the measured values around the prediction location. Model parameters and kriging results were evaluated with the use of cross-validation in which several statistics were computed. These included mean and standard mean prediction errors, root-mean-square prediction errors, average standard errors, and standardized root-mean-square prediction errors. For each variable multiple spherical and exponential models were compared and evaluated and the best model selected based on the above model comparison statistics. ESRI's ArcGIS v8.3 with the geostatistical analyst extension was used in the spatial analyses (ESRI, Redlands, CA).

The goal of the spatial analyses is to determine the spatial distribution and quantities of each measured parameter throughout the study region. Although the data are not synoptic, the geostatistical method was employed since it uses the spatial correlation inherent in the data to produce the maps. The maps are not intended to represent small-scale processes but rather elucidate broad-scale patterns in the surface zooplankton community and the accompanying ocean conditions. To confirm that the ocean conditions did not change significantly over the course of each cruise, the geostatistically produced sea surface temperature maps were compared with maps derived from satellite data and temperature measured by SeaSoar (see Barth et al., 2005). In addition, the geostatistically produced chlorophyll (at 3 m depth) maps were compared with chlorophyll (at 5 m depth) as measured by SeaSoar. The geostatistically produced maps were found to closely resemble both the satellite derived maps and the SeaSoar maps, thus supporting the assumption that the geostatistically produced maps are representative of ocean conditions during the cruises.

Community structural analysis

Community structural analyses were performed using PC-ORD v4.25 (McCune and Mefford, 1999). Original data from each of the two cruises formed complementary species and environmental matrices. The environmental matrices consisted of temperature and salinity data collected at 1 m, chlorophyll concentrations collected at 3 m, depth, and latitude. The June and August cruises were analyzed individually to look at spatial patterns of species composition in relation to environmental gradients. For all multivariate analyses, temperature and salinity data at 1 m depth were used. Stations with no species present were eliminated from the data set to allow for analysis of sample units in species space. Data transformations and their effects on the summary statistics were examined prior to analysis (McCune and Grace, 2002). For both cruises the original data showed moderate row and column skewness, high percent covariation (CV), and moderate beta diversity. Deletion of rare species (those species occurring in less than approximately 8% and 5% of sample units (stations) in June and August, respectively), log transformation and subsequent relativization by species maximum markedly reduced row and column skewness and CV. The decision to relativize the data by species maximum was based on the interest in species occurrence rather than overall abundance relative to environmental parameters.

Cluster analysis

Agglomerative hierarchical cluster analysis (AHCA) using Sorensen (Bray-Curtis) distance and flexible beta (β = -0.25) linkage function was applied to arrange zooplankton species assemblages into cluster groups. Flexible beta with β = -0.25 is a space-conserving method that avoids distortion and has less propensity to chain (McCune and Grace, 2002). The community data were relativized by species maximum to equalize common and uncommon species. The cutoff level for determining the optimum number of cluster groups was based on several criteria: (1) biological meaning; (2) test significance and effect size (*A*) of groups using a multi-response permutation procedure (MRPP, Sorensen distance); and (3) compare cutoff level MRPP results with those groups obtained from one cutoff level below and above the level of interest. A non-parametric procedure, MRPP compares the a priori groupings from AHCA to the environmental data, and tests the hypothesis of no difference between two or more groups (McCune and Grace, 2002). The weighting factor employed was:

$$C_i = \frac{n_i}{\sum n_i}.$$

Description of the primary species encompassing each group was done using Indicator Species Analysis (ISA) (Dufrene and Legendre, 1997). Indicator Species Analysis examines the fidelity of occurrence of a species within a particular group, which is based on the combined proportional measurements of the abundance of each particular species in a group relative to its abundance in all groups, and the percent frequency of that species in each group. From this, an indicator value is calculated for a given species across all groups. The statistical significance of each group is examined by a Monte Carlo method, in which sample units are randomly reassigned *n*-times to test if the indicator species values are higher than would be expected by chance. For this study, 1000 runs were applied to each Monte Carlo simulation. Although the community data were relativized by species maximum for cluster analysis to minimize the effect of the highly abundant taxa, Indicator Species Analysis relies on total differences between species, thus the original untransformed data were used for this method.

Ordination

Non-metric Multidimensional Scaling (NMS; Kruskal, 1964) was used to ordinate sample units in species space and to compare cluster groups to environmental gradients. NMS was chosen for this analysis because it is robust to data that are non-normal and contain high numbers of zeros. The Sorensen distance measure was used because it is less sensitive to outliers than some other distance measures. Random starting configurations with 200 maximum iterations were used for the NMS analysis with 15 runs conducted using real data. Non-metric multidimensional scaling uses an iterative search for the best positions of *n* entities on *k* dimensions (axes) that minimizes the stress of the *k*-dimensional configuration (McCune and Grace, 2002). The analysis uses random starting configurations and then runs through them until a predefined stability criterion is met. Instability is calculated as the standard deviation in stress over the previous 10 iterations. If the instability is less than a pre-set cutoff value (0.0001), iterations are stopped and the solution is considered final. The best solution, one with a particular random starting configuration and number of dimensions, is selected from the run with the lowest final stress from a real run and is reapplied to determine the final ordination. To evaluate whether NMS extracted stronger axes than expected by chance, a randomization (Monte Carlo) test was used. Monte Carlo simulations were conducted with 30 runs of randomized data which were then compared to the results obtained from the real data. The *p*-values were calculated as the proportion of randomized runs with stress less than or equal to the observed stress. The dimensionality of the ordination was assessed by comparing the results of the NMS runs using real data to the results obtained using the Monte Carlo simulations using randomized data. Dimensionality was increased if the addition of an axis resulted in a significant improvement compared to the randomized data ($p \leq 0.05$) and the reduction in stress was greater than 5. Sample units were then plotted in the reduced species space. Relationships between the environmental variables and ordination scores were shown with a joint plot. The coefficient of determination (r^2) between distances in the ordination space and distances in the original space was used to determine the proportion of variation represented by each axis. Pearson and Kendall correlations with each ordination axis were used to measure strength and direction of individual species and environmental parameters.

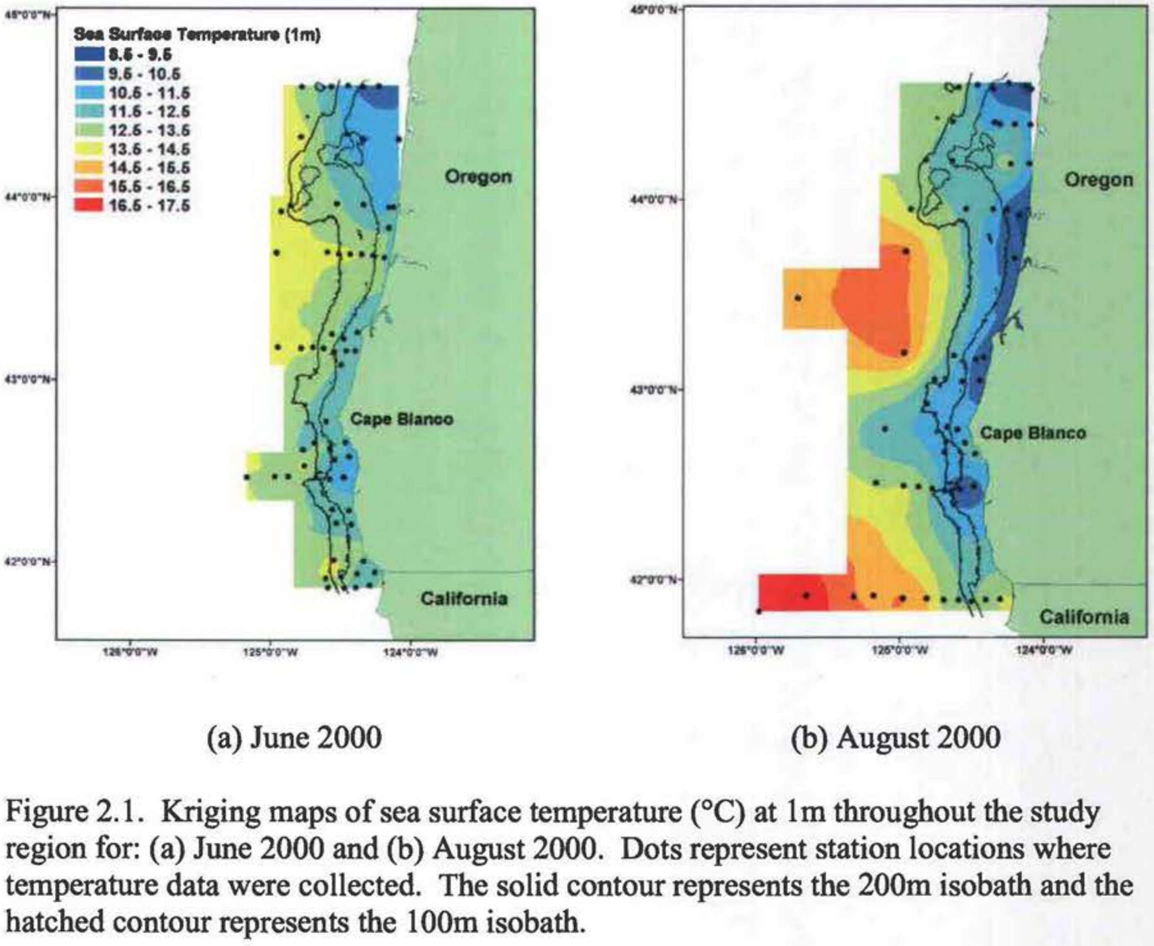
Results

Spatial analysis

The surface water characteristics varied substantially between the June and August 2000 cruises. Although no significant differences were detected in overall mean surface temperatures (two sample t-test = 1.02, p = 0.31) (Table 2.1), the spatial patterns differed with temperatures spanning a greater range in August (Figure 2.1). Since the August cruise included stations that were further offshore which introduces bias in the data since offshore waters tend to be warmer, the test was also computed with the offshore stations from the August cruise eliminated. The results did not change. During June, temperature values ranged from 10.0° to 14.6°C and in August from 8.7° to 17.5°C. In June, the spatial correlation of temperature was best fit by an exponential semivariogram model and the major range indicated a spatial dependence of 41 km (Table 2.2). Anisotropy was not detected; therefore an isotropic model was used. In August, the spatial correlation was best fit by a spherical semivariogram model. Directional influences were present in August with the axis of rotation for the major axis at 359.6° from North indicating the strongest gradient was generally across the shelf (Table 2.2; Figure 2.2). The direction of the major axis represents the direction over which spatial scales are longest, whereas the minor axis represents the direction of the strongest gradient. Essentially, this indicates that temperature at 1m varied more markedly in the onshore-offshore direction, and less so in the north-south direction. The small-scale spatial variation was low during both June and August ($C_0 = 0.133$ and $C_0 = 0.459$, respectively). Nearshore water temperatures in June were greater than 11°C in most regions except near Newport, OR and near Cape Blanco (Figure 2.1). Nearshore

Table 2.1. Seasonal mean (± SD) surface water characteristics, zooplankton concentration, and species richness in the study region: Temperature at 1 m (°C); Salinity at 1 m (psu); Chlorophyll concentration at 3 m (μg/l); Surface zooplankton concentration (ml/100m^3); and Zooplankton species richness (number of species per station). Note: sample sizes differ per cruise due to missing CTD values at 1 m or sample not collected.

Variable	**Season**					
	June 2000			**August 2000**		
	Mean	**SD**	**n**	**Mean**	**SD**	**n**
Temperature	12.4	1.1	71	12.1	2.2	58
Salinity	31.6	0.8	71	33.0	0.6	58
Chlorophyll Concentration	1.3	1.8	84	3.6	4.6	75
Zooplankton Concentration	96.8	153.3	81	56.0	63.3	73
Zooplankton Species Richness	3.3	2.3	81	2.5	2.4	73



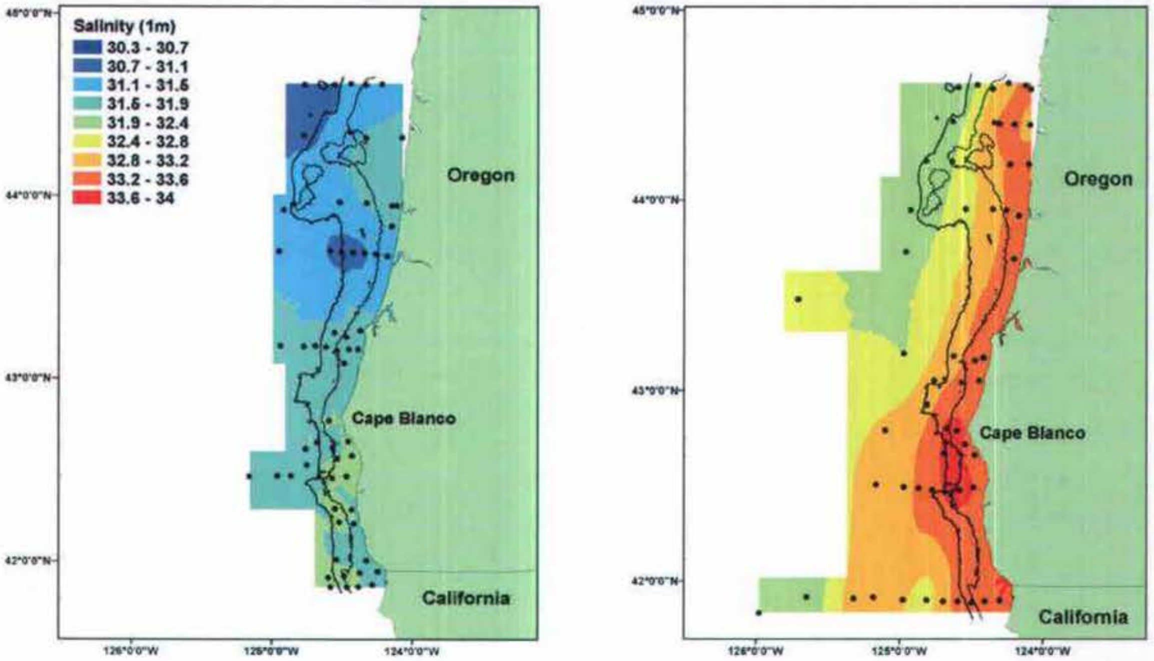
(a) June 2000

(b) August 2000

Figure 2.1. Kriging maps of sea surface temperature (°C) at 1m throughout the study region for: (a) June 2000 and (b) August 2000. Dots represent station locations where temperature data were collected. The solid contour represents the 200m isobath and the hatched contour represents the 100m isobath.

Table 2.2. Statistics and model parameters of the models fitted to the environmental and biological empirical semivariograms during the June and August 2000 cruises. Temperature was taken at 1 m depth in °C; Salinity was taken at 1 m depth and measured in psu; Chlorophyll concentration has units μg/l; Zooplankton concentration has units ml/100m^3; Zooplankton species richness is the number of species present at a particular station. C_0 is the nugget effect or y-intercept of the model; C_0+C is the sill or model asymptote; Major and Minor Ranges represent the range over which spatial dependence is apparent (measured in kilometers); Angle is the axis of rotation for the major axis for anisotropic models.

Spatial Process	**Month**	**Model**	**Nugget C_0**	**Sill C_0+C**	**C_0/C_0+C**	**Major Range**	**Minor Range**	**Major Angle**
Temperature	June 2000	Exponential	0.133	0.857	0.155	40.5 km	-	-
	Aug 2000	Spherical	0.459	6.405	0.072	148.9 km	142.2 km	359.6°
Salinity	June 2000	Exponential	0.341	0.688	0.495	306.0 km	-	-
	Aug 2000	Spherical	0.040	0.392	0.102	190.2 km	90.6 km	12.4°
Chlorophyll Concentration	June 2000	Exponential	0.123	0.736	0.167	69.1 km	-	-
	Aug 2000	Spherical	0.080	1.091	0.073	30.7 km	-	-
Zooplankton Concentration	June 2000	Exponential	0.265	1.623	0.163	49.6 km	-	-
	Aug 2000	Exponential	0.247	0.758	0.326	22.2 km	-	-
Zooplankton Species Richness	June 2000	Exponential	0.198	4.309	0.046	28.8 km	-	-
	Aug 2000	Exponential	0.054	0.271	0.199	72.8 km	-	-



(a) June 2000

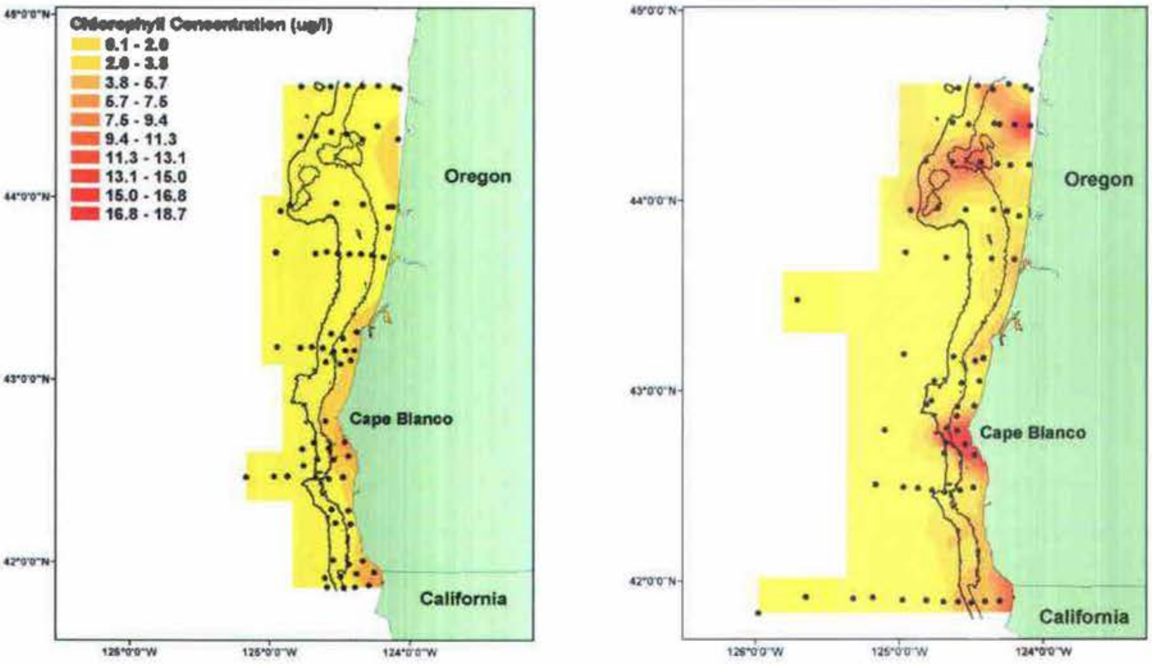
(b) August 2000

Figure 2.2. Kriging maps of sea surface salinity (psu) at 1m throughout the study region for: (a) June 2000 and (b) August 2000. Dots represent station locations where salinity data were collected. The solid contour represents the 200m isobath and the hatched contour represents the 100m isobath.

water temperatures in August were less than 10°C everywhere except immediately south of Cape Blanco and off Crescent City, CA (Figure 2.1). During August, the southernmost transect line was sampled further offshore than during June and resulted in the warmest recorded water temperatures. During both sampling periods, temperatures were generally coolest at the coast and warmest furthest offshore (Figure 2.1).

Salinity was significantly different among seasons (two sample t-test = -11.38, $p < 0.001$), being lower during June 2000 (Table 2.1). During June, values ranged from 28.87 to 32.77 and during August, values ranged from 31.79 to 33.94. In June, the spatial correlation of salinity was best fit by an exponential semivariogram model and the major range indicated a spatial dependence of 306 km (Table 2.2). Anisotropy was not detected; therefore an isotropic model was used. In August, the spatial correlation was best fit by a spherical semivariogram model. Directional influences were present in August with the axis of rotation for the major axis at 12.4° from North indicating the strongest gradient was generally across the shelf (Table 2.2; Figure 2.2). The small-scale spatial variation was moderately high in June ($C_0 = 0.341$) and extremely low in August ($C_0 = 0.040$). The larger small-scale spatial variation in June indicates that the variogram model explained a smaller portion of the variability compared to August. This is most likely due to spatial sources of variation at distances smaller than the sampling interval. Variation at scales smaller than the sampling distances typically appear as part of the nugget value. Nonetheless, the variogram did account for most of the variability and therefore was used. During both seasons, lower salinity values were apparent offshore in the northern portion of the study area (Figure 2.2). The highest salinity values during both cruises were observed nearshore in the southern region near Cape Blanco continuing to the south (Figure 2.2). A more pronounced gradient was observed during August 2000 with salinity decreasing from nearshore to offshore (Figure 2.2).

Chlorophyll concentration differed significantly between seasons (Wilcoxon Rank-Sum Test, $Z = -4.16$, $p < 0.001$) (Table 2.1). During June, values ranged from 0.11 to 10.29 μg/l and during August, values ranged from 0.07 to 18.70 μg/l. In June, the spatial correlation of chlorophyll concentration was best fit by an exponential semivariogram model and the major range indicated a spatial dependence of about 69 km (Table 2.2). Anisotropy was not detected; therefore an isotropic model was used. In August, the spatial correlation was best fit by a spherical semivariogram model. Again, anisotropy was not detected; therefore an isotropic model was used. The major range indicated a spatial dependence of approximately 30.7 km (Table 2.2). The small-scale spatial variation was low ($C_0 = 0.123$) in June and extremely low ($C_0 = 0.080$) in August. During both seasons, highest chlorophyll concentrations were observed nearshore (Figure 2.3). During June, highest values were observed very nearshore in three regions: to the north near Newport, OR, around Cape Blanco, and in the southernmost region near Crescent City, CA (Figure 2.3). During August, several patches of elevated chlorophyll concentration were observed. In the northern part of the study region, higher chlorophyll concentrations extended further offshore than were observed in June. Near Cape Blanco, very high chlorophyll concentrations (>14 μg/l) were observed very nearshore just south of the cape. High chlorophyll concentrations were also observed nearshore in the south around Crescent City (Figure 2.3).

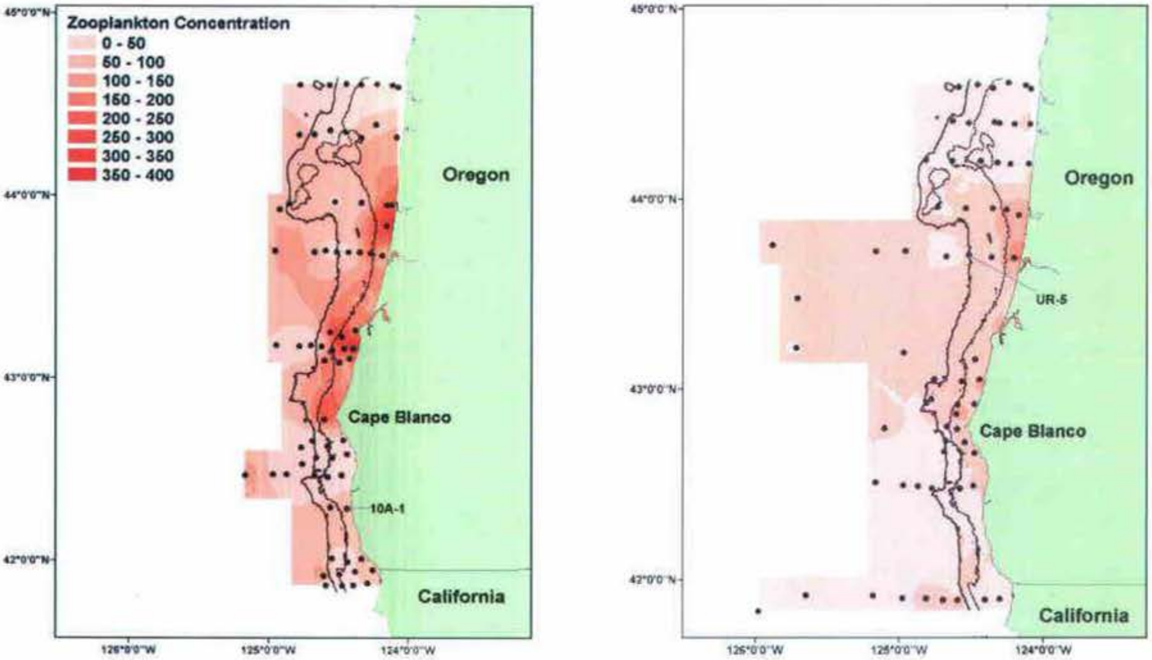


(a) June 2000 (b) August 2000

Figure 2.3. Kriging maps of chlorophyll concentration (μg/l) at 3m throughout the study region for: (a) June 2000 and (b) August 2000. Dots represent station locations where chlorophyll-*a* was estimated. The solid contour represents the 200m isobath and the hatched contour represents the 100m isobath.

Near-surface zooplankton concentrations did not differ significantly between seasons despite the higher absolute values observed during June (Wilcoxon Rank-Sum Test, Z = -0.01, p = 0.995) (Table 2.1). During June, values ranged from 4.6 to 987.8 ml/100 m^3 and during August, values ranged from 4.4 to 332.8 ml/100 m^3. In June and August, the spatial correlation of zooplankton concentrations best fit exponential semivariogram models and anisotropy was not detected; therefore isotropic models were used (Table 2.2). The major range indicated a spatial dependence of about 49.6 km in June and only 22.2 km in August. The small-scale spatial variation during both June and August was low (C_0 = 0.265 and C_0 = 0.247, respectively). Two very large concentrations were encountered during each cruise: (1) during June, station 10A-1 near the coast south of Cape Blanco had a concentration of 987.8 ml/100m^3, and (2) during August, station UR-5 on the shelf-break north of Cape Blanco had a concentration of 332.8 ml/100m^3. To reduce the influence of these extreme outliers, these stations were removed from the spatial analyses which improved the fit to the semivariogram models. Highest zooplankton concentrations were observed along the coast during both seasons (Figure 2.4). During June, with the exception of station 10A-1 south of Cape Blanco, larger values tended to occur north of Cape Blanco. During August, largest values were only observed north of Cape Blanco; however, surface zooplankton concentrations were more consistent throughout the entire region than in June. Zooplankton concentration values were consistently lower farther offshore during both seasons.

Although near-surface zooplankton species richness was higher in June, no significant difference was found between seasons (two sample t-test = 1.43, p = 0.15)

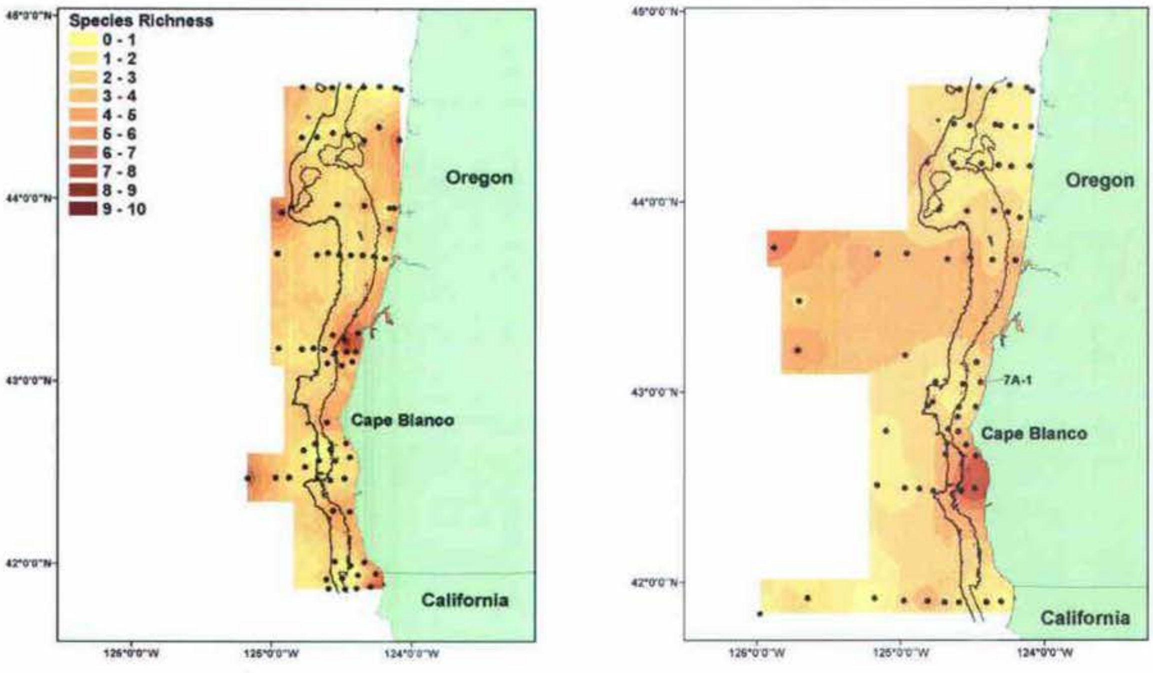


(a) June 2000

(b) August 2000

Figure 2.4. Kriging maps of surface zooplankton concentration (ml/100m^3) throughout the study region for: (a) June 2000 and (b) August 2000. Dots represent station locations. The solid contour represents the 200m isobath and the hatched contour represents the 100m isobath. During June and August, large zooplankton concentrations were collected at stations 10A-1 (987.8 ml/100m^3) and UR-5 (332.8 ml/100m^3), respectively.

(Table 2.1). Despite the lack of a significant seasonal difference in mean zooplankton species richness, the spatial patterns differed between seasons (Figure 2.5). During June, values ranged from 0 to 9 species per station and during August, values ranged from 0 to 15 species per station. In June, the spatial correlation of zooplankton species richness best fit an exponential semivariogram model and the major range indicated a spatial dependence of about 28.8 km (Table 2.2). Anisotropy was not detected; therefore an isotropic model was used. In August, the spatial correlation again best fit an exponential semivariogram model and the major range indicated a spatial dependence of about 72.8 km (Table 2.2). The small-scale spatial variation during both June and August was very low ($C_0 = 0.198$ and $C_0 = 0.054$, respectively). During June, species richness was usually highest near the coast and decreased offshore over the shelf, and in some locations increased again further offshore (Figure 2.5). The highest values were observed nearshore in patches where surface zooplankton concentration was also relatively high. Offshore, highest values occurred near the Heceta Bank region. In some areas no zooplankton greater than 5 mm were collected in the net resulting in patches of very low species richness within this size class. These low diversity regions were encountered relatively nearshore immediately south of Cape Blanco and further offshore north of Cape Blanco (Figure 2.5). During August, absolute species richness was higher (max = 15 species); however, this was the result of one extreme and one moderate outlier. At one station (Station 7A-1) located just north of Cape Blanco, 15 species were observed and at another station (Station RR-1) just south of Cape Blanco, 9 species were observed.



(a) June 2000

(b) August 2000

Figure 2.5. Kriging maps of surface zooplankton species richness throughout the study region for: (a) June 2000 and (b) August 2000. Dots represent station locations. The solid contour represents the 200m isobath and the hatched contour represents the 100m isobath. During August, a comparatively large number of species (15 species) were collected at station 7A-1.

To reduce the influence of the extreme outlier, Station 7A-1 was removed from the spatial analysis, however, the less extreme station (RR-1) remained in the analysis. The decision to leave station RR-1 in the analysis was made due to similar high values at neighboring stations and because leaving it out did not improve the fit to the semivariogram model whereas removing Station 7A-1 did. The patchiness of species richness observed in June was not as apparent in August with the exception of the relatively high values obtained nearshore and just south of Cape Blanco. In August, species richness was still highest near the coast but similar values were observed across the shelf and further offshore as well (Figure 2.5). Surface zooplankton species richness in general tended to be more diffuse in August than in June.

Taxonomic composition

A total of 85 taxa belonging to five phyla were identified from 158 neuston samples taken in June and August (Table 2.3). Fifty-three taxa were represented in 81 June samples, and 65 taxa were in 77 August samples. Three samples from June had no contents greater than 5 mm, and eight samples from August had no plankton measuring 5 mm or more. Only 18 taxa were present in any sample in densities greater than 10 ind./100m^3. Lists of the most common taxa for each cruise are given in Tables 2.4 and 2.5.

Polychaetes were present only in four samples taken in August. However, *Tomopteris septentrionalis* was present in high densities at the one station where it was caught. A second unidentified *Tomopteris* species was less abundant. Molluscs included

Table 2.3. Frequency of occurrence (FO), mean abundance (MA), and standard deviation (SD) of taxa from two cruises in 2000. Mean abundance is given as number of individuals/100m^3 for the tows in which those taxa occurred. Data in this table represent all stations sampled.

Species	June FO (n=81)	June MA	June SD	August FO (n=77)	August MA	August SD
ANNELIDA: Polychaeta						
Tomopteris septentrionalis	–	–	–	1	11.43	–
Tomopteris sp.	–	–	–	2	1.83	1.08
Nereis sp.	–	–	–	2	1.30	1.21
MOLLUSCA: Gastropoda						
Clio pyramidata	–	–	–	3	1.42	1.19
Clio sp.	–	–	–	3	2.25	0.93
Clionidae	1	0.47	–	–	–	–
Dendronotus sp.	–	–	–	1	5.20	–
Eolidacea	–	–	–	1	0.54	–
MOLLUSCA: Cephalopoda						
Chiroteuthis calyx	–	–	–	1	0.38	–
ARTHROPODA: Crustacea						
Copepoda						
Eucalanus sp.	–	–	–	1	0.49	–
Euchaeta sp.	–	–	–	2	1.26	1.25
Cirripedia						
Lepas sp.	1	1.56	–	2	2.97	3.41
Mysidacea						
Archaeomysis grebnitzkii	1	0.43	–	1	4.47	–
Neomysis kadiakensis	–	–	–	1	1.56	–
Alienacanthomysis macropsis	3	0.71	0.52	1	11.47	–
Isopoda						
Excirolana linguifrons	–	–	–	1	0.45	–
Idotea fewkesi	10	2.74	2.80	5	1.09	0.68
Idotea rufescens	–	–	–	2	1.03	0.83
Idotea resecata	1	0.43	–	–	–	–
Idotea wosnesenskii	1	0.40	–	2	0.76	0.45
Amphipoda						
Gammaridea						
Peramphithoe humeralis	1	0.47	–	4	2.76	2.73
Atylus tridens	3	0.40	0.03	18	2.66	4.19
Calliopius cf. columbianus	1	0.40	–	2	8.02	10.71
Eogammarus confervicolus	1	0.40	–	–	–	–
Allorchestes angustus	8	0.76	0.64	4	0.58	0.34

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Table 2.3 continued

Species	June			August		
	FO (n=81)	MA	SD	FO (n=77)	MA	SD
Hyale frequens	5	0.45	0.02	10	2.50	3.45
Microjassa sp.	–	–	–	1	0.46	–
Aruga oculata	–	–	–	1	0.45	–
Gnathopleustes simplex	1	0.46	–	–	–	–
Hyperiidea						
Hyperia medusarum	5	0.57	0.25	6	2.60	3.92
Hyperoche medusarum	22	1.48	1.28	28	1.77	1.94
Themisto pacifica	6	10.14	22.24	10	13.27	20.02
Primno brevidens	–	–	–	1	0.66	–
Lycaea pulex	25	11.35	45.29	–	–	–
Brachyscelus crusculum	1	0.69	–	–	–	–
Tryphana malmi	4	1.38	1.15	–	–	–
Vibilia australis	18	6.20	19.40	–	–	–
Paraphronima crassipes	–	–	–	1	0.44	–
Hyperiidea unidentified	2	0.41	0.01	1	0.38	–
Caprellidea						
Caprella incisa	–	–	–	1	10.40	–
Caprella ferrea	1	0.46	–	–	–	–
Caprellidea unidentified	–	–	–	1	0.54	–
Euphausiacea						
Euphausia pacifica	30	1.69	2.13	24	10.34	33.44
Thysanoessa inspinata	1	1.31	–	1	0.46	–
Thysanoessa spinifera	13	1.17	1.72	17	9.07	20.04
Decapoda						
Alpheidae	–	–	–	2	0.75	0.32
Hippolytidae	3	1.19	0.74	5	7.67	16.11
Crangon sp.	1	3.92	–	2	0.48	0.05
Cancer magister	34	14.48	29.27	13	16.97	31.04
Cancer oregonensis/productus	27	11.26	25.39	7	18.79	40.85
Pagurus sp.	1	0.43	–	1	0.52	–
Hemigrapsus nudus	1	0.40	–	–	–	–
ARTHROPODA: Insecta						
Odonata	–	–	–	1	0.51	–
Plecoptera	–	–	–	1	0.46	–
Hemiptera	1	0.40	–	3	0.46	0.07
Homoptera	1	0.40	–	1	0.46	–
Coleoptera	4	0.41	0.03	5	0.80	0.76
Neuroptera	8	1.01	0.92	–	–	–
Trichoptera	1	0.37	–	–	–	–
Lepidoptera	–	–	–	2	0.49	0.07

Continued on next page

Table 2.3 continued

		June			August	
Species	**FO** (n=81)	**MA**	**SD**	**FO** (n=77)	**MA**	**SD**
Diptera	12	0.86	0.71	3	0.52	0.06
Hymenoptera	1	0.37	–	3	0.68	0.35
Insecta unidentified	1	0.42	–	–	–	–
CHAETOGNATHA						
Sagitta minima	1	0.42	–	1	66.53	–
Sagitta elegans	1	108.91	–	7	1.22	1.77
Sagitta euneritica	–	–	–	3	36.54	61.98
Sagitta scrippsae	–	–	–	4	1.31	0.52
Chaetognatha unidentified	–	–	–	1	0.52	–
CHORDATA: Osteichthyes						
Clupea pallasi	–	–	–	9	0.68	0.43
Osmeridae	1	0.43	–	1	2.16	–
Lestidiops ringens	–	–	–	1	0.42	–
Tarletonbeania crenularis	1	0.69	–	5	4.56	3.40
Myctophidae	1	0.45	–	–	–	–
Cololabis saira	28	2.79	3.30	17	1.67	2.43
Sebastes alutus	–	–	–	1	1.08	–
Sebastes diploproa	–	–	–	3	4.66	1.37
Sebastes flavidus	1	0.69	–	–	–	–
Sebastes rufus	1	0.50	–	1	0.33	–
Sebastes zacentrus	–	–	–	4	1.79	1.72
Hexagrammos decagrammus	1	0.39	–	–	–	–
Clinocottus embryum	1	0.43	–	–	–	–
Hemilepidotus spinosus	1	0.47	–	–	–	–
Radulinus asprellus	1	0.47	–	–	–	–
Scorpaenichthys marmoratus	1	0.69	–	2	0.47	0.08
Psettichthys melanostictus	1	0.43	–	–	–	–
Fish unidentified	–	–	–	2	0.54	0.12

Table 2.4. The ten most abundant species in June 2000 by total abundance.

Species	**Total abundance (no./100m^3)**
Cancer magister	492.28
Cancer oregonensis/productus	303.93
Lycaea pulex	283.71
Vibilia australis	111.68
Sagitta elegans	108.91
Cololabis saira	78.21
Themisto pacifica	60.86
Euphausia pacifica	50.80
Hyperoche medusarum	32.59
Idotea fewkesi	27.43

Table 2.5. The ten most abundant species in August 2000 by total abundance.

Species	**Total abundance (no./100m^3)**
Euphausia pacifica	248.14
Cancer magister	220.59
Thysanoessa spinifera	154.16
Themisto pacifica	132.66
Cancer oregonensis/productus	131.56
Sagitta euneritica	109.62
Sagitta minima	66.53
Hyperoche medusarum	49.50
Atylus tridens	47.93
Hippolytidae	38.35

pteropods, nudibranchs, and a cephalopod and were uncommon in samples from either cruise.

Among the crustaceans, smaller copepods were common in many samples from both the June and August cruises, but only six individuals (*Eucalanus* sp. and *Euchaeta* sp.) from three stations in August measured more than 5 mm total length. The *Eucalanus* sp. was caught at one station during the day and the *Euchaeta* sp. were caught at two stations during early morning or night. Examples of smaller copepods include, among others, many *Epilabidocera* sp. and smaller members of the genera *Eucalanus* and *Euchaeta*.

Isopods were commonly collected but most were of the genus *Idotea*, with the species *Idotea fewkesi* being the most common in occurrence and abundance. Most isopods were found in samples taken within 5 miles of shore and were found in samples with macroalgae, seagrass, or other plant material and it is assumed that the isopods were attached to these substrata.

Amphipods were abundant in both cruises, and some species were among the most abundant taxa in the collections. Hyperiid amphipods were more abundant and occurred in more samples than gammarids or caprellids. Four species, *Lycaea pulex*, *Vibilia australis*, *Themisto pacifica*, and *Hyperoche medusarum*, were among the 10 most abundant taxa in June samples (Table 2.4). Hyperiid diversity and abundance decreased in August. *Themisto pacifica* and *Hyperoche medusarum* were the most abundant hyperiids in August samples and among the dominant taxa for the cruise (Table 2.5). Gammarid amphipods occurred more frequently and were more abundant in August than in June. Although no gammarid species was present in 10% of samples from June, two species, *Atylus tridens* and *Hyale frequens*, occurred in more than 10% of samples from August and *Atylus tridens* was the ninth most abundant taxon in August. Caprellid amphipods were present in only three samples and were associated with macroalgae and seagrass.

Three species of euphausiids were caught in June and August cruises. *Euphausia pacifica* was common in samples from June and August, and was the dominant species in August. *Thysanoessa spinifera* was found in more than 15% of the samples from both cruises, and was the third most abundant species in August. A third species, *Thysanoessa inspinata*, was caught at one station in each cruise and was not abundant. The increase in euphausiid abundance from June to August is a result of the increase in younger stages of *Euphausia pacifica* and *Thysanoessa spinifera.* All *Euphausia pacifica* and most *Thysanoessa spinifera* in June were adults. In August, *E. pacifica* juveniles were more abundant than furcilia and adults. *T. spinifera* furcilia were more common than juveniles and adults in August. The standard deviations are larger in August for both *E. pacifica* and *T. spinifera* which may be due to clumped distribution of the younger stages.

Decapod larvae were present in 60% of all samples, especially in the June cruises (80% of samples). Frequency of occurrence and abundance of decapods decreased from June to August due to the decrease in occurrence of *Cancer* crabs, which were the most common decapod taxa. *Cancer* species made up over 50% (by number) of the plankton over 5 mm in June and over 25% in August. *Cancer magister* was the most abundant species in June and the second most abundant species in August. All *Cancer magister* were megalopae except one late-stage zoea in June. *Cancer oregonensis/productus* (all megalopae) was the second most abundant taxon in June and the fifth most abundant taxon in August. Hippolytid larvae were the tenth most abundant taxon in the August cruise, mostly due to a large catch of 70 individuals at one nearshore station in the early morning.

Several insect orders were represented in samples from both cruises. Because only adults were found and most stations where insects were present were within 5 km of land, it is likely that these individuals were blown offshore. No taxa were very abundant, although the order Diptera was represented in 14% of the samples from June. Other more common insect orders represented included Coleoptera, Hymenoptera, and Neuroptera.

Although chaetognaths were not present at many stations, three species were among the most abundant taxa. All identified chaetognaths in the neuston samples were of the genus *Sagitta*. *Sagitta elegans* was the fifth most abundant species in June. This species was present at only one station nearshore, but was represented by 304 individuals. *S. euneritica* and *S. minima* were the sixth and seventh most abundant taxa in August. *Sagitta euneritica* was present in low numbers at two stations and by over 200 specimens at one station. This species has not previously been reported from plankton samples in northern California and Oregon, but this may be a result of misidentification of individuals as *S. elegans*, as it can be similar in appearance (M. Terazaki, Ocean Research Institute, Tokyo, pers. comm.).

Fish species collected by the surface tows during the cruises were diverse, but generally not abundant. Fewer species were present in August than in June, but the species that were present in August were taken more frequently. Only *Cololabis saira* occurred frequently and in relatively large numbers, and was one of the dominant taxa collected in June. *Cololabis saira* was caught frequently during day and twilight/night hauls. Other frequently encountered fish were *Clupea pallasi*, *Sebastes* spp., and *Tarletonbeania crenularis*.

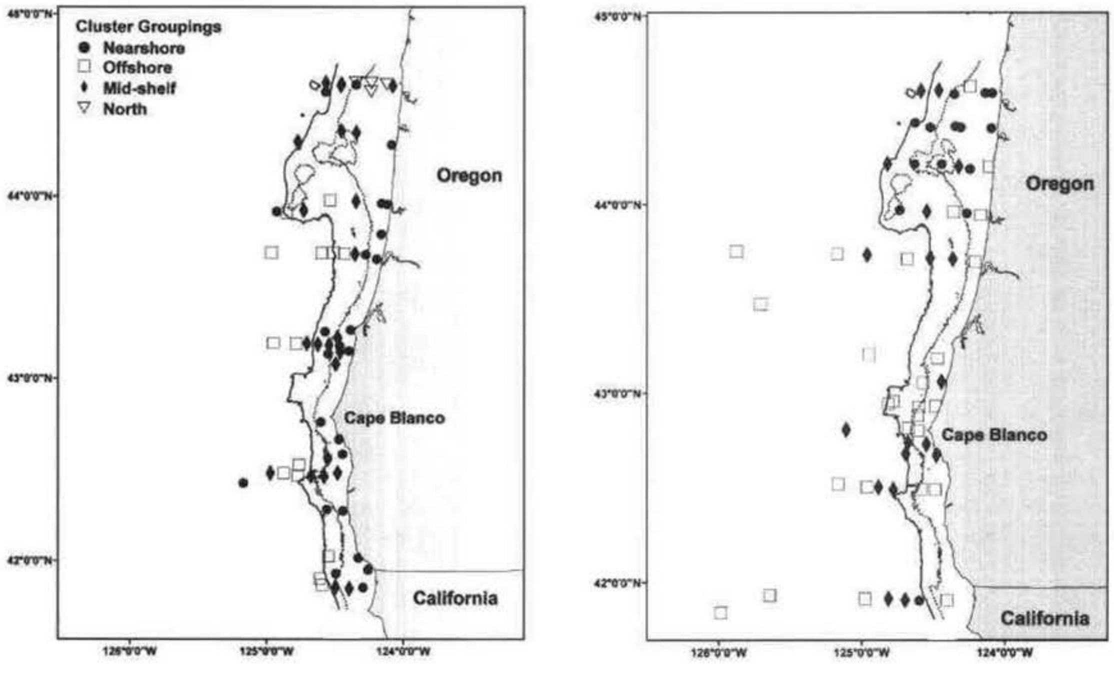
Cluster analysis

Cluster analysis of the June community data provided a dendogram containing one likely meaningful cutoff level with 4 cluster groups (Table 2.6, cutoff level 2). One cutoff level below and above the scale of cutoff level 2 was also investigated to determine if the optimum number of clusters was chosen. Results from MRPP analysis found high within group agreement (A) at all three cutoff levels (Table 2.6), although level 2 was the most biologically significant. In community ecology, values for A are commonly below 0.1, so an $A > 0.3$ is determined to be high (McCune and Grace, 2002). Level 2 shows a distinct cross-shelf zonation pattern with a nearshore, intermediate mid-shelf, and offshore group (Figure 2.6). A fourth group was also found representing a north-group (Figure 2.6). Indicator Species Analysis of the four groups within cutoff level 2 showed significant species associations for all four groups (Table 2.7).

The August community data resulted in less clear distinctions of groups and their association with shelf zonation (Figure 2.6). Cutoff level 2, containing 3 groups, was selected and compared to lower and upper dendogram scale levels (levels 1 and 3). Results from MRPP analysis found high within group agreement at cutoff levels 1 and 2,

Table 2.6. Multiresponse permutation procedure (MRPP) results comparing the different number of cluster groups and information remaining for June and August 2000 surface zooplankton collections.

Cutoff level	Number of groups	Information remaining (%)	Test statistic	Within-group agreement	p-value
June					
1	5	27	-25.87	0.61	<0.0001
2	4	16	-26.77	0.54	<0.0001
3	3	10	-26.87	0.43	<0.0001
August					
1	4	20	-21.78	0.45	<0.0001
2	3	11	-21.91	0.36	<0.0001
3	2	0	-18.36	0.21	<0.0001



(a) June 2000

(b) August 2000

Figure 2.6. Locations of station cluster groupings for the (a) June 2000 and (b) August 2000 cruises based on surface zooplankton composition. The solid contour represents the 200m isobath and the hatched contour represents the 100m isobath.

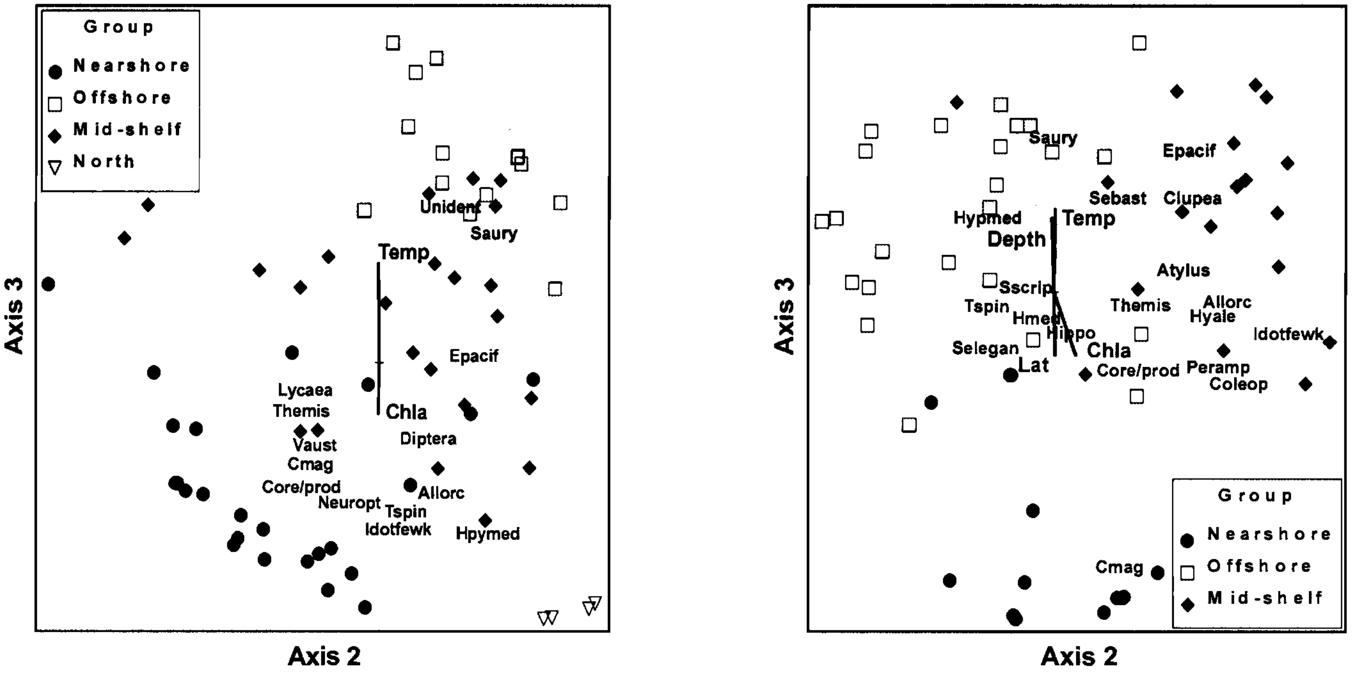
Table 2.7. Results of Indicator Species Analysis from the level 2 cutoff point showing species with significantly high indicator values and their associated group membership for June and August 2000 zooplankton samples. Values for Groups are as follows: 1 = nearshore, 2 = offshore, 3 = mid-shelf, and 4 = north.

Species	Indicator value	*p*-value	Group
June			
Cancer magister	86.1	<0.001	1
Cancer oregonensis/productus	89.7	<0.001	1
Vibilia australis	44.6	0.041	1
Cololabis saira	77.6	<0.001	2
Euphausia pacifica	84.7	<0.001	3
Hyperoche medusarum	81.0	<0.001	4
August			
Cancer magister	78.4	<0.001	1
Cololabis saira	32.2	0.009	2
Hyperoche medusarum	69.7	<0.001	2
Atylus tridens	40.3	0.007	3
Clupea pallasi	30.4	0.004	3
Euphausia pacifica	56.6	<0.001	3
Hyale frequens	37.2	0.004	3
Idotea fewkesi	27.8	<0.001	3
Sebastes sp.	22.2	0.009	3

and moderate within group agreement for cutoff level 3 (Table 2.6). In this instance, cutoff level 2 was determined to be more biologically significant in terms of geographic distribution. For grouping level 2, distribution of cluster groups showed nearshore, mid-shelf, and offshore distributions, with mid-shelf and offshore cluster groups having similar temperature and depth characteristics but differed somewhat relative to the chlorophyll concentration present (Figure 2.6). Indicator Species Analysis of the level 2 cluster groups indicated distinct species for all three cluster groups (Table 2.7).

Ordination

Non-metric multidimensional scaling (NMS) of the June community data confirmed that the a-priori cluster groups from cutoff level 2 were distinct in ordination space (Figure 2.7a). The 3-dimensional solution was able to explain 76.3% of the variation between original and ordination space (stress = 15.69). Axes 2 and 3 collectively represented 60.6% of the variation and are displayed in Figure 2.7a. Of the environmental parameters measured, temperature and chlorophyll concentration exhibited moderate levels of correlation ($r^2 = 0.34$ and 0.17, respectively, along axis 3). Marginal contribution came from depth ($r^2 = 0.12$, axis 3) and latitude ($r^2 = 0.09$, axis 3). Temperature and depth were positively correlated with axis 3, whereas chlorophyll concentration and latitude were negatively correlated. Species centroid distributions in ordination space were more aggregated toward nearshore and mid-shelf sample station groups (Figure 2.7a). Abundances of four species were found to correlate moderately with r = -0.56, respectively, axis 3 ordination scores) characteristic of the nearshore group. The fourth species, *Cololabis saira*, was more abundant in warmer



(a) June 2000

(b) August 2000

Figure 2.7. Ordination plots of stations in species space from a 3-dimensional solution for: (a) June 2000 and (b) August 2000. Most significant vectors shown denote temperature (Temp), depth (Depth), chlorophyll concentration (Chla), and latitude (Lat). Species locations are based on species-specific centroids, denoted by the following: *Allorchestes angustus* (Allorc), *Atylus tridens* (Atylus), *Cancer magister* (Cmag), *Cancer oregonensis/productus* (Core/prod), *Clupea pallasi* (Clupea), Coleoptera (Coleop), *Cololabis saria* (Saury), Diptera (Diptera), *Euphausia pacifica* (Epacif), Hippolytidae (Hippo), *Hyale frequens* (Hyale), *Hyperia medusarum* (Hmed), *Hyperoche medusarum* (Hypmed), *Idotea fewkesi* (Idotfewk), *Lycaea pulex* (Lycaea), Neuroptera (Neuropt), *Peramphithoe humeralis* (Peramp), *Sagitta elegans* (Selegan), *Sagitta scrippsae* (Sscrip), *Sebastes* spp. (Sebast), *Themisto pacifica* (Themis), *Thysanoessa spinifera* (Tspin), Unidentified (Unident), *Vibilia australis* (Vaust).

water with lower chlorophyll concentrations characteristic of the mid-shelf and offshore groups (r = 0.48, axis 3 ordination scores). However, *C. saira* had a polymodal distribution along axis 3, therefore, using a linear correlation coefficient between species abundance and ordination scores are likely misleading given the non-linear response. Nevertheless, abundance tended to be higher in warmer temperatures and lower chlorophyll concentrations.

Non-metric multidimensional scaling of the August community data confirmed that the a-priori cluster groups from cutoff level 2 were distinct in ordination space (Figure 2.7b). The 3-dimensional solution was able to explain 68.6% of the variation between original and ordination space (stress = 17.00). Axes 2 and 3 collectively represented 56.9% of the variation and are displayed in Figure 2.7b. Of the environmental parameters measured, temperature, depth, chlorophyll concentration, and latitude exhibited moderate levels of correlation (r^2 = 0.29, 0.26, 0.22, and 0.22, respectively, along axis 3). Temperature and depth were positively correlated with axis 3 whereas chlorophyll concentration and latitude were negatively correlated. Temperature and depth increased from nearshore to midshelf/offshore groups. Species centroid distributions in ordination space were more aggregated toward mid-shelf and offshore sample station groups with the exception of *C. magister* which was found within the nearshore cluster group (Figure 2.7b). Abundances of three species were found to correlate moderately with ordination scores from axis 3. As in June, *C. magister* was more abundant in cooler temperatures and higher chlorophyll concentrations (r = -0.65). *Euphausia pacifica* was more abundant in warmer temperatures and lower chlorophyll (r = 0.46). As in June, the third species *C. saira*, was more abundant in warmer water with lower chlorophyll concentrations, again characteristic of the mid-shelf and offshore groups (r = 0.43).

Discussion

Temperature varied markedly between June and August 2000 due to the development of the upwelling season (Figure 2.1). Along the Oregon coast, the upwelling season extends from May to September; however, during this time upwelling is often sporadic, occurring in events lasting from a few days to a few weeks (Huyer, 1976; Small and Menzies, 1981; Landry et al., 1989). During June, strong upwelling conditions were not yet present (Barth et al., 2005), thus warmer water remained near the coast. However, by August, substantial strong upwelling had occurred and produced low surface temperatures all along the coast throughout most of the study region (Figure 2.1).

Salinity also varied markedly according to the seasonal flux of freshwater from the Columbia River to the north (Figure 2.2). The Columbia River releases significant amounts of freshwater into the marine environment off Oregon. The freshwater plume is observable as a surface lens of low-salinity water that is carried south with the prevailing currents during the summer resulting in the input of low salinity water to the study area (Cross and Small, 1967; Landry et al., 1989). During June, the greater input of freshwater to the study area was evident from overall lower levels of salinity throughout the entire study area which led to less of a salinity gradient, as was observed in August. In addition, the lack of strong upwelling kept nearshore salinity levels low. During

August, salinity showed a clear spatial gradient from nearshore to offshore with higher salinity observed near the coast and decreasing offshore.

Chlorophyll concentrations varied seasonally coincident with the upwelling activity. Upwelling brings colder, nutrient-rich water to the surface, availing phytoplankton of abundant necessary nutrients for growth (Lalli and Parsons, 1997). The increased availability of nutrients, along with the increased availability of light at this time of year, stimulates increased primary production and increased chlorophyll concentrations (Landry et al., 1989). During June, since strong seasonal upwelling had not yet occurred, chlorophyll concentrations tended to be lower overall with only a few nearshore locations having elevated chlorophyll concentrations. However, by August upwelling was much stronger, and patches of elevated chlorophyll concentration became evident. In fact, the range over which spatial dependence was apparent for chlorophyll concentration was much less during August than during June confirming the presence of patches. The highest concentrations of chlorophyll were found in the north extending offshore with an additional patch over the Heceta Bank region, and in the southern part of the study area around Cape Blanco and Crescent City. In all areas with higher chlorophyll concentrations, elevated levels extended offshore further during August than during June, presumably as the upwelled water was displaced further offshore.

The analysis of temperature, salinity, and chlorophyll concentration using semivariograms determined varying spatial dependence along the Oregon and northern California coast (Table 2.2). Different degrees of spatial correlation described ranges of dependence from 41 km to 149 km for temperature, 91 km to 306 km for salinity, and 31 km to 69 km for chlorophyll concentration, which provides an idea of patch size for each variable. During June, salinity showed a fairly weak degree of autocorrelation with an exceptionally large range over which correlation was evident (major range of 306 km). This is the result of the gradual change in salinity values from the southeast to the northwest of the study area during this time of year.

Near-surface zooplankton concentrations tended to mimic the chlorophyll concentration pattern in June with higher concentrations of each nearshore, most likely because the zooplankton were taking advantage of the increased food supply. However, during August the patterns differed with low zooplankton concentrations in the north coincident with relatively high levels of chlorophyll. The highest zooplankton concentrations were encountered north of Cape Blanco and further offshore whereas these areas were represented by having only moderate chlorophyll concentrations. The degrees of spatial correlation describing the major ranges of dependence for the zooplankton concentrations between seasons were comparable, indicating the patch sizes were similar between the two seasons along the major axis (Table 2.2). The relatively high nugget value and lower sill for the semivariogram model in August indicates that a smaller amount of correlation was present in the data resulting in a loss of predictive power. Nonetheless, in August, higher zooplankton concentrations were directed offshore, whereas in June, zooplankton were concentrated more along shore (Table 2.2; Figure 2.4). This is most likely due to the lower degree of upwelling occurring during June such that organisms in the surface water were being transported in a more southerly direction along the coast with the prevailing currents. However, during August upwelling appeared stronger which most likely resulted in the net transport of organisms more offshore than was observed in June. Hydrographic surveys, drifter studies, and satellite observations of sea surface temperature and chlorophyll conducted concurrently with our survey indicate numerous meanders pushing surface water offshore during August (Barth et al., 2005).

Zooplankton species richness was highest along the coast in regions where chlorophyll concentration and zooplankton biomass were also relatively high. This was particularly evident during June. With the increase in light availability and the sporadic upwelling occurring during June, both primary and secondary production typically begin to increase. Many species take advantage of the increasingly abundant food resources early in the productive season. Later (August), some of the near-surface meroplankton we collected, especially the larval fish and decapod larvae, have settled to the bottom as juveniles in late summer.

Near-surface zooplankton concentration was relatively low compared to subsurface estimates and previous neuston collections, which may be due in part to the fact that our collections were taken during the day. In a previous study conducted along a transect off Newport, OR, Shenker (1988) collected most (> 90%) of the fish larvae and juveniles in his neuston collections at night. The only species in Shenker's study that did not show any day/night differences in catch was Pacific saury (*Cololabis saira*), a dominant species in our collections. Similar to what Shenker (1988) found, we found that Dungeness crab larvae (*Cancer magister*) were the dominant neustonic species off Oregon.

Our results are most comparable to the collections off of Washington and Oregon conducted during June through September, 1984 (Brodeur, 1989). Both collections had many species in common (>50% of taxa) despite some differences in geographic coverage of sampling, with many of the dominant species in June 1984 occurring also in our June sampling (Brodeur et al., 1987). Among the most notable differences in the present study were the low number of insects collected and the complete absence of the dominant fish species (northern ronquil, *Ronquilus jordani*) collected in the earlier study. The dominance of insects in 1984 apparently resulted from unusual wind conditions that transported many terrestrial insects to the coastal environment (Brodeur, 1989).

Cluster analyses for both June and August cruises provided statistically and biologically meaningful results. Onshore and offshore groups were consistent between the two sampling periods, and were in agreement with general knowledge of the hydrography off of Oregon and Northern California. During June the transition toward strong sustained levels of upwelling had not yet occurred. This would explain the strong delineation of the different shelf-related cluster groups. Cross-shelf delineation was less obvious in August because sustained levels of upwelling had caused substantial transport from nearshore to offshore. Another interesting feature was the persistence of an in-shore intrusion along the Umpqua River transect (43.7 – 44°N) by an offshore cluster group. This transect was influenced by an eddy that pushed water shoreward in the lee of Heceta Bank (Barth et al., 2005). Plots of sea surface temperature from the two cruises confirm that this eddy was present at the time of sampling and may have influenced the geographic distribution of the offshore cluster groups. Similar cluster patterns were evident in the more mobile nektonic fauna collected in surface trawls during these cruises (Brodeur et al., 2004).

Results from NMS confirm cross-shelf zonation of certain zooplankton species within the neuston off Oregon and Northern California. Temperature was the most consistent environmental gradient in explaining zooplankton distribution. Depth was nearly as explanatory as temperature for the August cruise, but this was due to the high correlation between depth and temperature (both increasing offshore). More indicative of specific water masses, it is understandable why temperature is the most consistent environmental measure of onshore/offshore groups. A relatively high correlation value for the latitude variable during August is likely due to the presence of the abundant Dungeness crab (*Cancer magister*) larvae to the north.

Since the prey field of many commercially important fish including salmon is comprised of near-surface zooplankton (Brodeur, 1989), understanding how the prey field changes and identifying the factors involved are important for understanding changes in fish assemblages (Brodeur et al., 2004). Furthermore, changes in zooplankton species composition are known to be significant indicators of environmental disturbance (Attayde and Bozelli, 1998). In fact, changes in species composition of zooplankton assemblages are considered to be among the earliest responses in aquatic ecosystems to environmental stress (Schindler, 1987). Early identification of perturbations in the marine environment may facilitate recovery or allow for better-informed management decisions, which is particularly important to commercial fisheries.

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IDENTIFYING AND CHARACTERIZING BIOLOGICAL HOTSPOTS IN THE NORTHERN CALIFORNIA CURRENT

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Abstract

Understanding how marine animals utilize their environment and identifying important habitats are crucial for understanding how marine ecosystems function. The goal of the present study is to identify biologically rich areas within the northern California Current and to determine the environmental characteristics occurring within these areas. We analyzed how surface nekton are distributed in the northern California Current, not only in space and time but also with reference to species assemblages, habitat characteristics, and environmental factors. Sampling was conducted during June and August of 2000 and 2002 as part of the U.S. GLOBEC mesoscale surveys from Newport, Oregon in the north to Crescent City, California in the south. A geostatistical approach was used to create surfaces to be used in a GIS to determine the presence or absence of biological hotspots throughout the region. Two biological hotspots were identified and determined to persist in space and time, yet differed with respect to biological and physical features and in the amount of area covered. We used indicator species analyses (ISA) and nonmetric multidimensional scaling (NMS) to explore patterns in community structure. Results indicate that although the locations of the biological hotspots persisted over the course of the study, the habitat characteristics and nekton community composition within each hotspot varied over time. The most consistent environmental parameters explaining the distributions were sea-surface

temperature, salinity, and density, indicating the likely structuring mechanism of the hotspots is related to the flow through the region and differing patterns of circulation.

Introduction

Traditionally, studies of fish in the marine environment have been conducted and analyzed by examining single species, which tend to be the most economically valuable species. The justification of this approach is the increased cost of sampling in the ocean realm compared to that of terrestrial systems. As such, our understanding of diversity and species assemblages that inhabit marine ecosystems tends to decrease with distance from shore (Cailliet, 1997). Nevertheless, changes in species composition have the potential to affect an entire ecosystem. In fact, the exclusion of certain species from communities often results in a rearrangement of the way in which abundances are partitioned among species, leading to changes in community structure and to further changes in the diversity within the system (McGowan, 1992). Alternatively, increasing species richness is thought to lead to more efficient use of resources and a greater capacity to ensure ecosystem stability under disturbance or ecosystem change (Tilman, 1996; Naeem and Li, 1997; Patrick, 1997; Duarte, 2000; Loreau et al., 2001). Biodiversity, in general, is a valuable indicator of ecological change, as stress in biological communities typically results in a reduction in biodiversity (Warwick and Clarke, 1995; Lovejoy, 1997). For these reasons, marine nekton studies are shifting to a more ecosystem-based approach in which communities are studied as opposed to the single-species approach of the past (e.g., Beamish and Mahnken, 1999).

The ocean is a heterogeneous environment with marine resources tending to be patchily distributed (Steele, 1976; Mackas and Boyd, 1979). As such, abundances of marine organisms tend to be higher in localized areas. The identification of these marine, biological hotspots is a growing area of research (Malakoff, 2004). Within terrestrial and coral reef systems, biological hotspots have traditionally been defined in terms of biodiversity (Myers, 1997; Hughes et al., 2002). In contrast, in pelagic systems, biological hotspots are typically defined as areas of high chlorophyll concentration (Valavanis et al., 2004). In the present paper, we define biological hotspots in terms of nekton community characteristics such as species richness, abundance, and biomass.

The California Current is a dynamic and highly productive ecosystem, characterized by substantial spatial and temporal variability. This system has undergone dramatic shifts in abundance and species composition at both the lower and higher trophic levels (Roemmich and McGowan, 1995; Emmett and Brodeur, 2000; Brodeur et al., 2003). Ocean characteristics are known to vary spatially and temporally. For example, northwest sea-surface temperatures had shown a strong warming trend since 1977 (Emmett and Brodeur, 2000), with a subsequent decline in recent years. In addition, recently there have been reports of the intrusion of cold, subarctic Pacific waters into the California Current which has greatly affected the entire ecosystem and led to anoxic events in the bottom water (Huyer, 2003; Wheeler et al., 2003). However, the causes of the ecosystem shifts and the association with oceanographic conditions are not well understood. The identification of persistent and therefore less variable, localized areas of biological activity within the larger region would be beneficial for furthering our understanding of how this system functions.

Localized biological hotspots are potentially important for migratory species as potential foraging sites, and would therefore be most advantageous if their locations were predictable in time and space. In addition, biological hotspots are likely important to endemic species as nursery areas, particularly those associated with retention features. These areas are also of particular interest as potential protected areas depending on the management goals of the areas. Marine protected areas (MPAs) have become increasingly popular tools to counter modern threats to marine biodiversity and the sustainability of fisheries (Bohnsack, 1993; Sobel, 1993; Agardy, 1994). There has been an increasing awareness of the need for protecting pelagic zones of predictable high productivity, which may serve as critical feeding habitats for higher trophic level predators. However, in order to better design MPAs, it is necessary to understand if and how community composition changes over time (seasonally and annually) and space within biological hotspots.

In the current paper, we describe a method to examine surface nekton community dynamics in the northern California Current in relation to habitat characteristics. A primary goal of the current study is to address how nektonic communities are distributed in the near surface environment. Specifically we examine whether these pelagic communities are distributed uniformly, randomly, or clumped within the region under study and whether the patterns persist through time. Three community characteristics are examined to determine the spatial structure within this environment: nekton species richness, total nekton density, and nekton biomass. Additionally, we examine how community composition within these areas varies over time relative to habitat conditions.

Methods

Field sampling

Sampling was conducted at each trawling station as part of a mesoscale and fine-scale sampling study within the U.S. GLOBEC Northeast Pacific Program (Batchelder et al., 2002). Samples were collected over four time periods to explore seasonal and interannual patterns of community dynamics: during early summer (29 May to 11 June, 2000 and 1 June to 18 June, 2002 (hereafter called June 2000 and June 2002 cruises, respectively) and during late summer (29 July to 12 August, 2000 and 1 August to 17 August, 2002 (hereafter called August 2000 and August 2002 cruises, respectively). During both years, sampling was conducted from chartered fishing vessels, the F/V *Sea Eagle* in 2000 and the F/V *Frosti* in 2002. The sampling area extended from Newport off central Oregon (latitude 44° 40' N) to Crescent City in northern California (approximately 42° N). Stations were sampled along five GLOBEC designated transects located 1, 5, 10, 15, 20, 25, and 30 nautical miles from shore and at fine-scale sampling stations in areas of particular physical and/or biological interest (e.g., areas associated with fronts or eddies). Most collections took place during daytime but occasionally tows were made during twilight or nighttime (June 2000, n = 84; Aug 2000, n = 75; June 2002, n = 90; Aug 2002, n = 94). The spatial and community analyses included in this paper were limited to collections made during daylight hours to avoid any changes in the day/night community structure.

At each station, nekton collections were made with a Nordic 264 rope trawl (Nor'Eastern Trawl Systems, Inc., Bainbridge Island, WA) towed in the surface layer for 30 minutes at a speed of 6 km/h (see Brodeur et al. (2004) for additional sampling details). Nekton abundance was then standardized for differences in effort between tows based on the volume of water filtered per trawl. Even though the volume of water sampled is approximately the same at each station, to ensure that observed values of nekton species richness were not confounded by slight variations in the volumes of water sampled, we used species richness values obtained only from volumes of water within two standard deviations of the mean volume sampled and then tested for correlations between sample volume and species richness to ensure that no relationship existed.

Immediately prior to setting the trawl, the physical and biological environment was sampled at each station. Salinity and temperature were measured at each station using a Seabird SBE 19 Seacat profiler CTD (Conductivity, Temperature, Depth) profiler to depths of 100 m or to within 10 m of the bottom. In addition, water from 3 m below the surface was collected with a 1-l Niskin water sampler for chlorophyll analysis. The near-surface zooplankton were sampled at each station using a neuston net measuring 0.3 m by 1.0 m in the mouth with 335-μm mesh towed for five minutes at 3 km/hr out of the wake of the vessel. Additional details on the sampling and analyses of the neuston tows are available in Reese et al. (2005). Occasionally, sampling of each variable was not possible due to equipment malfunction or poor weather conditions.

Biomass calculations

In order to obtain total nekton biomass estimates, the weight of each fish was either obtained at sea or determined from a length-weight regression for that species (Ricker, 1975) using the length (L) and weight (W) relationship expressed by the equation:

$$W = aL^b$$

For fish that were not weighed at sea, individual fish weights were obtained either by calculating a length-weight regression using field data or by acquiring length-weight regressions from the literature. Once individual weights were obtained, the total weight for each species was calculated for each station. The total nekton biomass estimate for each station was calculated by summing the weights for each species at each station and then standardized for differences in effort between tows.

Environmental data analysis

Differences in temperature, salinity, density, and zooplankton biovolume were compared between cruises using a Kruskal-Wallis test (Zar, 1996). A non-parametric test was chosen because assumptions of normality and homoscedasticity were not met. When significant differences were found, Mann-Whitney *U* tests were performed to compare between the different cruises. The significance level associated with the test was adjusted because more than one test was carried out (Shott, 1991). To obtain an overall significance level of 0.05, a Bonferroni-adjusted significance level of $0.05/4 = 0.0125$ for each Mann-Whitney test was used. Differences in chlorophyll concentration, nekton species richness, density, and biomass were compared with a 1-way ANOVA, following previous confirmation of normality and homoscedasticity assumptions. Data were log transformed when necessary to prevent violations of normality and homoscedasticity. Where significant differences were found, a multiple comparison test was performed using the Tukey Honestly Significant Difference (HSD) test to identify differences between means. For these analyses, alpha was set at 0.05.

Spatial analysis

To identify spatial patterns of distribution and, thus identify hotspot regions, geostatistical modeling techniques were employed. Geostatistics can be a powerful tool for spatial analyses, especially in a patchy environment. The first step in the analysis is to calculate the empirical semivariogram. The semivariogram is a geostatistical procedure in which variables tend to be more similar in value the closer they are geographically. Each spatial process consisted of observations measured at a location x, where x is station location defined by latitude and longitude in a 2-dimensional space for each cruise. It was assumed that: (1) the spatial distribution of each process was stable throughout the period of each cruise (approximately 2 weeks), and (2) the observations and spatial processes are the result of random processes (Johnston et al., 2001). The intrinsic stationarity assumption was examined with semivariance data clouds in which the variance of the difference between two locations is the same between any two points that are at similar distances and direction (Johnston et al., 2001). Two types of directional components can affect the surface predictions: global trends and anisotropy (Johnston et al., 2001). Global trends are dominant processes that affect all measurements in a deterministic manner and can result from such things as prevailing winds or currents. Once identified, global trends may be removed from the analysis by detrending (Johnston et al., 2001). Anisotropy differs from global trends in that the cause of the anisotropy in the semivariogram is not usually known, so it is alternatively modeled as random error (Johnston et al., 2001). Anisotropy is simply a characteristic of a random process where autocorrelation changes with both the distance and direction between two locations resulting in higher autocorrelation in one direction than in another. Directional influences were therefore examined for each variable and incorporated into the analyses when present.

Data were normalized with a log transformation when necessary to prevent violations of normality and homoscedasticity. Large outliers result in an increased nugget effect which consequently results in higher predicted values with higher uncertainty (Chiles and Delfiner, 1999). Chiles and Delfiner (1999) suggest a reasonable compromise in handling outliers such that the largest outlier values are reduced to the value of the upper limit of the range not including the outlier. Empirical semivariograms $\{\gamma(h)\}$ were estimated by pooling pairs of observations using the following equation given by Matheron (1971):

$$\gamma(h) = \frac{\sum_{i=1}^{N_h} \{Z(x_i + h) - Z(x_i)\}^2}{2N(h)}$$

where $Z(x_i)$ is the value of the variable at location x_i, $Z(x_i + h)$ is the value separated from x_i by distance h (measured in meters), and $N(h)$ is the number of pairs of observations separated by distance h. Although a small number of stations were sampled more than once, only one sampling from each station was used in the analyses which were those that minimized the time between sampling other nearby stations. Exponential and spherical theoretical models were fit to the empirical semivariograms to estimate the semivariogram values for each distance within the range of observations (Cressie, 1993). The following parameters were estimated based on the resulting models: (1) the nugget effect (C_0), which represents independent error, measurement error, and/or variation at distances less than the sample spacing in the dataset; (2) the sill ($C_0 + C$), which represents the asymptotic value of semivariance; and (3) the range, which indicates the maximum distance over which autocorrelation exists. When anisotropy was encountered, the range over which autocorrelation was present consisted of a major range (the length of the longer axis to reach the sill) and a minor range (the length of the shorter axis to reach the sill). With anisotropy, the angle of rotation from north of the line that forms the major range was a fourth parameter estimated.

Expected values of the variables were estimated for each cruise by kriging. Kriging forms weights from surrounding measured values to predict values at unmeasured locations such that the closest measured values have the most influence (Johnston et al., 2001). The weights of each measured value are derived from the modeled semivariogram that characterizes the spatial structure of the data. The predictor is then formed as the weighted sum of the data such that:

$$\hat{Z}(X_0) = \sum_{i=1}^{n} \lambda_i Z(X_i)$$

where, $Z(X_i)$ is the measured value at the ith location; λ_i is an unknown weight for the measured value at the ith location that minimizes prediction error (Cressie, 1993), and X_0 is the prediction location. The weighting factor, λ_i, therefore depends on the semivariogram, the distance to the prediction location, and the spatial relationships among the measured values around the prediction location.

Cross-validation was used to evaluate model parameters and kriging results. The cross-validation procedure involved the calculation and comparison of several statistics. These included mean and standard mean prediction errors, root-mean-square prediction errors, average standard errors, and standardized root-mean-square prediction errors. For each variable multiple exponential and spherical models were compared and evaluated and the best model selected based on the above model comparison statistics. ESRI's ArcGIS v8.3 with the Geostatistical Analyst extension was used in the spatial analyses (ESRI, Redlands, CA).

In the absence of spatial correlation an alternative interpolation method was employed to obtain the required spatial coverage. We chose to use Inverse Distance Weighting which is similar to kriging in that it weights the surrounding measured values to derive a prediction for each location, however, the weights are based only on the distance between the measured points and the prediction location and does not depend on spatial correlation in the data (Johnston et al., 2001).

Although the data are not synoptic, the geostatistical method was employed since it is ideal for identifying spatial patterns in a patchy environment by using the spatial correlation inherent in the data to produce the maps. The maps are not intended to represent small-scale processes but rather elucidate broad-scale patterns in the surface nekton community and the accompanying ocean conditions. To confirm that the ocean conditions did not change significantly over the course of each cruise, the geostatistically produced sea surface temperature maps were compared with maps derived from satellite data and temperature measured by a SeaSoar package (Barth et al., 2005 and unpub. data). In addition, geostatistically produced chlorophyll maps at 3 m were compared with SeaSoar chlorophyll measured at 5 m. The geostatistically produced maps were found to closely resemble both the satellite derived maps and the SeaSoar maps, thus supporting the assumption that the geostatistically produced maps are representative of ocean conditions during the four cruises (Reese et al., 2005).

In the present study, a biological hotspot is defined as an area with greater than average biological activity in terms of nekton species richness, nekton density, and/or nekton biomass. In order to identify areas within the sample region meeting these criteria, the geostatistically produced layers for these variables were combined and analyzed with ArcGIS v8.3 Spatial Analyst (ESRI, Redlands, CA).

Community structural analysis

Community structural analyses were performed using PC-ORD v4.25 (McCune and Mefford, 1999). Original data from each of the four cruises formed complementary species and environmental matrices. The environmental matrices consisted of temperature, salinity, and density data and chlorophyll concentrations collected at 3 m, surface zooplankton biovolume, surface zooplankton species richness, depth, distance from shore, latitude, and a categorical code for geographical hotspot association as determined by the spatial analyst. In addition, to represent the vertical structure of the surface waters, three additional parameters were calculated and included vertical gradients for temperature, salinity, and density. The gradients were calculated as the difference in parameter values between 3 m and 15 m depth, divided by the depth range, with greater values representing larger gradients and smaller values representing a more homogeneous surface water column. All cruises were analyzed individually to examine the community responses to the different seasonal and interannual conditions occurring throughout the study area. Stations with no nekton species present were eliminated from the community data set to allow for analysis of sample units in species space. Data transformations and their effects on the summary statistics were examined prior to analysis (McCune and Grace, 2002). Log transformation and, in some cases, the deletion of rare species (those which only occurred once throughout a cruise), markedly reduced the row and column skewness and coefficient of variation (CV).

In order to test for group differences in species composition between hotspots and non-hotspots, a multi-response permutation procedure (MRPP) was used (Mielke and Berry, 2001; McCune and Grace, 2002). MRPP is a nonparametric procedure used to test the hypothesis of no difference between two or more groups of entities (McCune and Grace, 2002). Groups were defined according to the geographic locations of the biological hotspots, such that any station within a particular hotspot area was assigned a code identifying it to that particular hotspot. Stations not associated with a hotspot were assigned a code indicating this. The weighting factor employed for weighting groups was:

$$C_i = \frac{n_i}{\sum n_i}.$$

Description of the primary species encompassing each hotspot was done using Indicator Species Analysis (ISA) (Dufrene and Legendre, 1997). Indicator Species Analysis examines the fidelity of occurrence of a species within a particular group, which is based on the combined proportional measurements of the abundance of each particular species in a group relative to its abundance in all groups, and the percent frequency of that species in each group. The method combines information on the concentration of species abundance in a particular group and the faithfulness of occurrence of a species in a particular group (McCune and Grace, 2002). The statistical significance of each group is examined by a Monte Carlo test, such that sample units are randomly reassigned *n*-times to test if the indicator species values are higher than would be expected by chance. For this study, 1000 runs were applied to each Monte Carlo simulation.

Community structure and habitat relationships

Non-metric Multidimensional Scaling (NMS; Kruskal, 1964) was used to ordinate sample stations in species space using the geographic location of the biological hotspots as a categorical variable and to compare the community structure within the hotspot groups to environmental gradients. NMS was chosen for this analysis because it is robust to data that are non-normal and contain high numbers of zeros as is typical for this type of ecological data. The Sorensen distance measure was used because it is less sensitive to outliers than some other distance measures. Random starting configurations with 200 maximum iterations were used for the NMS analysis with 15 runs conducted using real data. Non-metric multidimensional scaling uses an iterative search for the best positions of n entities on k dimensions (axes) that minimizes the stress of the k-dimensional configuration (McCune and Grace, 2002). The best solution, one with a particular random starting configuration and number of dimensions, is selected from the run with the lowest final stress from a real run and is reapplied to determine the final ordination. To evaluate whether NMS extracted stronger axes than expected by chance, a randomization (Monte Carlo) test was used. The p-values were calculated as the proportion of randomized runs with stress less than or equal to the observed stress. The dimensionality of the ordination was assessed by comparing the results of the NMS runs using real data to the results obtained using the Monte Carlo simulations with randomized data. Dimensionality was increased if the addition of an axis resulted in a significant improvement compared to the randomized data ($p \leq 0.05$) and the reduction in stress was greater than 5. Relationships between the environmental variables and ordination scores are shown with a joint plot. The coefficient of determination (r^2) between distances in the ordination space and distances in the original space was used to determine the proportion of variation represented by each axis. Pearson and Kendall correlations with each ordination axis were used to measure the strength and direction of individual species and environmental parameters.

Results

Environmental analysis

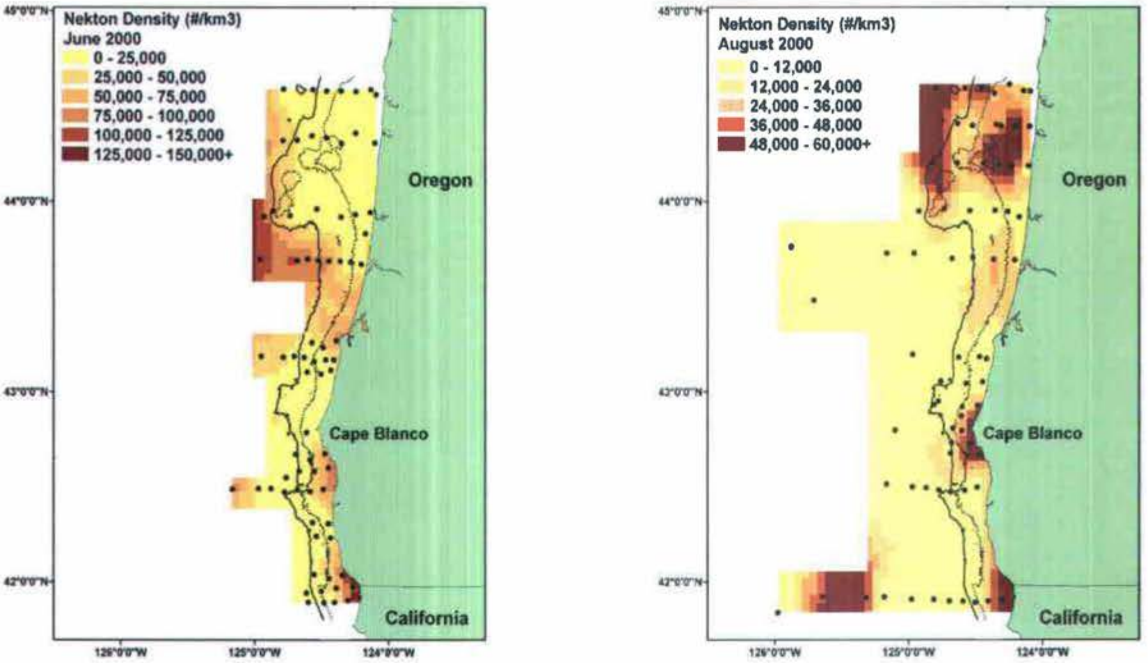
Surface water characteristics varied substantially between the four cruises (Table 3.1). Temperature differed significantly between the four cruises (Kruskal-Wallis test, $H_{3,302} = 68.23$, $p < 0.001$), being higher during the 2000 cruises and lowest during August 2002 (*U*-test, $p < 0.001$). The August 2000 cruise included stations that were further offshore which introduced bias in the data since offshore waters tend to be warmer. Thus the test was also computed for this cruise with the elimination of the offshore stations and the results did not change. Salinity was significantly different among cruises (Kruskal-Wallis test, $H_{3,302} = 145.57$, $p < 0.001$) being lower during June cruises and higher during August cruises. Salinity was significantly higher during the August 2002 cruise compared to all other cruises (*U*-test, $p < 0.005$) (Table 3.1). Water density differed significantly between cruises (Kruskal-Wallis test, $H_{3,302} = 113.30$, $p < 0.001$) with lower density values obtained during June cruises and higher values during August cruises (*U*-test, $p < 0.006$) (Table 3.1). Chlorophyll concentrations differed significantly between the cruises as well ($F_{3,305} = 22.13$, $p < 0.001$), with significantly lower concentrations during both June and August 2000 cruises compared to the 2002 cruises (Tukey, $p < 0.025$). Near-surface zooplankton concentrations significantly differed between the cruises (Kruskal-Wallis test, $H_{3,292} = 34.90$, $p < 0.001$) with generally higher concentrations occurring during the June cruises. Significantly higher surface zooplankton concentrations were observed during June 2002 (*U*-test, $p < 0.001$) (Table 3.1).

Table 3.1. Mean (± SE) surface water characteristics, surface zooplankton concentration, nekton density, nekton biomass, and nekton species richness in the study region: Temperature at 3 m (°C); Salinity at 3 m (psu); Density at 3 m (kg/m^3); Chlorophyll concentration at 3 m (μg/l); Surface zooplankton concentration (ml/100m^3); Nekton density (number/km^3); Nekton biomass (kg/km^3); Nekton species richness (number of species/station). Note: sample sizes differ per cruise due to missing CTD values at 3 m or samples not collected.

	Cruise											
Variable	**June 2000**			**August 2000**			**June 2002**			**August 2002**		
	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n
Temperature	12.3	0.1	74	12.3	0.3	74	11.4	0.2	71	10.3	0.2	83
Salinity	31.9	0.1	74	33.0	0.1	74	32.2	0.1	71	33.3	0.1	83
Density	24.1	0.1	74	25.0	0.1	74	24.5	0.1	71	25.6	0.1	83
Cholorophyll	1.4	0.2	74	3.5	0.5	74	5.4	0.8	71	5.8	0.8	86
Zooplankton	100.8	18.9	71	59.2	7.9	68	115.8	11.5	71	72.2	7.7	82
Nekton Density	53,851	15,051	73	103,514	85,466	70	1,192,307	737,760	70	137,602	49,122	84
Nekton Biomass	2,319	1,057	73	24,004	10,534	70	61,345	31,102	70	14,781	3,365	84
Nekton Species Richness	3.4	0.4	73	2.6	0.2	70	5.3	0.3	70	3.6	0.2	84

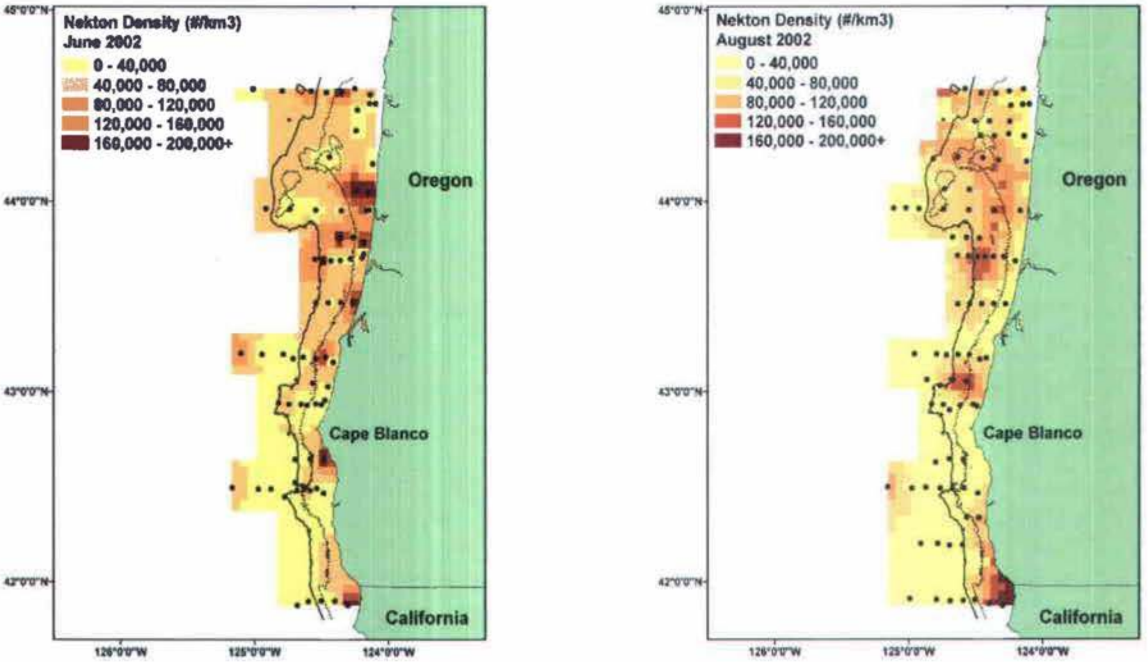
Spatial analysis

Surface nekton densities differed significantly between the four cruises ($F_{3,297}$ = 7.44, $p < 0.001$) (Figure 3.1). During June 2002, nekton densities were significantly higher than during any other cruise (Tukey, $p < 0.01$). Mean values were lowest in June 2000 and highest in June 2002 (Table 3.1). August cruises had intermediate mean densities. The larger density of nekton in June 2002 was the result of several large collections of adult Pacific herring occurring at four nearshore stations immediately inshore of Heceta Bank. Different degrees of spatial correlation were fitted to nekton densities according to the cruises (Table 3.2), with a spatially structured density component $[C/(C_0 + C)]$ ranging from 64 to 92%. In June 2000, the spatial correlation of nekton density best fit an isotropic, spherical model with a major range of spatial dependence of about 31 km. In August 2000 and 2002, the spatial correlations best fit exponential models, whereas in June 2002 there was an absence of spatial correlation. The ranges of spatial dependence differed markedly between these cruises with the largest distance observed in August 2000. During this cruise directional influences were present (Table 3.2; Figure 3.1). The direction of the major axis represents the direction over which spatial scales are longest (here roughly parallel with the coastline), whereas the minor axis represents the direction of the strongest gradient (across the shelf). In June 2000 and August 2002 the major range indicated a much smaller spatial dependence compared to August 2000. In the absence of spatial correlation during June 2002, Inverse Distance Weighting (IDW) was used to obtain the spatial coverage. Highest densities



a) June 2000

b) August 2000



c) June 2002

d) August 2002

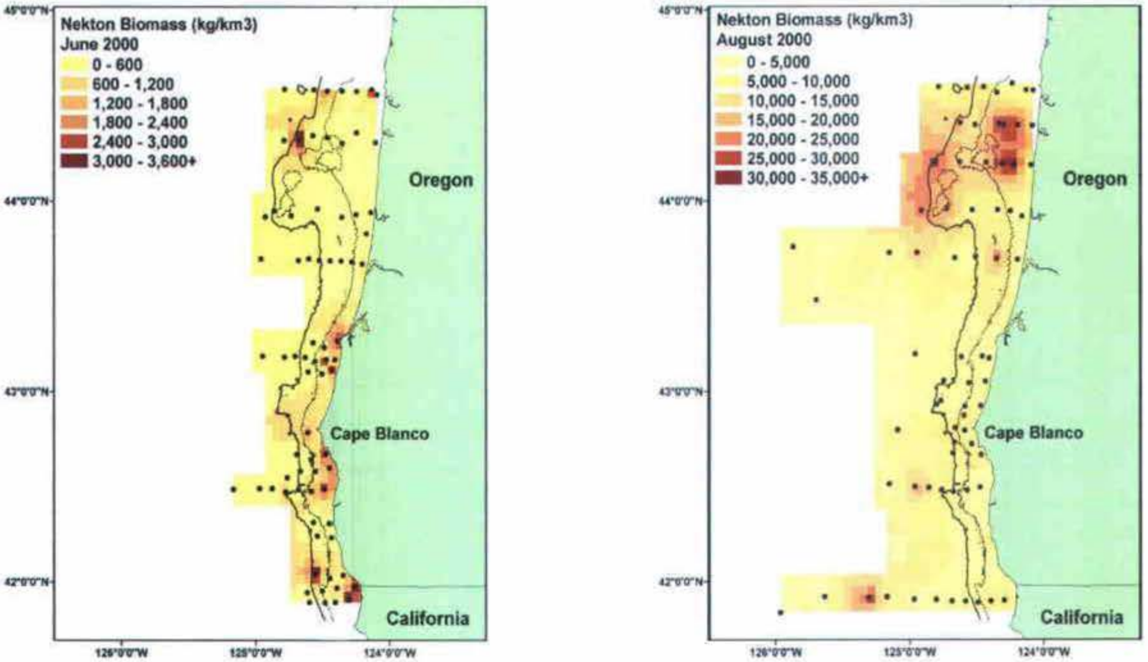
Figure 3.1. Kriging maps of surface nekton density throughout the study region for: (a) June 2000; (b) August 2000; (c) June 2002; and (d) August 2002. Dots represent station locations. The solid contour represents the 200 m isobath and the hatched contour represents the 100 m isobath. Note: scales differ between cruises.

Table 3.2. Statistics and model parameters of the models fitted to the empirical semivariograms during the June and August 2000 and 2002 cruises. Nekton species richness is the number of species present at a particular station; Nekton density is the number of nekton standardized for the volume of water filtered; and Nekton biomass is the weight (kg) of nekton landed standardized by the volume of water filtered. C_0 is the nugget effect or y-intercept of the model; C_0+C is the sill or model asymptote; $C/(C_0+C)$ is the spatially structured component; Major and Minor Ranges represent the range over which spatial dependence is apparent; Angle is the axis of rotation for the major axis for anisotropic models.

Spatial Process	**Month**	**Model**	**Nugget** C_0	**Sill** C_0+C	$C/(C_0+C)$	**Major Range**	**Minor Range**	**Major Angle**
Nekton Density	June 2000	Spherical	3.70x10^{8}	1.27x10^{9}	0.71	31 km	-	-
	Aug 2000	Exponential	0.63	7.92	0.92	238 km	144 km	9.9°
	June 2002	IDW	-	-	-	-	-	-
	Aug 2002	Exponential	1.50x10^{9}	4.24x10^{9}	0.64	20 km	-	-
Nekton Biomass	June 2000	IDW	-	-	-	-	-	-
	Aug 2000	Exponential	5.59x10^{6}	9.4x10^{7}	0.94	27 km	-	-
	June 2002	Spherical	1.87x10^{7}	1.10x10^{8}	0.83	16 km	-	-
	Aug 2002	Exponential	3.91x10^{7}	1.87x10^{8}	0.79	141 km	30 km	16.5°
Nekton Species Richness	June 2000	Spherical	2.54	11.36	0.78	141 km	73 km	1.5°
	Aug 2000	Exponential	0.18	0.31	0.63	149 km	144 km	10.9°
	June 2002	Exponential	2.03	8.33	0.76	83 km	-	-
	Aug 2002	Exponential	0.44	3.94	0.89	32 km	-	-

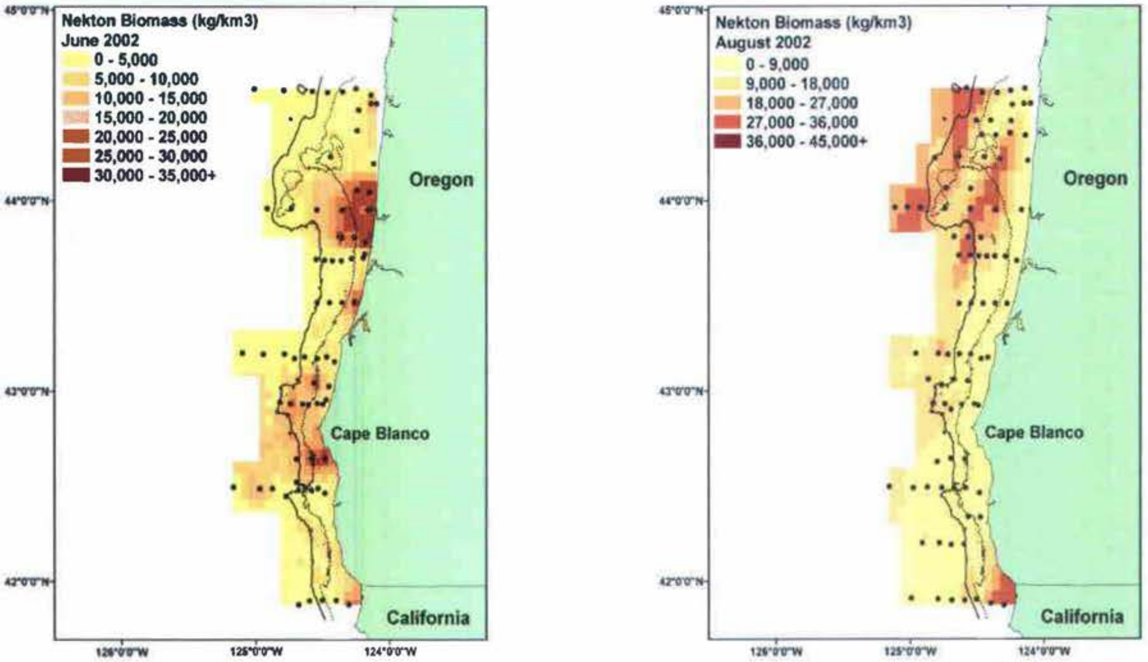
were observed in three general areas throughout the study region: 1) over or near the Heceta Bank region and immediately inshore, 2) nearshore around Cape Blanco, and 3) nearshore around Crescent City, CA in the south extending northward into southern Oregon (Figure 3.1).

In addition to nekton densities, nekton biomass was also significantly different between the four cruises ($F_{3,297} = 15.85$, $p < 0.001$) (Figure 3.2). Although biomass is correlated with density (Pearson $r = 0.54$, $p < 0.001$), there are instances where high densities do not necessarily occur with high biomasses (Table 3.1). During June 2000, nekton biomass was significantly lower than during any other cruise (Tukey, $p < 0.01$). Mean values were lowest in June 2000 and highest during June 2002 (Table 3.1). Mean biomasses were again intermediate during both August cruises. No other significant differences were detected. The large biomass of nekton in June 2002 was the result of several large collections of adult Pacific herring occurring at four nearshore stations immediately inshore of Heceta Bank. Different degrees of spatial correlation were fitted to nekton biomass (Table 3.2), with a spatially structured density component $[C/(C_0 + C)]$ ranging from 79 to 94%. In June 2000, there was an absence of spatial correlation. In August 2000, nekton biomass best fit an isotropic, exponential model whereas in June 2002, nekton biomass best fit an isotropic, spherical model. In August 2002, biomass best fit an anisotropic, exponential model with a major range of spatial dependence roughly parallel to the coast and the strongest gradient in biomass generally across the shelf (Table 3.2; Figure 3.2). In other words, nekton biomass varied more markedly in the onshore-offshore direction, and less so in the north-south direction. Highest biomass



a) June 2000

b) August 2000



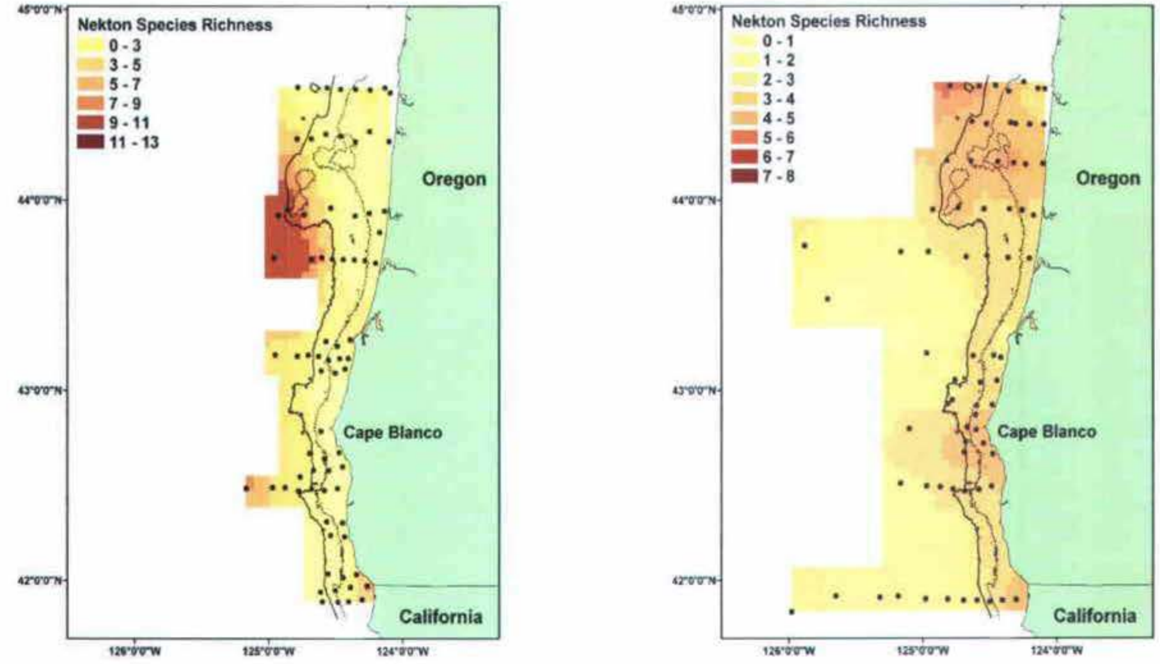
c) June 2002

d) August 2002

Figure 3.2. Kriging maps of nekton biomass throughout the study region for: (a) June 2000; (b) August 2000; (c) June 2002; and (d) August 2002. Dots represent station locations. The solid contour represents the 200 m isobath and the hatched contour represents the 100 m isobath. Note: scales differ between cruises.

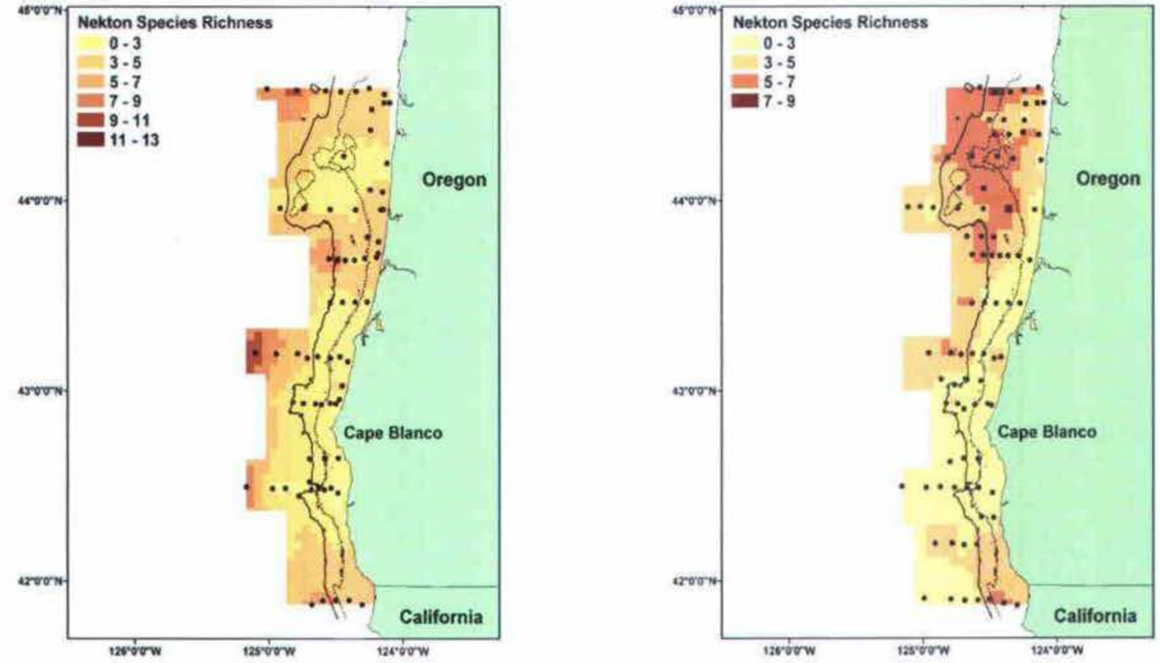
values were observed in the same three general areas as seen for nekton densities (Figure 3.2).

Nekton species richness also differed significantly between the four cruises ($F_{3,297} = 14.48$, $p < 0.001$) (Figure 3.3). Nekton species richness was significantly higher in June 2002 than during any other cruise (Tukey, $p < 0.01$). Mean values were lowest in August 2000 and highest during June 2002 (Table 3.1). During June 2000 and August 2002, intermediate mean species richness values were observed. No other significant differences were detected. Different degrees of spatial correlation were fitted to species richness (Table 3.2), with a spatially structured density component $[C/(C_0 + C)]$ ranging from 63 to 89%. In June 2000, species richness best fit an anisotropic, spherical model. In August 2000, however, species richness best fit an anisotropic, exponential model. In both cases, the directional influences indicated the strongest gradient in species richness was across the shelf, however this effect was more pronounced in June 2000. In June and August 2002, species richness best fit isotropic, exponential models (Table 3.2). During all cruises, nekton species richness varied more across the shelf than in the north-south direction. Highest species richness values were observed in two general areas throughout the study region: 1) over or near the Heceta Bank region and/or immediately inshore and 2) in the nearshore region around Crescent City, CA in the south extending northward into southern Oregon (Figure 3.3). During August 2000, nekton species richness in general tended to be more diffuse than during the other cruises in which species richness tended to be more concentrated in localized areas.



a) June 2000

b) August 2000



c) June 2002

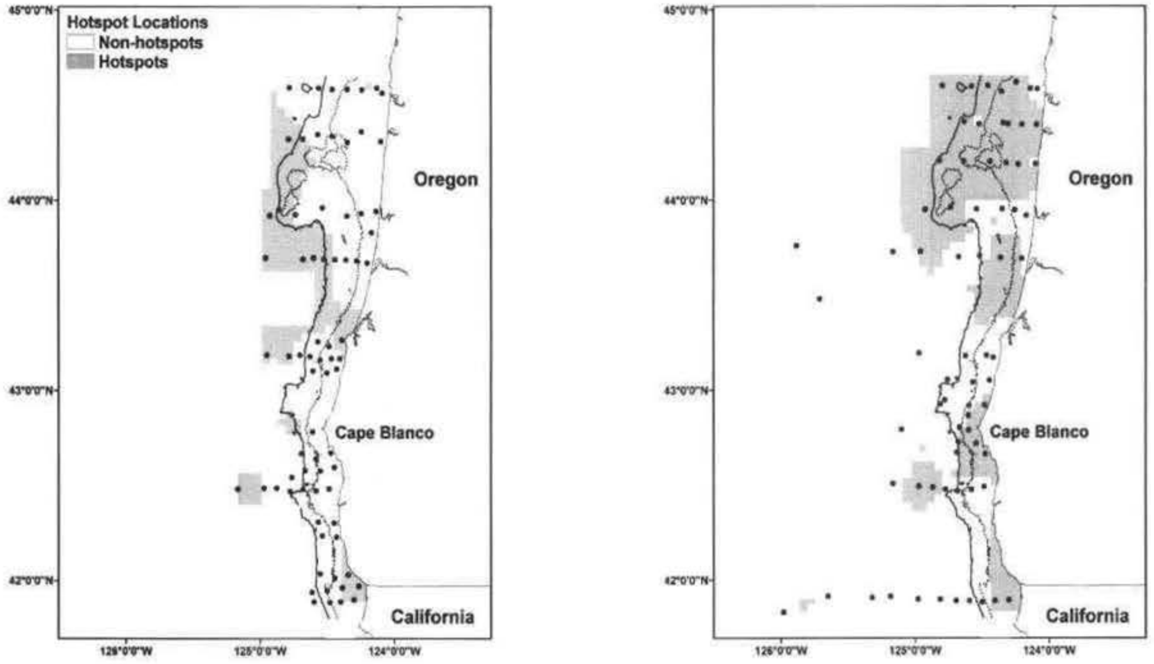
d) August 2002

Figure 3.3. Kriging maps of nekton species richness throughout the study region for: (a) June 2000; (b) August 2000; (c) June 2002; and (d) August 2002. Dots represent station locations. The solid contour represents the 200 m isobath and the hatched contour represents the 100 m isobath. Note: scales differ between cruises.

Hotspot determination

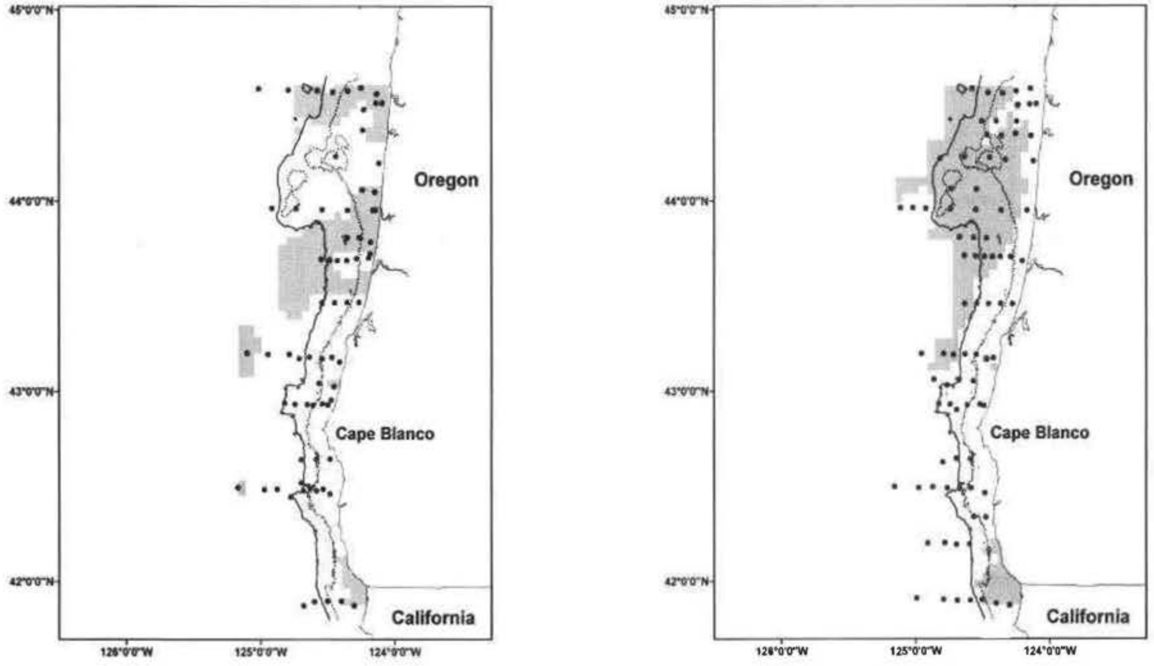
Combining the geostatistically produced spatial coverages for nekton species richness, density, and/or biomass resulted in persistent locations of elevated values when compared to the overall mean values (Figure 3.4). Although the general locations of the hotspot areas were persistent, the sizes of the hotspots varied by season and year. Two hotspot regions were identified for further community analyses: a northern hotspot region near Heceta Bank and a southern hotspot region off the coast from Crescent City. These two hotspot regions are hereafter referred to as the Heceta Bank hotspot and the Crescent City hotspot. The Heceta Bank hotspot region occupies a much larger area than the Crescent City hotspot. During June 2002, fewer stations were sampled around Heceta Bank, therefore it is not surprising that the hotspot region was not detected directly over the Bank during this time period. During the June 2000 cruise, the Heceta Bank hotspot extended from beyond the shelf-break, across the shelf to the southeast towards the coast to about 43.2° N. During the August 2000 and June and August 2002 cruises, the Heceta Bank hotspot region extended further north from beyond the shelf-break to the most nearshore stations.

The Crescent City hotspot region was relatively small compared to the Heceta Bank hotspot region (Figure 3.4). The size of this hotspot region was more persistent than the Heceta Bank hotspot and was consistently located around the nearshore region at the California and Oregon border (about 42° N). The size of the Crescent City hotspot tended to expand slightly north toward Cape Blanco and further over the shelf during August of both 2000 and 2002 whereas in June of both years the hotspot tended to be



a) June 2000

b) August 2000



c) June 2002

d) August 2002

Figure 3.4. Hotspot locations within the study region for: (a) June 2000; (b) August 2000; (c) June 2002; and (d) August 2002. Dots represent station locations. The solid contour represents the 200 m isobath and the hatched contour represents the 100 m isobath.

more limited to the coast. Another hotspot region was identified in August 2000 around Cape Blanco, however, this hotspot was not identified during the other cruises. It is possible that this hotspot was an extension of the Crescent City hotspot, since the Crescent City hotspot expanded furthest north during this time period.

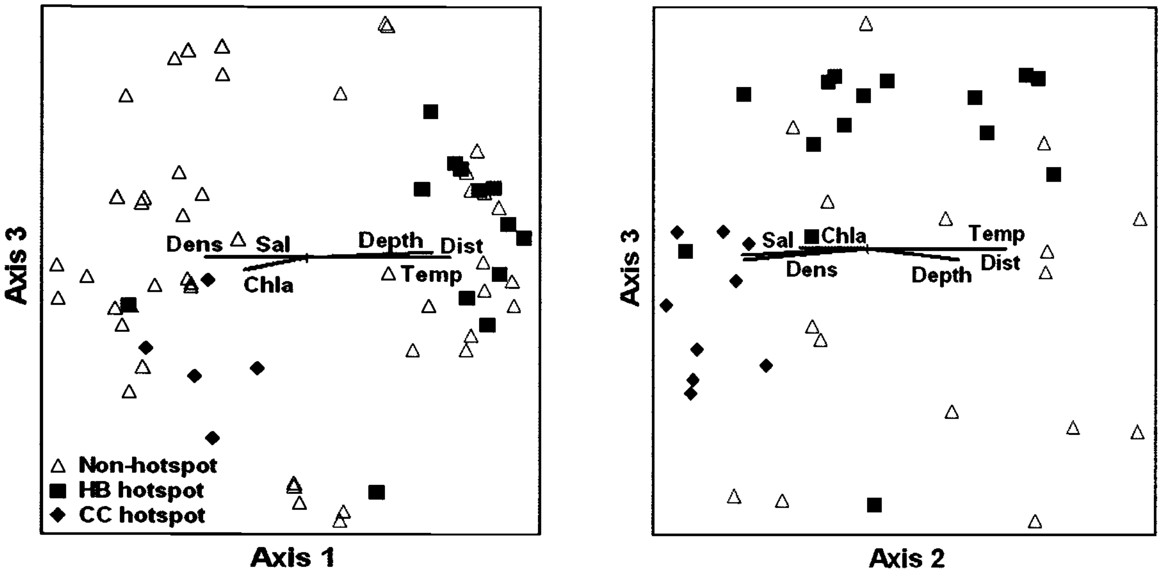
Community analysis

A multi-response permutation procedure (MRPP) was used to compare nekton community composition between the two hotspot regions and non-hotspot region for each cruise. Results from MRPP analysis found moderate within-group agreement (*A*) during all cruises (Table 3.3). In community ecology, values for *A* are commonly below 0.1, so an $A > 0.3$ is determined to be high (McCune and Grace, 2002). During each cruise, significant within-group agreement was obtained (Table 3.3). The largest within-group agreement occurred during August 2000 and the lowest value occurred during August 2002. Intermediate values were obtained for both June 2000 and 2002. These results suggest that community composition varied between the hotspot regions and non-hotspot regions.

Non-metric multidimensional scaling (NMS) of the community data for each cruise further indicated that the nekton communities differed between the Heceta Bank and Crescent City hotspots (Figure 3.5). However, the degree to which the dissimilarity in community composition was represented by the environmental gradients differed between the cruises. In June 2000, most of the variance in the nekton communities was captured by two dimensions containing 25.3% and 23.3%, respectively, of the

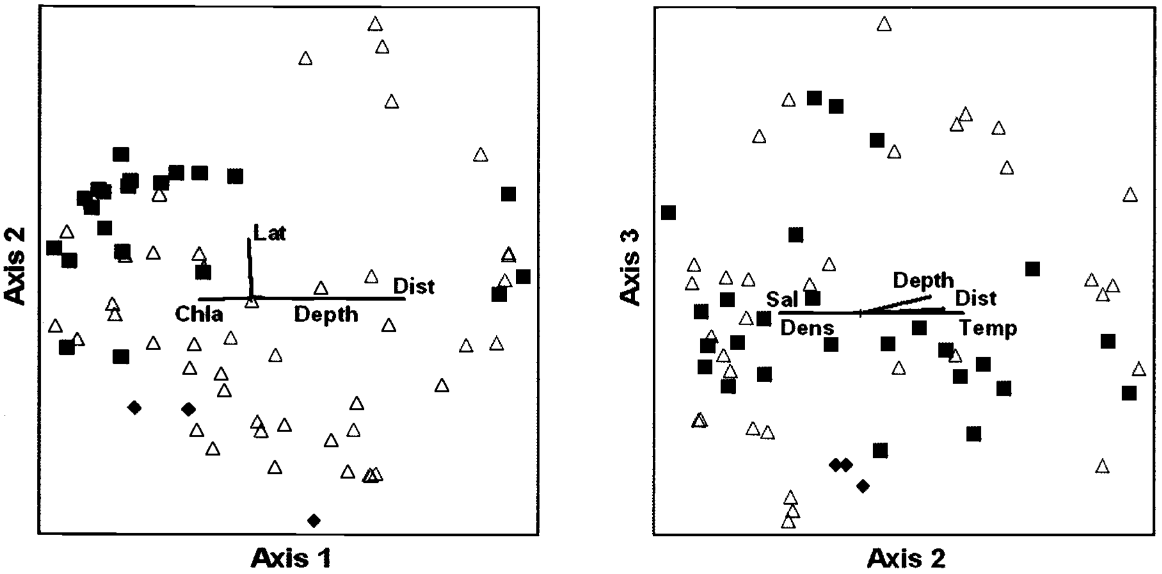
Table 3.3. Multi-response permutation procedure (MRPP) results comparing the nekton collections from the Heceta Bank and Crescent City hotspot regions and non-hotspot region for June and August of 2000 and 2002.

Cruise	**Number of groups**	**Test statistic**	**Within-group agreement (*A*)**	**p-value**
June 2000	3	-7.25	0.104	<0.0001
August 2000	3	-7.46	0.180	<0.0001
June 2002	3	-7.82	0.117	<0.0001
August 2002	3	-4.27	0.071	<0.0001



a) June 2000

b) August 2000



c) June 2002

d) August 2002

Figure 3.5. Ordination plots of stations in species space from a 3-dimensional solution for: (a) June 2000, (b) August 2000, (c) June 2002, and (d) August 2002. Stations are categorized according to their location relative to hotspot location: Non-hotspots, HB (Heceta Bank) hotspot, and CC (Crescent City) hotspot. Most significant vectors ($r^2 > 0.20$) shown denote: chlorophyll concentration (Chla), density (Dens), depth (Depth), distance from shore (Dist), latitude (Lat), salinity (Sal), and temperature (Temp).

information in the analytical data set (cumulative for 3-dimensional solution = 65.8%; stress = 19.43). Of the environmental parameters measured, temperature and distance offshore exhibited the strongest levels of correlation ($r^2 = 0.54$ and 0.48, respectively, along axis 1). Marginal contribution along axis 1 came from density ($r^2 = 0.38$), salinity ($r^2 = 0.26$), depth ($r^2 = 0.24$), and chlorophyll concentration ($r^2 = 0.23$). Temperature, distance from shore, and depth were positively correlated with axis 1, whereas density, salinity, and chlorophyll concentration were negatively correlated. Stations within the Heceta Bank hotspot were associated with warmer, offshore water in deeper depths whereas the Crescent City hotspot was associated with cooler, denser, more saline, nearshore water with higher chlorophyll concentrations (Figure 3.5a).

Abundances of five species were found to correlate with ordination scores from axis 1. Adult Chinook salmon (*Oncorhynchus tshawytscha*) and coho yearlings (*O. kisutch*) were more abundant with lower temperatures and higher chlorophyll concentrations ($r = -0.57$ and $r = -0.47$, respectively, axis 1 ordination scores) which was characteristic of the Crescent City hotspot. In contrast, juvenile rex sole (*Errex zachirus*), juvenile darkblotched rockfish (*Sebastes crameri*), and juvenile speckled sanddabs (*Citharichthys stigmaeus*) were more abundant in warmer, deeper, offshore water ($r = 0.57$, $r = 0.57$, and $r = 0.53$, respectively, axis 1 ordination scores) characteristic of the Heceta Bank hotspot. Indicator Species Analysis (ISA) of the three groups showed significant species associations only for the hotspot regions and not for the non-hotspot region (Table 3.4). Juveniles of several species of rockfish (genus *Sebastes*), rex sole juveniles, speckled sanddab juveniles, curlfin sole juveniles (*Pleuronichthys decurrens*),

Table 3.4. Results of Indicator Species Analysis from the hotspot regions showing species with significantly high indicator values and their associated group membership. HB and CC indicate the Heceta Bank and Crescent City hotspots, respectively. (j) denotes juvenile stage; (sy) subyearling; (y) yearling; (a) adult; no denotation represents adults. Note: No species were found to be significant indicators for the non-hotspot region during any cruise.

Species		**Indicator value**	***p*-value**	**Hotspot Group**
Common name	**Scientific name**			
June 2000				
Yellowtail rockfish (j)	*Sebastes flavidus*	75.0	0.003	HB
Darkblotched rockfish (j)	*Sebastes crameri*	67.7	0.001	HB
Rex sole (j)	*Errex zachirus*	49.6	0.012	HB
Speckled sanddab (j)	*Citharichthys stigmaeus*	42.2	0.012	HB
Pacific clubhook squid	*Onychoteuthis borealijaponicus*	38.1	0.007	HB
Cabezon (j)	*Scorpeanichthys marmoratus*	36.3	0.015	HB
Bocaccio (j)	*Sebastes paucispinis*	30.4	0.029	HB
Curlfin sole (j)	*Pleuronichthys decurrens*	23.1	0.019	HB
Stripetail rockfish (j)	*Sebastes saxicola*	23.1	0.024	HB
Market squid	*Loligo opalescens*	76.5	0.001	CC
Whitebait smelt (j)	*Allosmerus elongates*	60.0	0.001	CC
Pacific herring	*Clupea pallasi*	56.4	0.003	CC
Steelhead trout (j)	*Oncorhynchus mykiss*	37.3	0.007	CC
August 2000				
Jack mackerel	*Trachurus symmetricus*	55.3	0.003	HB
Coho salmon (a)	*Oncorhynchus kisutch*	50.1	0.006	HB
Pacific sardine	*Sardinops sagax*	44.3	0.005	HB
Coho salmon (j)	*Oncorhynchus kisutch*	34.2	0.018	HB
Chub mackerel	*Scomber japonicus*	22.0	0.018	HB
Chinook salmon (sy)	*Oncorhynchus tshawytscha*	85.7	0.001	CC
Surf smelt	*Hypomesus pretiosus*	55.5	0.001	CC
Steelhead trout (j)	*Oncorhynchus mykiss*	48.4	0.003	CC
Chinook salmon (a)	*Oncorhynchus tshawytscha*	44.9	0.003	CC
Wolf-eel (j)	*Anarrhichthys ocellatus*	42.3	0.001	CC
Medusafish	*Icichthys lockingtoni*	29.0	0.003	CC
Chinook salmon (y)	*Oncorhynchus tshawytscha*	22.1	0.022	CC
June 2002				
Chinook salmon (y)	*Oncorhynchus tshawytscha*	58.1	0.016	HB
Coho salmon (j)	*Oncorhynchus kisutch*	58.1	0.020	HB
Wolf-eel (j)	*Anarrhichthys ocellatus*	91.1	0.001	CC
Rex sole (j)	*Errex zachirus*	56.4	0.024	CC
Surf smelt	*Hypomesus pretiosus*	33.2	0.035	CC
Pacific tomcod (j)	*Microgadus proximus*	30.3	0.046	CC
Steelhead trout (j)	*Oncorhynchus mykiss*	28.3	0.037	CC
Pacific hake	*Merluccius productus*	28.2	0.032	CC
August 2002				
Northern anchovy	*Engraulis mordax*	30.8	0.060	HB
Surf smelt	*Hypomesus pretiosus*	100.0	0.001	CC
Pacific herring	*Clupea pallasi*	96.2	0.001	CC
Market squid	*Loligo opalescens*	89.9	0.011	CC
King-of-the-salmon (j)	*Trachipterus altivelis*	30.3	0.017	CC

cabezon juveniles (*Scorpeanichthys marmoratus*), and Pacific clubhook squid (*Onychoteuthis borealijaponicus*) all had significant indicator values within the Heceta Bank hotspot. Market squid (*Loligo opalescens*), juvenile whitebait smelt (*Allosmerus elongates*), Pacific herring (*Clupea pallasi*), and juvenile steelhead trout (*O. mykiss*) were all significant indicators of the Crescent City hotspot.

In August 2000, most of the variance in the nekton communities was captured by two dimensions containing 31.2% and 30.8%, respectively, of the information in the analytical data set (cumulative for 3-dimensional solution = 75.6%; stress = 16.42). To reduce stress, stations with only one species present were not included in the ordination. Of the environmental parameters measured distance from shore, density, salinity, depth, temperature, and chlorophyll concentration exhibited the strongest levels of correlation ($r^2 = 0.56$, 0.52, 0.49, 0.39, 0.34 and 0.27, respectively, along axis 2). Temperature, distance from shore, and depth were positively correlated with axis 2, whereas density, salinity, and chlorophyll concentration were negatively correlated. Stations within the Heceta Bank hotspot were associated with warmer and deeper offshore water whereas stations within the Crescent City hotspot were associated with cooler, denser, more saline water closer to shore (Figure 3.5b). With the exception of one station classified within the Heceta Bank hotspot, community composition within the Heceta Bank and Crescent City hotspot stations tended to fall out along a gradient associated with axis 3. A vertical temperature gradient had the highest correlation and was positive along axis 3 ($r^2 = 0.17$). The vertical temperature gradient indicates that there was a larger vertical temperature gradient associated with the Heceta Bank hotspot than with the Crescent City hotspot. The Crescent City hotspot surface water was more uniformly cool.

Abundances of three species were found to correlate with ordination scores from axis 2. Chinook yearlings and adults were more abundant with lower temperatures, denser, more saline, nearshore water ($r = -0.71$ and -0.52, respectively, axis 2 ordination scores) which were more characteristic of the Crescent City hotspot. In contrast, blue sharks (*Prionace glauca*)and adult jack mackerel (*Trachurus symmetricus*) were more abundant in warmer, less saline water ($r = 0.50$ and 0.38, respectively, axis 2 ordination scores) characteristic of the Heceta Bank hotspot. Jack mackerel were also positively correlated with axis 3 ($r = 0.70$ with axis 3). Indicator Species Analysis (ISA) of the three groups showed significant species associations only for the hotspot regions and not for the non-hotspot region (Table 3.4). Adult jack and chub mackerel (*Scomber japonicus*), adult and juvenile coho salmon, and Pacific sardines (*Sardinops sagax*) all had significant indicator values within the Heceta Bank hotspot. Chinook salmon adults and juveniles, juvenile steelhead trout, surf smelt (*Hypomesus pretiosus*), juvenile wolf-eels (*Anarrhichthys ocellatus*), and medusafish (*Icichthys lockingtoni*) were all significant indicators of the Crescent City hotspot.

In June 2002, most of the variance in the nekton communities was captured by two dimensions containing 38.3% and 20.9%, respectively, of the information (cumulative for 3-dimensional solution = 75.9%; stress = 17.72). Distance from shore, depth, and chlorophyll concentration exhibited the strongest levels of correlation ($r^2 = 0.56$, 0.29, and 0.20, respectively, along axis 1). Distance from shore and depth were positively correlated with axis 1, whereas chlorophyll concentration was negatively correlated. Latitude had the highest correlation and was positive along axis 2 ($r^2 = 0.24$) indicating the communities within the Heceta Bank and Crescent City hotspots differed somewhat with respect to latitudinal differences. Although stations within the Heceta Bank hotspot were distinct from those within the Crescent City hotspot, latitude was the only parameter able to explain the difference since the two hotspots tended to fall out along axis 2 more so than along axis 1. Three stations classified as Heceta Bank hotspots were clumped together apart from the rest of the Heceta Bank hotspot stations (Figure 3.5c). These stations are all located offshore near the shelf-break (200 m isobath) and are therefore associated with deeper depths and less chlorophyll concentrations.

Abundances of several species were found to correlate with ordination scores from axis 1. Adult and yearling Chinook salmon ($r = -0.73$ and -0.53, respectively) and market squid ($r = -0.79$) were more abundant closer to shore, in shallower water, with higher chlorophyll concentrations. All but one of the remaining species that correlated with axis 1 were juvenile rockfish species (genus *Sebastes*): darkblotched rockfish ($r = 0.67$), Pacific ocean perch (*S. alutus*) ($r = 0.64$), yellowtail rockfish (*S. flavidus*) ($r = 0.59$), widow rockfish (*S. entomelas*) ($r = 0.57$), canary rockfish (*S. pinniger*) ($r = 0.56$), black rockfish (*S. melanops*) ($r = 0.53$), and blue rockfish (*S. mystinus*) ($r = 0.46$). The remaining species that correlated with axis 1 was juvenile Pacific sandlance (*Ammodytes hexapterus*) ($r = 0.50$). All of the juvenile rockfish and Pacific sandlance were more abundant in the Heceta Bank hotspot stations located further offshore, associated with deeper depths and lower chlorophyll concentrations. Again, ISA of the three groups showed significant species associations only for the hotspot regions and not for the non-hotspot region (Table 3.4). Chinook yearlings and juvenile coho salmon had significant indicator values within the Heceta Bank hotspot. Juvenile rex sole, juvenile wolf-eels, surf smelt, juvenile steelhead, juvenile Pacific tomcod (*Microgadus proximus*), and Pacific hake (*Merluccius productus*) were all significant indicators of the Crescent City hotspot.

In August 2002, most of the variance in the nekton communities was captured by two dimensions containing 34.3% and 22.6%, respectively, of the information in the analytical data set (cumulative for 3-dimensional solution = 73.3%; stress = 18.17). Temperature, distance from shore, density, depth, and salinity exhibited the strongest levels of correlation (r^2 = 0.41, 0.33, 0.32, 0.28, and 0.20, respectively, along axis 2). Temperature, distance from shore, and depth were positively correlated with axis 2, whereas density and salinity were negatively correlated. During August 2002, the distinction between community composition within the Heceta Bank and Crescent City hotspots was less apparent compared to previous cruises (Figure 3.5d). The Heceta Bank hotspot stations were distributed along the temperature, density, salinity, and depth gradients. The Crescent City hotspot stations clumped together generally away from the Heceta Bank hotspot stations with respect to axis 3, however latitude was not found to be correlated with any axis. Therefore, of the environmental parameters measured, none of the parameters sufficiently explains this pattern.

Abundances of six species were found to correlate with ordination scores from axis 2. Blue sharks, Pacific saury (*Cololabis saira*), and Pacific sardine (r = 0.71, 0.49, and 0.47, respectively) were more abundant in warmer, deeper and less dense, offshore water characteristic of the Heceta Bank hotspot stations. Rex sole juveniles, market squid, and adult Chinook ($r = -0.60$, $r = -0.48$, and -0.45, respectively) were more abundant in cooler, denser, nearshore water. Indicator Species Analysis of the three groups again showed significant species associations only for the Heceta Bank and Crescent City hotspot regions and not for the non-hotspot region (Table 3.4). Northern anchovies (*Engraulis mordax*) had the highest indicator values from the Heceta Bank hotspot whereas surf smelt, Pacific herring, market squid, and king-of-the-salmon juveniles (*Trachipterus altivelis*) were all significant indicators of the Crescent City hotspot.

Temporal community analysis

To examine the extent to which nekton community composition persists or changes through seasons or years, we examined the nekton community within the Heceta Bank hotspot across seasons and years. High within-group agreement was obtained (MRPP, $A = 0.28$, $p < 0.001$) indicating that nekton community composition was more similar within the Heceta Bank hotspot area during each cruise than between cruises. The distinction between the nekton communities is evident in the ordination of sample stations in species-space (Figure 3.6). Most of the variance in the nekton communities was captured by two dimensions containing 43.0% and 22.3%, respectively, of the information (cumulative for 3-dimensional solution = 76.8%; stress = 17.33). Of the parameters measured, distance from shore, density, depth, temperature, and salinity

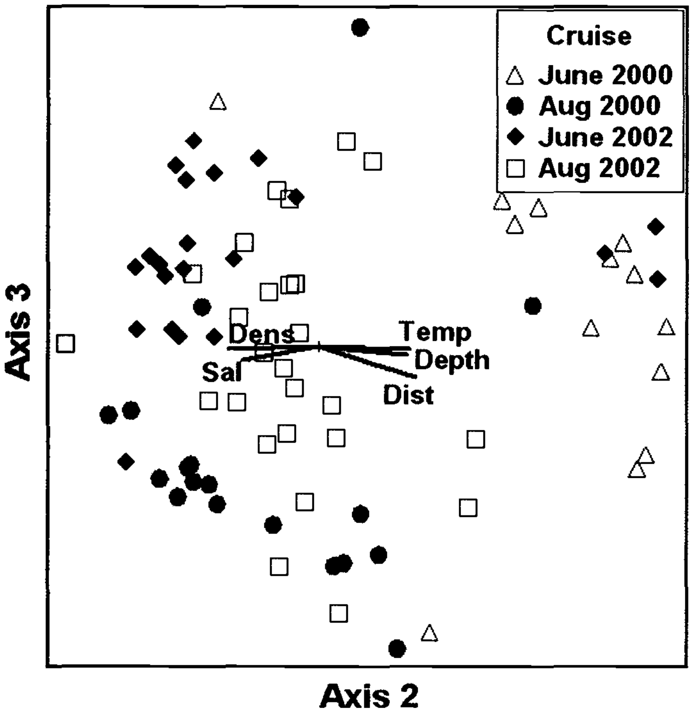


Figure 3.6. NMS ordination of the Heceta Bank hotspot stations by cruise. Stations are categorized by cruise. Most significant vectors shown denote: density (Dens), depth (Depth), distance from shore (Dist), salinity (Sal), and temperature (Temp).

exhibited the strongest levels of correlation ($r^2 = 0.31$, 0.29, 0.29, 0.28, and 0.24, respectively, along axis 2). Distance from shore, temperature, and depth were positively correlated with axis 2, whereas density and salinity were negatively correlated. In June 2000, stations within the Heceta Bank hotspot were associated with deeper, warmer, and less saline offshore water. In August 2000, the stations were characterized by cooler, more saline water. During June 2002, community composition was more similar to those observed in August 2000 than to the previous sampling year (June 2000) being characterized by cooler, more saline water. During August 2002, community composition was less distinct compared to the previous cruises and appeared to be intermediate of all other cruises.

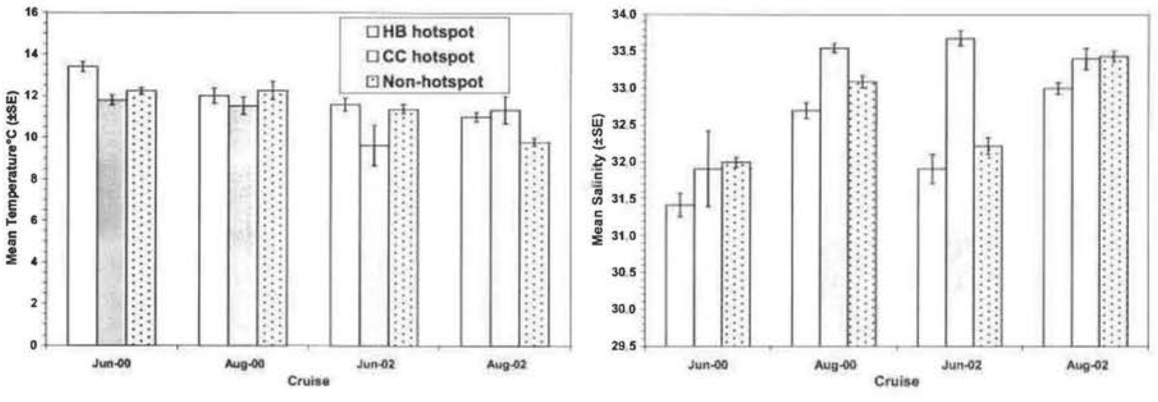
Abundances of several species were found to correlate with ordination scores from axis 2. Adult Chinook salmon and coho adults and yearlings were found to be negatively correlated with axis 2 indicating that they were more abundant with lower temperatures and higher salinity ($r = -0.65$, $r = -0.46$, and $r = -0.61$, respectively, axis 2 ordination scores) which were characteristic of the Heceta Bank hotspot during August 2000, June 2002, and August 2002. Five species of juvenile rockfish were found to positively correlate with axis 2: darkblotched rockfish ($r = 0.75$), yellowtail rockfish ($r = 0.74$), canary rockfish ($r = 0.51$), bocaccio (*S. paucispinis*) ($r = 0.47$), and stripetail rockfish (*S. saxicola*) ($r = 0.46$). All rockfish species were more abundant in warmer, deeper, less saline, offshore waters characteristic of the June 2000 and June 2002 cruises. Both juvenile speckled sanddabs and juvenile sablefish (*Anoplopoma fimbria*) were also more abundant in warmer, deeper, less saline water ($r = 0.50$ and $r = 0.48$, respectively) again characteristic of the June 2000 and June 2002 cruises. Indicator Species Analysis of the four cruises showed significant species associations for each cruise (Table 3.5). Juveniles tended to be more important indicators during the June cruises whereas adults were more prevalent during August cruises. Juveniles of several species of rockfish (genus *Sebastes*), rex sole, speckled sanddab, cabezon, and Pacific clubhook squid, sablefish, and curlfin sole all had significant indicator values in June 2000. In August 2000, jack mackerel, adult coho salmon, chub mackerel, and Pacific sardines were significant indicators. In June 2002, Chinook adults and yearlings, coho juveniles, chum juveniles (*O. keta*), Pacific sanddabs (*C. sordidus*), Pacific sandlance, and spiny dogfish (*Squalus acanthias*) were all significant indicators. In August 2002, market squid, Pacific tomcod, and juvenile wolf-eels were significant indicators (Table 3.5).

Hotspot habitat characteristics

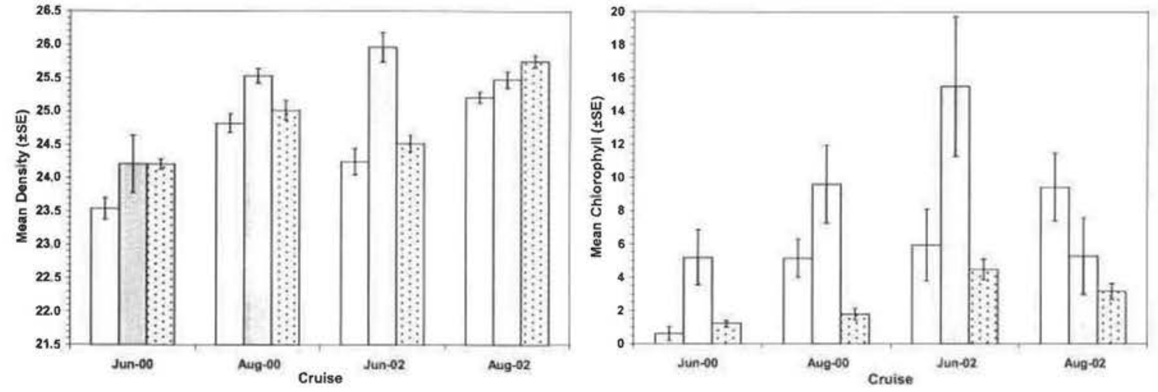
Surface water characteristics varied substantially between the hotspots and non-hotspot during each of the four cruises (Figure 3.7). Temperature in the Heceta Bank hotspot tended to be warmer than in the Crescent City hotspot, except during August 2002 (Figure 3.7a). Temperature within the non-hotspot area was intermediate for the June cruises and cooler than the hotspot areas in August 2002. Overall, surface water temperatures were lower during the 2002 cruises (Table 3.1). Salinity and density followed similar patterns during all cruises (Figure 3.7b and c). Salinity and density were consistently lowest in the Heceta Bank hotspot and tended to be higher in the Crescent City hotspot with the exception of August 2002. Chlorophyll concentrations were

Table 3.5. Results of Indicator Species Analysis from the Heceta Bank hotspot region by cruise showing species with significantly high indicator values. Denotation is as is in Table 3.4.

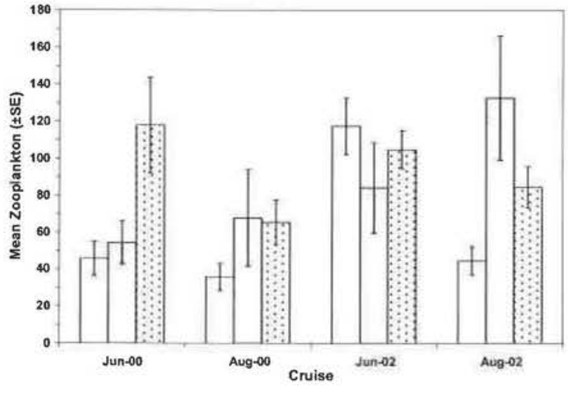
Species		Indicator	
Common name	**Scientific name**	**value**	***p*-value**
June 2000			
Yellowtail rockfish (j)	*Sebastes flavidus*	76.8	0.001
Darkblotched rockfish (j)	*Sebastes crameri*	61.3	0.001
Rex sole (j)	*Errex zachirus*	48.5	0.004
Speckled sanddab (j)	*Citharichthys stigmaeus*	45.5	0.001
Cabezon (j)	*Scorpeanichthys marmoratus*	38.5	0.001
Pacific clubhook squid	*Onychoteuthis borealijaponicus*	38.5	0.001
Sablefish (j)	*Anoplopoma fimbria*	36.9	0.003
Bocaccio (j)	*Sebastes paucispinis*	29.8	0.003
Curlfin sole (j)	*Pleuronichthys decurrens*	23.1	0.008
Stripetail rockfish (j)	*Sebastes saxicola*	22.1	0.006
August 2000			
Jack mackerel	*Trachurus symmetricus*	49.2	0.002
Coho salmon (a)	*Oncorhynchus kisutch*	42.3	0.002
Pacific sardine	*Sardinops sagax*	37.1	0.041
Chub mackerel	*Scomber japonicus*	22.0	0.011
June 2002			
Chinook salmon (y)	*Oncorhynchus tshawytscha*	42.4	0.001
Coho salmon (j)	*Oncorhynchus kisutch*	36.2	0.017
Chinook salmon (a)	*Oncorhynchus tshawytscha*	33.2	0.023
Chum salmon (j)	*Oncorhynchus keta*	28.5	0.002
Pacific sanddab	*Citharichthys sordidus*	27.4	0.009
Pacific sandlance (j)	*Ammodytes hexapterus*	23.8	0.006
Spiny dogfish	*Squalus acanthias*	23.8	0.001
August 2002			
Market squid	*Loligo opalescens*	52.0	0.026
Pacific tomcod (j)	*Microgadus proximus*	20.1	0.019
Wolf-eel (j)	*Anarrhichthys ocellatus*	18.3	0.035



a) Temperature b) Salinity



c) Density d) Chlorophyll



e) Surface Zooplankton

Figure 3.7. Mean (± SE) surface water characteristics within each hotspot and non-hotspot region by cruise. Temperature at 3 m (°C); Salinity at 3 m (psu); Density at 3 m (kg/m^3); Chlorophyll concentration at 3 m (μg/l); Surface zooplankton concentration (ml/100m^3).

consistently higher in the Crescent City hotspot area except during August 2002 when concentrations were highest in the Heceta Bank hotspot (Figure 3.7d). Chlorophyll concentrations were consistently lowest in the non-hotspot areas except during June 2000. There was also less variability in chlorophyll concentrations in the non-hotspot areas, indicative of consistently low values. Overall, chlorophyll concentrations were highest during June and August 2002 (Table 3.1). Surface zooplankton biovolume tended to be lowest in the Heceta Bank hotspot with the exception of June 2002 when biovolume was highest in this area (Figure 3.7e). Surface zooplankton biovolume was highest during August 2002 within the Crescent City hotspot. In general, surface zooplankton biovolume was higher in the Crescent City hotspot or non-hotspot areas. This pattern may be due to top-down effects by juvenile nekton reducing the surface zooplankton biovolume within the Heceta Bank hotspot area. Overall, surface zooplankton biovolume was highest during June 2002 (Table 3.1).

Discussion

In this analysis, we identified two biological hotspots with different physical and biological characteristics associated with each. Both hotspots persisted through space and time, although the sizes of the hotspots tended to fluctuate, being larger during August than during June cruises (Figure 3.4). In June 2000, the Heceta Bank hotspot was located furthest offshore compared to other cruises and was characterized by warmer temperatures and lower salinity and density. During all cruises, the Heceta Bank hotspot was associated with Heceta Bank, which is a region along the northwest coast where the isobaths extend offshore, whereas the isobaths are otherwise somewhat parallel with the coastline. The presence of Heceta Bank results in the shelf-break being located further offshore. Therefore, the Heceta Bank hotspot is more influenced by warmer, offshore water. Flow is to the south during the summer over the shelf and switches to flow north during the fall and winter (Hickey and Banas, 2003). The location of the Heceta Bank hotspot in the northern part of the study region is in closer proximity to the Columbia River, and results in more influence from the plume which is observable as a surface lens of low-salinity water. The Columbia River releases large amounts of fresh water into the marine environment which then flows to the south off Oregon in the summer with prevailing currents (Landry et al., 1989). The result is lower salinity and consequently less dense water within the Heceta Bank hotspot.

In terms of biology, the Heceta Bank hotspot typically had lower chlorophyll concentrations than the Crescent City hotspot, and typically lower surface zooplankton biovolume relative to both the Crescent City hotspot and the non-hotspot areas (Figure 3.7). Chlorophyll concentrations vary seasonally, coincident with upwelling activity. Upwelling brings cooler, nutrient-rich water to the surface, which along with the increased light availability, stimulates increased primary production and increased chlorophyll concentrations (Landry et al., 1989). During June, strong seasonal upwelling had not yet occurred, so chlorophyll concentrations tended to be lower overall with only a few nearshore locations having elevated chlorophyll concentrations (Reese et al., 2005). The Heceta Bank hotspot, being further offshore and near the shelf-break during June 2000 (Figure 3.4), was therefore characterized with low chlorophyll concentrations (Figure 3.7) presumably because the upwelled water had not yet been displaced offshore.

By August 2000, upwelling was much stronger and elevated chlorophyll concentrations extended further offshore as the upwelled water was displaced. During June and August 2002, there was an anomalous input of Subarctic Pacific water into the region (Huyer, 2003; Wheeler et al., 2003) resulting in increased nutrients and at least a doubling of phytoplankton biomass along the Oregon coast. Offshore, maximum chlorophyll levels were observed at about 50 m depth and were 2-4 times greater in the subsurface layer in 2002 compared with 2000 (Wheeler et al., 2003). Within the Heceta Bank hotspot in June 2002, mean chlorophyll concentration was roughly 6 times higher than in June 2000. Highest chlorophyll concentrations in the Heceta Bank hotspot were observed in August 2002, presumably as the upwelled water was displaced further offshore.

The Crescent City hotspot was consistently located close to shore in the southern part of the study area near Crescent City, CA. In contrast to the Heceta Bank hotspot, the Crescent City hotspot was characterized by cooler temperatures and higher salinity and density. Seasonal upwelling brings cooler, higher salinity, nutrient-rich water to the surface all along the U.S. West Coast (Huyer, 1983). In the Pacific Northwest, the strength and duration of upwelling increases to the south along the coast (Hickey and Banas, 2003). The characteristics within the Crescent City hotspot are explained by the proximity of this hotspot near the coast in the south where the influence of upwelled water is greatest. With the exception of August 2002, chlorophyll levels were consistently higher in the Crescent City hotspot compared to the Heceta Bank hotspot and non-hotspot areas (Figure 3.7). Given the small size of the Crescent City hotspot, comparisons must be taken with caution. Nonetheless, the patterns are evident among the different cruises. With respect to surface zooplankton biovolume, the Crescent City hotspot area typically had higher biovolumes than the Heceta Bank hotspot with the exception of June 2002.

The non-hotspot areas were characterized, in general, by having intermediate values of temperature, salinity, and density. This is most likely due to the wide variety of habitats covered by the non-hotspot areas. During all cruises, these areas contained stations that were both very nearshore and offshore beyond the shelf. In addition, chlorophyll concentrations were lowest within the non-hotspot areas with the exception of June 2000 when chlorophyll concentrations were particularly low within the Heceta Bank hotspot. An interesting finding, however, was that surface zooplankton biovolumes tended to be relatively high within the non-hotspot area compared to one or both of the hotspot areas, particularly during June 2000. This is most likely due to offshore displacement and the smaller areas denoted as hotspots during June 2000. In particular, the Heceta Bank hotspot area was mostly limited to near the shelf and did not include many nearshore stations during this cruise.

Nekton community composition was distinct between the Heceta Bank and Crescent City hotspot areas, particularly during June and August 2000 and June 2002. During June 2000, nekton communities differed between the Heceta Bank and Crescent City hotspot areas along several environmental gradients (Figure 3.5) consistent with properties of the water masses between the two areas. Temperature, distance from shore, depth, salinity, and density were the most consistent gradients in explaining the community distributions. Temperature, distance from shore, and depth are highly correlated as temperature increases offshore with increasing depth. Temperature, salinity, and density are more indicative of the specific water masses discriminating between Columbia River water versus upwelled water, so it is understandable why these parameters are the most consistent environmental measures of the two groups.

During August 2000, community composition varied in the Heceta Bank hotspot area and spanned a larger range of temperatures, salinities, and densities whereas the community composition within the Crescent City hotspot was limited to the end of the gradient represented by the coolest, most saline and dense water. Again, the stronger upwelling that occurred in the southern portion of the study area supports this finding. The larger ranges of temperatures, salinities, and densities within the Heceta Bank hotspot are due to the large area denoted as a hotspot. Therefore, the larger area spans a greater range of habitats and consequently more variability in water characteristics, yet still differs from those observed in the Crescent City hotspot.

During June and August 2002, the Heceta Bank and Crescent City hotspot regions were still somewhat distinct with respect to community composition, however, the differences were not associated with the measured gradients. In June 2002, communities within the Heceta Bank hotspot clumped together but differed from the communities in the Crescent City hotspot with respect to an axis with no correlations to the measured environmental parameters. This suggests that the communities differ according to some undetermined gradient. The influence of the Subarctic water into the California Current resulted in much cooler and less saline waters throughout the study area. In addition, the nutrient-rich water fueled primary production throughout the area resulting in a less discernable explanation as to the differences between the communities. A similar pattern was observed in August 2002.

Indicator species analysis suggests that not only do the Heceta Bank hotspots differ from the Crescent City hotspots with respect to which species are significant indicators, but also that within a particular hotspot the significant indicators change with time. During the June cruises, nearly all of the significant indicators were juveniles, with rockfish species being particularly important in the Heceta Bank hotspot in 2000. During both June cruises, juvenile steelhead trout were significant indicators within the Crescent City hotspot. As the season progressed, juveniles were not nearly as important during the August cruises. By August, most of the juveniles have migrated out of the system or settled to the bottom. During June 2000 and August 2002, significant indicator species were juveniles or forage fish, however, during August 2000 there was a greater proportion of predatory fish relative to forage fish or juveniles (Table 3.4). Juveniles are most abundant in spring coincident with the increases in food resources, and juveniles typically greatly outnumber adults given the life-history and high mortality rates of juvenile fish. Therefore, it is not surprising that juveniles are significant indicators during June since ISA combines information on the concentration of species abundance in a particular group and the faithfulness of occurrence of a species to a particular group. As the seasons progress, the juveniles migrate out of the area so that the proportion remaining is less, yielding a relatively greater proportion of adults. During August 2000, both forage fish and predatory fish were found to be significant indicators within the Heceta Bank and Crescent City hotspots (Table 3.4). During June 2002, several species of juvenile fish were significant indicators within the Crescent City hotspot, as were a forage fish species (surf smelt) and a predatory species (hake). It is interesting to note that during none of the cruises were significant indicator species found within the non-hotspot areas. This is likely due to a combination of factors such as less fidelity of any species to these areas, lower abundances of individual species, and the relatively large number of stations within this area each cruise.

The varying community composition and coincident varying water properties of the Heceta Bank and Crescent City hotspot areas can be explained by the flow through the region and the different physical processes within each area. Flow through the system is generally from the north during spring and summer with meanders and jets associated with topographical features (Barth, 2003; Barth et al., 2005). Barth et al. (2005) noted two significant features associated with the flow around Heceta Bank. There is an onshore component to the flow on the southern flank of Heceta Bank at about (44° N) and relatively weak flow inshore of the Bank. The result of this flow is the potential for retention of water over the Bank (Barth et al., 2005). This flow would likely lead to favorable conditions for juvenile fish, especially those that will take up residence on the bank after further development, as well as forage fish that will take advantage of the accumulated phytoplankton biomass and accompanying zooplankton. Ressler et al. (2005) found high concentrations of acoustically-determined euphausiids near Heceta Bank which they suggest are due to retention mechanisms. Euphausiids are a major food of many of the nekton species we examined here (Brodeur and Pearcy, 1992). Higher trophic level predators can then take advantage of the higher abundances of potential prey. In fact, the distributions of top-level predators have been reported to occur within, at least, the Heceta Bank hotspot region (Tynan et al., 2005). Further to the south, coastal upwelling increases, which leads to cooler, nutrient-rich waters near the surface that are able to support higher chlorophyll levels, in turn supporting higher trophic levels and resulting in the formation of the Crescent City hotspot.

Given the large number of sample stations within the Heceta Bank hotspot, it was possible to examine the nektonic communities through time (Figure 3.6). The results of the ordination indicate distinct differences in community composition within the Heceta Bank hotspot over time. The environmental parameters that best explain the differences are temperature, salinity, and density. So, although the locations of the hotspots persist through time and space, the communities that occupy them tend to vary between seasons and years. In other words, community composition tends to vary yet nekton species richness, abundance, and/or biomass tend to be conserved resulting in the presence and persistence of local hotspots in the northern California Current ecosystem.

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SPECIES ASSOCIATIONS IN RELATION TO BIOLOGICAL HOTSPOTS OF THE NORTHERN CALIFORNIA CURRENT

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Abstract

The associations among organisms are known to affect the local distributions and abundances of species. Evaluating the associations among species is therefore one means to help explain observed spatial patterns and distributions. The primary goal of this study is to identify species associations in relation to previously determined biological hotspots within the northern California Current. Sampling was conducted during June and August of 2000 and 2002 as part of the U.S. GLOBEC mesoscale surveys from Newport, Oregon in the north to Crescent City, California in the south. Species associations were examined to identify potentially complementary and redundant species. Strong positive and negative associations were found between species. The strongest negative associations were between jellyfish species and fish species. Strong positive associations were determined between several fish species. Dominant species from the hotspots varied seasonally and annually, however, there appeared to be some evidence of replacement of dominant species by other similar species with respect to functional group and preferred habitat. This finding suggests that the persistence of these hotspots is related to species redundancy and is an important attribute contributing to the stability within this highly variable system.

Introduction

Interrelations among organisms are known factors that limit local distributions and abundances of species. In the pelagic marine environment, however, acquiring knowledge about nekton communities has proven to be problematic, primarily due to the high cost of sampling in the ocean. As such, our understanding of species diversity, community structure, and species associations that inhabit marine ecosystems tends to decrease with distance from shore (Cailliet, 1997). It is important, however, to evaluate biodiversity and community structure to assess the status of marine communities as they are susceptible to impacts related to environmental change. Biodiversity has become an increasingly popular subject, stimulated in part by the need to determine the extent of damage caused by human activities to the health of communities and abundance of species on earth (Lubchenco et al., 1991; Peterson, 1992; Schulze and Mooney, 1994; Heywood, 1995; Cailliet, 1997). In addition to understanding how biodiversity is distributed within a system, it is necessary to understand how those species are associated. Evaluating the interactions among species is one means to help explain the patterns and distributions we observe.

Since changes in diversity and species assemblages could potentially be indicators of large-scale changes in the environment, knowledge of how diversity is affected by both natural and anthropogenic processes is essential to our understanding of ecological conditions and will allow for wiser management decisions. In the past, however, emphasis has been on terrestrial systems, but interest has increased in recent years in studying marine habitats (Peterson, 1992; Hawksworth and Kalin-Arroyo, 1995; Cailliet, 1997; Duarte, 2000; Turpie et al., 2000).

The California Current is a dynamic and highly productive ecosystem, characterized by considerable spatial and temporal variability (McGowan et al., 1998).

Within the northern portion of this highly variable system, changes in species composition and production of all trophic levels in this region are known to occur due to varying environmental conditions (Pearcy et al., 1985; Brodeur and Pearcy, 1992; Pearcy, 2002; Peterson et al., 2002; Brodeur et al., 2005; Reese et al., 2005). On a seasonal scale, variability within the system is the result of the seasonal reversal in wind pattern north of 37° N, blowing equatorward during the summer and poleward during the winter (Huyer, 2003). The equatorward winds during the summer produce strong upwelling-favorable winds along the coast which result in increased primary production (Barth et al., 2005). Interannual variability is typically linked with El Niño events (Chelton et al., 1982) and decadal variability appears to be associated with large-scale regime shifts that alter ocean characteristics over periods of decades (Mantua et al., 1997; Chavez et al., 2003).

In a study involving two years of sampling at the beginning and end of the upwelling season, Reese and Brodeur (2006) identified two persistent biological hotspots within the northern portion of this highly variable system. These nekton hotspots, which were characterized in terms of diversity, abundance, and/or biomass, persisted despite changes in environmental conditions and nekton community structure (Reese and Brodeur, 2006). One hotspot was located further offshore near the shelf-break and was associated with a retention area near Heceta Bank (about 44° N). The other hotspot was located closer to shore near Crescent City, CA (about 42° N) and was an upwelling-based hotspot.

One mechanism for the persistence of these biological hotspots in the Northern California Current may be the ecological redundancy present in these biologically diverse hotspot communities (Walker, 1992; Naeem, 1996). Frost et al. (1995) examined species compensation and functional complementarity in ecosystem function in a lake system and found that biomass of zooplankton remained at high levels despite the loss of component species from each group. Compensatory increases by other taxa were determined to be responsible for the complementarity of function. A key factor increasing the degree of compensation among species in response to environmental change was the functional similarity of associated species (Frost et al., 1995). Species redundancy, as reflected in more biologically diverse areas, may therefore preserve ecosystem functioning despite changes in the environment (Naeem, 1996). Likewise, the persistence of the biological hotspots in the Northern California Current system may therefore be related to species complementarity.

The local distribution and abundance of some species are known to affect the presence of other species due to biological interactions such as competition and predation. Identifying which species are indicators of specific habitats and which species associate with them would be important in understanding ecosystem structure. Positive associations between species whose dominance fluctuates may facilitate the complementary functioning of species within a system such that if one species becomes limited in abundance another associated, and functionally similar, species may replace it thus preserving ecosystem function. On the other hand, negative associations are also possible. For instance, jellyfish abundance is increasing in many marine ecosystems (Mills, 2001; Brodeur et al., 2002; Kideys, 2002; Xian et al., 2005) and this increase is suggested to adversely affect fish populations (Lynam et al., 2005; Purcell and

Sturdevant, 2001). Given the large abundances of jellies encountered in the Northern California Current, jellies may be significant competitors with some nekton species. For instance, Suchman et al. (2006) found that jellies and sardines both feed heavily on euphausiid eggs. Therefore, if there is significant competition between these marine organisms, this may indicate a change in food web dynamics and a potential loss in diversity if the system becomes dominated by jellies which could lead to a potential loss of ecosystem function.

In this paper, we describe the distribution and abundance of nekton and jellyfish within the Northern California Current ecosystem in relation to habitat characteristics and species associations. A primary goal was to identify species associations in relation to biological hotspots. In particular, we were interested in the associations of hotspot indicator species with other species. Associated species with similar diets may be competitors and have the potential to be complementary species, thus providing insight into the persistence of these biological hotspots despite changing environmental conditions and community structure. Traditionally, redundancy has simply been defined as the number of species within a functional group. We took a more conservative approach by adding to this definition the requirement that redundant species be complementary species, such that they occupy similar habitats and have overlapping geographic distributions. Since such a definition requires that redundant species have similar diets and occupy similar habitats, fluctuations in abundances would be predicted in a variable environment. Therefore, a compensatory increase in the abundance of one species would be related to a decrease in abundance of another species. Given the spatial and temporal overlap of jellyfish and nekton, we were also interested in determining whether any positive or negative associations occur between or among jellyfish and nektonic species. The distribution of rare species is also discussed as they relate to biological hotspots or non-hotspot regions.

Methods

Study region and sampling design

Sampling was conducted at multiple trawling stations as part of a mesoscale and fine-scale sampling study within the U.S. GLOBEC Northeast Pacific Program (Batchelder et al., 2002). Samples were collected over four time periods to examine seasonal and interannual patterns of community dynamics: during early summer (29 May to 11 June, 2000 and 1 June to 18 June, 2002 (hereafter called June 2000 and June 2002 cruises, respectively) and during late summer (29 July to 12 August, 2000 and 1 August to 17 August, 2002 (hereafter called August 2000 and August 2002 cruises, respectively). All sampling was conducted from chartered fishing vessels, the F/V *Sea Eagle* was used in 2000 and the F/V *Frosti* in 2002. The sampling area extended from Newport, Oregon (latitude 44° 40' N) to Crescent City in northern California (approximately 42° N). Stations were sampled along five GLOBEC designated transects located 1, 5, 10, 15, 20, 25, and 30 nautical miles from shore and also at fine-scale sampling stations in areas of particular physical and/or biological interest (e.g., areas associated with fronts or eddies). Most collections took place during daytime but occasionally tows were made during twilight or nighttime (June 2000, n = 84; Aug 2000, n = 75; June 2002, n = 90; Aug 2002, n = 94). The spatial and community analyses included in this paper were limited to collections made during daylight hours to avoid any changes in the day/night community structure.

Surface nekton tows of the surface layer were made at each station for 30 minutes at a speed of 6 km/hr with a Nordic 264 rope trawl (Nor'Eastern Trawl Systems, Inc., Bainbridge Island, WA) (see Brodeur et al. (2004) for additional sampling details). Then, based on the volume of water filtered per trawl, nekton and jellyfish abundance were standardized for differences in effort between tows. We only used species richness values obtained from volumes of water within two standard deviations of the mean volume sample to ensure that observed values of species richness were not confounded by variations in the volumes of water sampled.

The following physical and biological variables were sampled at each station prior to setting the trawl. Salinity and temperature were measured using a Seabird SBE 19 Seacat profiler CTD profiler to depths of 100 m or to within 10 m of the bottom. Water samples for chlorophyll analysis were collected from 3 m below the surface with a 1-l Niskin water sampler. In addition, the near-surface zooplankton were sampled using a 335-μm mesh neuston net measuring 0.3 m by 1.0 m in the mouth. The net was towed for five minutes at 3 km/hr out of the wake of the vessel. A more detailed description of the sampling and analyses of the neuston tows are available in Reese et al. (2005). On occasion, equipment malfunction or poor weather conditions prevented sampling of some variables.

Environmental data analysis

Differences in total jellyfish densities were compared between cruises using a Kruskal-Wallis test (Zar, 1996). A non-parametric test was chosen because assumptions of normality and homoscedasticity were not met. When significant differences were found, Mann-Whitney U tests were performed to compare between the different cruises. The significance level associated with the test was adjusted because more than one test was carried out (Shott, 1991). To obtain an overall significance level of 0.05, a Bonferroni-adjusted significance level of $0.05/4 = 0.0125$ for each Mann-Whitney test was used. Statistical tests were not performed between hotspot and non-hotspot regions during each cruise due to the low sample sizes associated with the Crescent City hotspot.

Spatial analysis

To identify spatial patterns of jellyfish distributions and thus identify relationships to nekton biological hotspot regions, geostatistical modeling techniques were employed and are discussed in detail in Reese and Brodeur (2006). Since the geostatistical methods employed in this paper for creating maps of jellyfish densities are the same as those used in Reese and Brodeur (2006) for identifying nekton biological hotspots, a brief description is presented here for illustrating the general approach. Densities for four species of large medusae common in surface waters off the coast of Oregon, consisting of three scyphomedusae (*Aurelia labiata*, *Chrysaora fuscescens*, and *Phacellophora camtschatica*) and one hydromedusa (*Aequorea* sp.), were combined to produce the total jellyfish density maps for each cruise.

The first step in the geostatistical analysis was to calculate the empirical semivariogram. Each spatial process consisted of observations measured at a location x which is the sample station defined by latitude and longitude for each cruise. It was assumed that: (1) the spatial distribution of each process was stable throughout the period of each cruise (approximately 2 weeks), and (2) the observations and spatial processes are the result of random processes (Johnston et al., 2001). The intrinsic stationarity assumption was examined with semivariance data clouds in which the variance of the difference between two locations is the same between any two points that are at similar distances and direction (Johnston et al., 2001). Two types of directional components were examined for each variable for their affect on surface predictions: global trends and anisotropy and when present were incorporated into the analyses (Johnston et al., 2001).

Data were normalized with a log (x+1) transformation when necessary to prevent violations of normality and homoscedasticity. Large outliers result in an increased nugget effect which consequently results in higher predicted values with greater uncertainty (Chiles and Delfiner, 1999). As suggested by Chiles and Delfiner (1999), the extreme outlier values were reduced to the value of the upper limit of the range not including the outlier. Empirical semivariograms {γ(h)} were estimated by pooling pairs of observations using the following equation given by Matheron (1971):

$$\gamma(h) = \frac{\sum_{i=1}^{N_h} \{Z(x_i + h) - Z(x_i)\}^2}{2N(h)}$$

where $Z(x_i)$ is the value of the variable at location x_i, $Z(x_i + h)$ is the value separated from x_i by distance h (measured in meters), and $N(h)$ is the number of pairs of observations separated by distance h. Exponential and spherical theoretical models were fit to the empirical semivariograms to estimate the semivariogram values for each distance within the range of observations (Cressie, 1993). Expected values of the variables were then estimated for each cruise by kriging. Kriging forms weights from surrounding measured values to predict values at unsampled locations such that the nearest measured values have the most influence (Johnston et al., 2001). The weights are derived from the modeled semivariogram that characterizes the spatial structure of the data. The predictor is then formed as the weighted sum of the data such that:

$$\hat{Z}(X_0) = \sum_{i=1}^{n} \lambda_i Z(X_i)$$

where, $Z(X_i)$ is the measured value at the *i*th location; λ_i is an unknown weight for the measured value at the *i*th location that minimizes prediction error (Cressie, 1993), and X_0 is the prediction location. The weighting factor, λ_i, therefore depends on the semivariogram, the distance to the prediction location, and the spatial relationships among the sampled values around the prediction location. Cross-validation was used to evaluate model parameters and kriging results. For each variable, multiple exponential and spherical models were evaluated and compared and the best model was selected. ESRI's ArcGIS v8.3 with the geostatistical analyst extension was used in the spatial analyses (ESRI, Redlands, CA).

Although the data are not synoptic, the geostatistical method was used since it is ideal for identifying spatial patterns in a patchy environment by using the spatial correlation inherent in the data to produce the maps. The maps are not intended to represent small-scale processes but rather elucidate broad-scale patterns in the surface nekton and jellyfish communities and the accompanying ocean conditions. The geostatistically produced maps were found to closely resemble both satellite-derived maps and in situ sampling (SeaSoar) maps of temperature and chlorophyll (Barth et al., 2005), thus supporting the assumption that the geostatistically produced maps are representative of ocean conditions during the four cruises (Reese et al., 2005).

Biological hotspots were previously described in Reese and Brodeur (2006) and were defined as areas with greater than average biological activity in terms of nekton species richness, nekton density, and/or nekton biomass. In order to identify the relationship of jellyfish densities with these biological hotspots, the geostatistically produced layers for the jellyfish densities and hotspots were combined and analyzed with ArcGIS v8.3 Spatial Analyst (ESRI, Redlands, CA).

Community structural analysis

Community structural analyses were performed using PC-ORD v4.25 (McCune and Mefford, 1999). Original data from each of the four cruises formed complementary species and environmental matrices. The environmental matrices consisted of temperature, salinity, density, and chlorophyll concentrations collected at 3 m, surface zooplankton biovolume, surface zooplankton species richness, nekton species richness, station depth and distance from shore, and a categorical code to represent the station's geographical position within or outside a biological hotspot as determined by the spatial analyst. In addition, to represent the vertical structure of the surface waters, three additional parameters were calculated: vertical gradients for temperature, salinity, and density. The gradients were calculated as the difference in parameter values between 3 m and 15 m depth, divided by the depth range, with greater values representing larger gradients and smaller values representing a more homogeneous surface water column. All cruises were analyzed individually to examine the community responses to the different seasonal and interannual conditions occurring throughout the study area. Stations with no species present were eliminated from the community data set to allow for analysis of sample units in species space. In addition, to avoid spurious effects caused by the presence of rare species, we excluded species from the species matrix that had a frequency of occurrence of less than 5% of the possible occurrences for each cruise (McCune and Grace, 2002). We examined the deletion of species which had a frequency of occurrence less than 10%, but there was not a significant improvement over the 5% deletion. Data transformations and their effects on the summary statistics were examined prior to analysis (McCune and Grace, 2002). Log $(x + 1)$ transformation and the deletion of rare species, markedly reduced the row and column skewness and coefficient of variation (CV).

Nekton and jellyfish species groupings were examined with agglomerative hierarchical cluster analyses (AHCA) using the Sorensen distance measure and flexible beta linkage function (McCune and Grace, 2002). This linkage function was chosen because the user can control its space-distorting properties, it is a space-conserving method, and it has less propensity to chain. A value of $\beta = -0.25$ gives results similar to Ward's method (Lance and Williams, 1967), therefore values of β in the present analyses ranged from -0.25 to -0.30. Analyses were performed on individual cruises to identify similar or changing patterns of species associations during different time periods.

Correlations between species were examined with Spearman's rho. Only strongly significant correlations ($p < 0.01$) between dominant species are presented here given the large number of significant correlations identified.

Non-metric multidimensional scaling (NMS; Kruskal, 1964) was used to ordinate sample units in species space. NMS was chosen for this analysis because it is robust to data that are non-normal and contain high numbers of zeros as is typical for this type of ecological data. The Sorensen distance measure was used because it is less sensitive to outliers than some other distance measures. Random starting configurations with 200 maximum iterations were used for the NMS analysis with 15 runs conducted using real data. Non-metric multidimensional scaling uses an iterative search for the best positions of n entities on k dimensions (axes) that minimizes-the stress of the k-dimensional configuration (McCune and Grace, 2002). The best solution, one with a particular random starting configuration and number of dimensions, is selected from the run with the lowest final stress from a real run and is reapplied to determine the final ordination. To evaluate whether NMS extracted stronger axes than expected by chance, a randomization (Monte Carlo) test was used. The p-values were calculated as the proportion of randomized runs with stress less than or equal to the observed stress. The dimensionality of the ordination was assessed by comparing the results of the NMS runs using real data to the results obtained using the Monte Carlo simulations with randomized data. Dimensionality was increased if the addition of an axis resulted in a significant improvement compared to the randomized data ($p \leq 0.05$) and the reduction in stress was greater than 5. Species were then represented as points on the ordinations to indicate their average position in the sample space. Although this method ignores the breadth of a species' distribution in sample space, the method allows for the general depiction of many species at once. Individual species distributions were examined using overlays on the ordinations. Relationships between the environmental variables and ordination scores were shown with a joint plot. The coefficient of determination (r^2) between distances in the ordination space and distances in the original space was used to determine the proportion of variation represented by each axis. Pearson and Kendall correlations with each ordination axis were used to measure the strength and direction of individual species and environmental parameters.

Results

Environmental analysis

Surface water characteristics varied substantially between the four cruises and between the hotspot and non-hotspot regions (Table 4.1). Mean surface temperatures at 3 m were higher during the 2000 cruises compared to the 2002 cruises for hotspot and non-hotspot regions. The lowest surface temperatures were typically found within the Crescent City (CC) hotspot region in the south and warmest in the Heceta Bank (HB) hotspot region (Table 4.1). Mean salinity and density at 3 m tended to be highest during the August cruises and in the CC hotspot region and lowest in the HB hotspot region. Mean values in the non-hotspot region during all cruises for these parameters were intermediate of the values from the hotspots (Table 4.1).

Table 4.1. Mean (±SE) surface water characteristics, zooplankton concentration and species richness, total jelly and nekton density, nekton biomass, and nekton species richness in each region during the four cruises. Temperature at 3 m (°C); salinity at 3 m (psu); density at 3 m (kg/m^3); chlorophyll concentration at 3 m (μg/l); surface zooplankton concentration (ml/100m^3); surface zooplankton species richness (number of species > 5 mm/station); jelly and nekton density (number/km^3); nekton biomass (kg/km^3); nekton species richness (number of species/station). No HS represents stations not within a hotspot region, whereas HBHS and CCHS represent the Heceta Bank Hotspot and the Crescent City Hotspot regions, respectively.

	June 2000			**August 2000**		
	No HS (n = 51)	**HBHS (n = 14)**	**CCHS (n = 8)**	**No HS (n = 39)**	**HBHS (n = 19)**	**CCHS (n = 9)**
Variable	Mean (SE)	Mean (SE)	Mean (SE)	Mean (SE)	Mean (SE)	Mean (SE)
Temperature	12.3 (0.2)	13.1 (0.3)	11.4 (0.3)	12.4 (0.5)	12.1 (0.4)	11.5 (0.4)
Salinity	32.0 (0.1)	31.5 (0.2)	32.2 (0.3)	33.1 (0.1)	32.7 (0.1)	33.5 (0.1)
Density	24.2 (0.1)	23.7 (0.2)	24.5 (0.3)	25.0 (0.1)	24.8 (0.1)	25.5 (0.1)
Chlorophyll concentration	1.0 (0.1)	0.8 (0.4)	5.0 (1.2)	1.7 (0.3)	5.0 (1.1)	9.6 (2.3)
Zooplankton concentration	110.5 (24.9)	104.1 (38.9)	44.3 (9.0)	66.7 (11.7)	35.7 (6.9)	67.8 (26.2)
Zooplankton species richness	3.8 (0.4)	4.7 (1.0)	4.5 (1.1)	4.0 (0.7)	1.6 (0.4)	4.1 (1.4)
Jelly density	294,268 (105,009)	604,484 (589,556)	140,713 (64,733)	3,352,739 (2,023,149)	670,280 (656,149)	1,033,720 (387,214)
Nekton density	9,839 (2,388)	156,520 (55,665)	154,756 (71,254)	4,585 (1,621)	347,738 (313,841)	49,637 (16,812)
Nekton biomass	1,007 (957)	5,102 (4,237)	2,605 (1,003)	3,904 (2,121)	66,628 (35,597)	899 (465)
Nekton species richness	2.4 (0.3)	6.4 (1.2)	4.6 (0.9)	1.7 (0.2)	3.7 (0.3)	4.1 (0.4)

Table continued on next page

Table 4.1 continued

	June 2002			August 2002		
	No HS (n = 45)	**HBHS (n = 22)**	**CCHS (n = 3)**	**No HS (n = 49)**	**HBHS (n = 28)**	**CCHS (n = 3)**
Variable	Mean (SE)	Mean (SE)	Mean (SE)	Mean (SE)	Mean (SE)	Mean (SE)
Temperature	11.4 (0.2)	11.6 (0.3)	9.6 (1.0)	9.9 (0.2)	10.9 (0.2)	11.4 (0.7)
Salinity	32.2 (0.1)	31.9 (0.2)	33.7 (0.1)	33.4 (0.1)	33.0 (0.1)	33.4 (0.1)
Density	24.5 (0.1)	24.3 (0.2)	26.0 (0.2)	25.7 (0.1)	25.2 (0.1)	25.5 (0.1)
Chlorophyll concentration	4.3 (0.6)	6.2 (2.1)	15.5 (4.2)	2.7 (0.4)	9.7 (1.9)	5.3 (2.3)
Zooplankton concentration	102.9 (10.3)	120.4 (14.9)	84.0 (21.5)	85.0 (11.3)	46.3 (7.4)	132.7 (33.6)
Zooplankton species richness	5.1 (0.5)	5.5 (0.8)	4.0 (1.5)	4.7 (0.5)	2.9 (0.3)	7.3 (0.9)
Jelly density	274,164 (133,247)	411,682 (246,821)	220,728 (101,162)	1,145,216 (538,495)	496,609 (345,304)	3,490,770 (3,400,163)
Nekton density	90,237 (53,678)	3,585,880 (2,291,060)	170,474 (147,663)	35,818 (15,620)	161,204 (65,218)	1,487,235 (1,060,948)
Nekton biomass	6,690 (3,306)	165,662 (95,232)	8,734 (8,632)	4,270 (2,010)	22,666 (8,567)	29,380 (17,217)
Nekton species richness	4.7 (0.4)	6.2 (0.4)	6.7 (1.5)	2.4 (0.3)	5.4 (0.3)	5.3 (0.7)

Mean surface chlorophyll concentrations tended to be highest in the hotspot regions, particularly within the CC hotspot region (Table 4.1). Highest mean near-surface zooplankton concentrations varied between the non-hotspot region and the CC hotspot region except during June 2002 when concentrations were highest in the HB hotspot region. Similarly, mean near-surface zooplankton species richness varied between regions but tended to be highest in the non-hotspot and CC hotspot regions. By definition, mean nekton species richness, density, and/or biomass were highest within the hotspot regions than in the non-hotspot region (Reese and Brodeur, 2006) (Table 4.1).

Spatial analyses

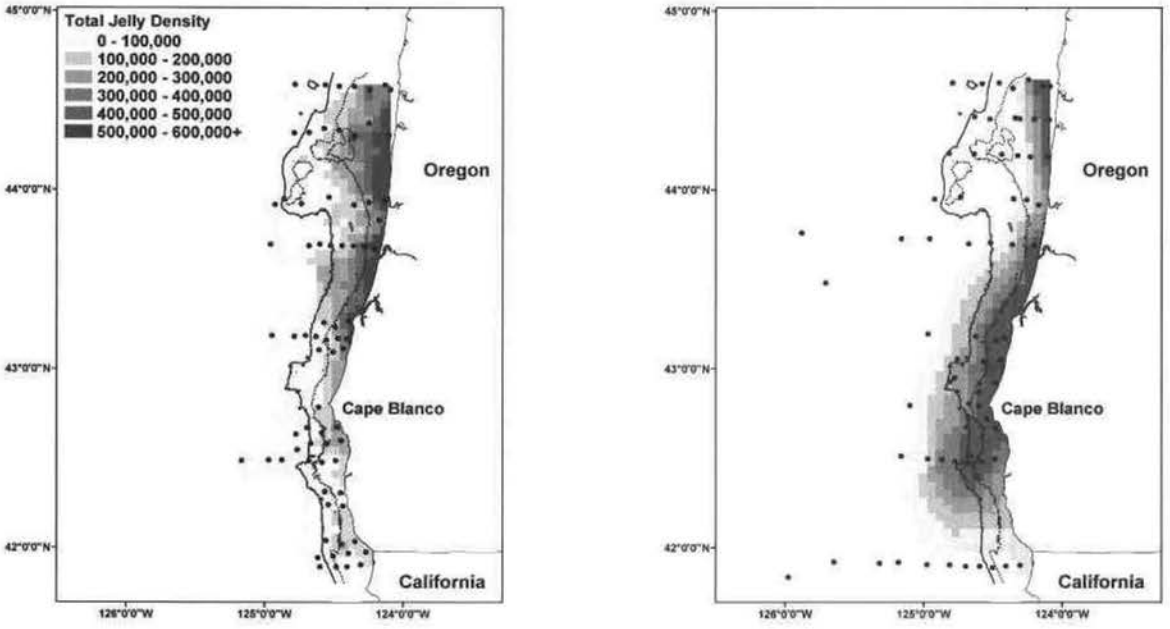
Total jellyfish densities differed significantly between the cruises (Kruskal-Wallis test, $H_{3,290} = 17.42$, $p < 0.001$) with higher densities occurring during the August 2002 cruise and lowest densities during both June and August 2000 (U-test, $p<0.01$). Total jellyfish densities varied between the hotspot and non-hotspot regions and during both June 2000 and 2002 were highest in the Heceta Bank (HB) hotspot region (Table 4.1). During August 2000, jellyfish density was highest in the non-hotspot region and during August 2002 highest in the Crescent City (CC) hotspot region.

Different degrees of spatial correlation were fitted to total jellyfish densities according to the cruises, with a spatially structured density component $[C/(C_0 + C)]$ ranging from 51 to 73%. The spatially structured density component is a measure of the degree of spatial correlation in the data and therefore can be used as a measure of goodness of fit. In June 2000, the spatial correlation of jellyfish density best fit an isotropic, exponential model with a major range of spatial dependence of about 12 km

(Figure 4.1) and a spatially structured component of 72.5%. In August 2000, the spatial correlation again best fit an exponential model; however, during this cruise directional influences were present. The direction of the major axis was determined to be about 5° from north and represents the direction over which spatial scales are longest (here roughly parallel with the coastline), whereas the minor axis represents the direction of the strongest gradient (onshore-offshore) (Figure 4.1). The major and minor ranges over which spatial dependence was apparent were about 162 and 89 km, respectively, and with a spatially structured component of 62.4%. During June 2002, the spatial correlation best fit a spherical model and again directional influences were present. The direction of the major axis was determined to be about 95° indicating the direction of the strongest gradient was generally in the north-south direction (Figure 4.1). The major and minor ranges over which spatial dependence was apparent were about 67 and 21 km, respectively, and with a spatially structured component of 51.7%. During August 2002, the spatial correlation of jellyfish density best fit an isotropic, exponential model with a major range of spatial dependence of about 29 km (Figure 4.1) and a spatially structured component of 61.4%.

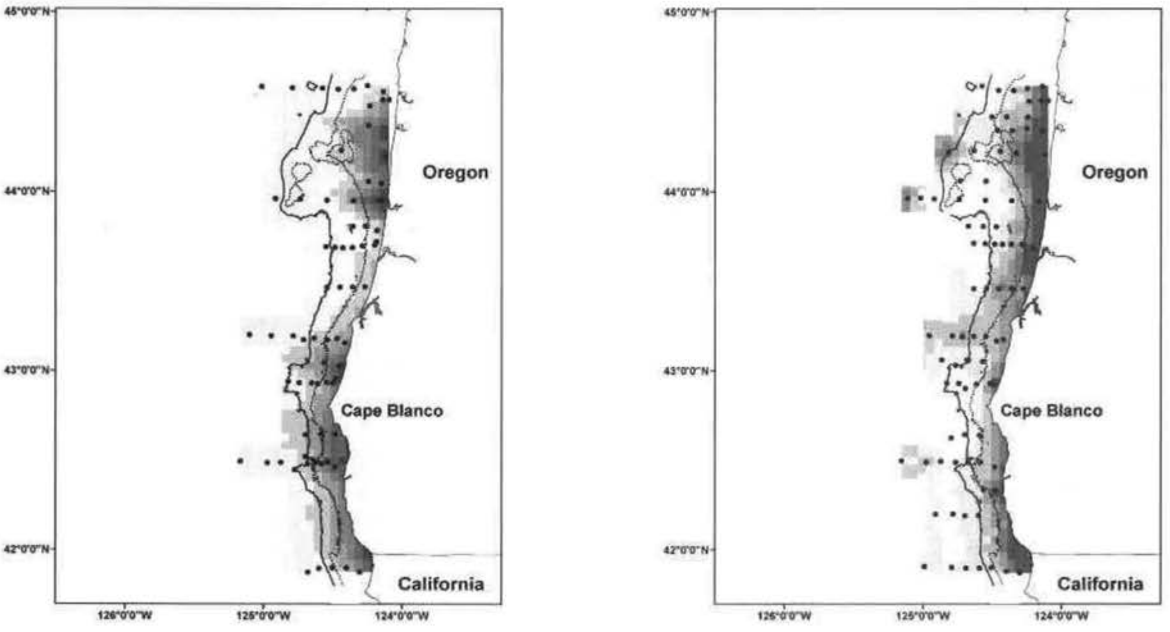
Locations of mean jellyfish densities greater than the cruise-wide mean were identified for each cruise and then all four cruises were combined. This allowed for the determination of persistent high jellyfish densities throughout the study region. Persistent high jellyfish densities were located near the coast, primarily north of Cape Blanco and immediately south of the Cape (Figure 4.2).

Nekton hotspots identified in Reese and Brodeur (2006) were used to examine the



a) June 2000

b) August 2000



c) June 2002

d) August 2002

Figure 4.1. Kriging maps of total jelly densities (#/km^3) throughout the study region for: (a) June 2000; (b) August 2000; (c) June 2002; and (d) August 2002. Dots represent station locations. The solid contour represents the 200 m isobath and the hatched contour represents the 100 m isobath.

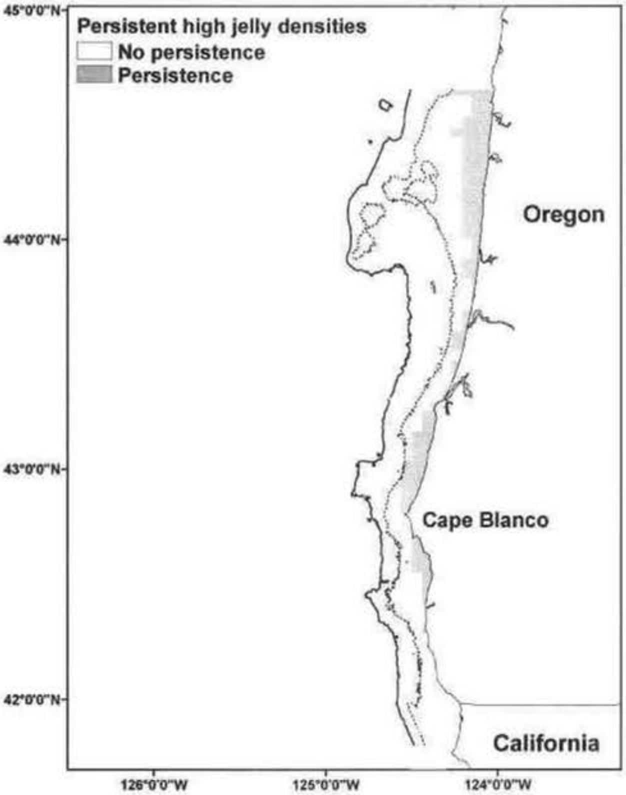
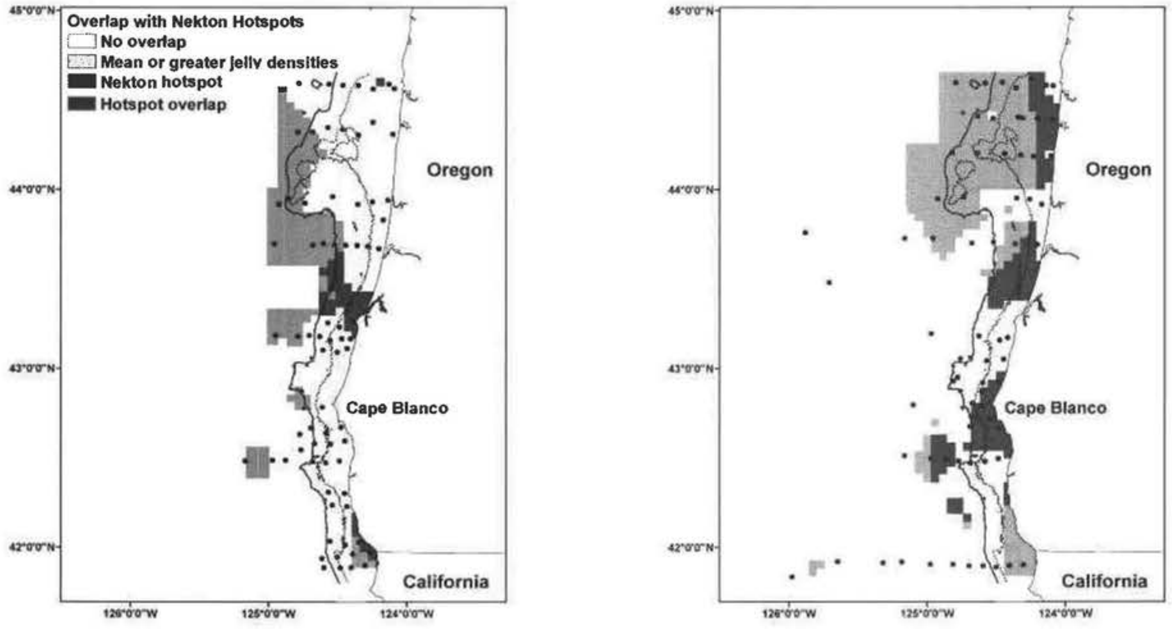


Figure 4.2. Persistent high jelly densities (#/km^3) over the four cruises. Shaded areas indicate 5km grid cells with density values equal to or greater than overall mean values for each cruise. The solid contour represents the 200 m isobath and the hatched contour represents the 100 m isobath.

overlap of nekton hotspots and above average jellyfish densities for each of the four cruises (Figure 4.3). Overlap is defined as the region of the above average densities that are within the hotspots (given as a percentage of overlap). The amount of overlap was similar between seasons and years with the exception of August 2002. During June and August 2000 and June 2002 the amount of overlap was 30%, 33%, and 36%, respectively; however, during August 2002 the amount of overlap increased to 46%. Jellyfish densities were consistently higher near the coast and consequently these areas are primarily where the overlap with the hotspots occurred (Figure 4.3). The greatest overlap occurred within the CC hotspot region during both the June and August 2002 cruises. Overlap with the HB hotspot tended to be along the nearshore side of the hotspot for all cruises. During August 2002, however, elevated jellyfish densities were encountered offshore near the shelf-break (200 m isobath) and thus led to the offshore overlap.

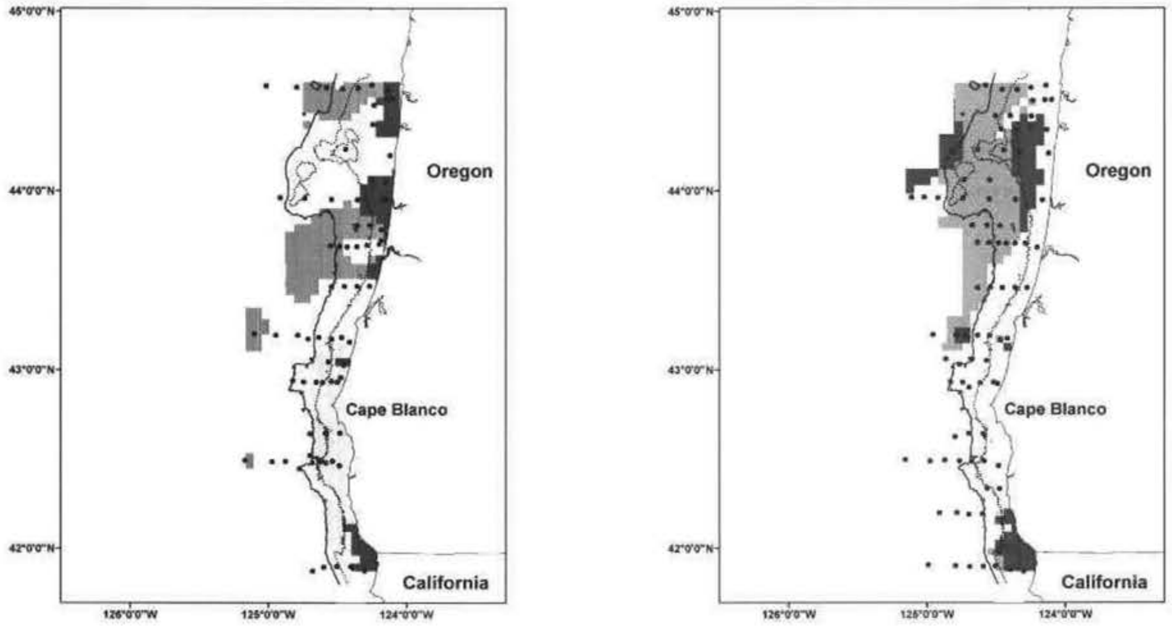
Distribution of nekton and jellies

A total of 41 dominant taxa were present in 290 surface trawls over the four cruises. Dominant taxa are those that were encountered in at least 5% of the samples for a given cruise and their frequency of occurrences within and outside hotspot regions are displayed in Table 4.2. The four large medusae were among the most frequently occurring organisms throughout the study region (Table 4.2). The hydromedusa *Aequorea* sp. was frequently encountered in both hotspot and non-hotspot regions. One of the scyphomedusae, *Chrysaora fuscescens*, was numerically the most abundant species



a) June 2000

b) August 2000



c) June 2002

d) August 2002

Figure 4.3. Spatial overlap of nekton hotspots and above average jelly densities (#/km^3) for the four cruises: (a) June 2000; (b) August 2000; (c) June 2002; and (d) August 2002. Shaded areas indicate 5km grid cells. Dots represent station locations. The solid contour represents the 200 m isobath and the hatched contour represents the 100 m isobath.

Table 4.2. Phylogenetic listing of the dominant jelly and nekton species caught within the hotspot and non-hotspot regions during each cruise. Numbers represent frequency of occurrence, dashed lines (-) represent the absence of that species during a particular cruise. Notation as in Table 4.1. (a) and (j) indicate adults and juveniles, respectively. The sample size associated with each region is given as n.

		June 2000			August 2000			June 2002			August 2002		
Class, Family, and Species	Common Name	No HS (n=51)	HBHS (n=14)	CCHS (n=8)	No HS (n=39)	HBHS (n=19)	CCHS (n=9)	No HS (n=45)	HBHS (n=22)	CCHS (n=3)	No HS (n=49)	HBHS (n=28)	CCHS (n=3)
Hydrozoa													
Aequoreidae													
Aequorea sp.	Jelly hydromedusa	27	7	4	16	3	2	34	14	3	27	19	0
Scyphozoa													
Pelagiidae													
Chrysaora fuscescens	Sea nettle	15	4	4	11	3	6	23	18	2	29	17	0
Ulmaridae													
Aurelia labiata	Moon jelly	16	1	7	16	1	9	19	5	3	34	5	3
Phacellophora camtschatica	Egg-yolk jelly	-	-	-	7	0	3	10	3	2	25	8	2
Cephalopoda													
Loliginidae													
Loligo opalescens	Market squid	4	4	5	-	-	-	17	18	2	15	21	3
Onychoteuthidae													
Onychoteuthis borealijaponicus	Pacific clubhook squid	1	5	0	-	-	-	6	0	0	-	-	-
Chondrichthyes													
Carcharhinidae													
Prionace glauca	Blue shark (a)	-	-	-	6	2	0	-	-	-	5	8	0
Squalidae													
Squalus acanthias	Spiny dogfish (a)	-	-	-	-	-	-	2	5	1	-	-	-

Table continued on next page

Table 4.2 continued

Class, Family, and Species	Common Name	June 2000 No HS (n=51)	June 2000 HBHS (n=14)	June 2000 CCHS (n=8)	August 2000 No HS (n=39)	August 2000 HBHS (n=19)	August 2000 CCHS (n=9)	June 2002 No HS (n=45)	June 2002 HBHS (n=22)	June 2002 CCHS (n=3)	August 2002 No HS (n=49)	August 2002 HBHS (n=28)	August 2002 CCHS (n=3)
Osteichthyes													
Ammodytidae													
Ammodytes hexapterus	Pacific sandlance (j)	4	0	0	-	-	-	7	5	0	-	-	-
Anarhichadidae													
Anarrhichthys ocellatus	Wolf-ell (j)	4	3	2	1	0	4	7	0	3	6	7	1
Anoplopomatidae													
Anoplopoma fimbria	Sablefish (j)	10	3	0	-	-	-	-	-	-	1	4	0
Bothidae													
Citharichthys sordidus	Pacific sanddab (j)	3	1	0	-	-	-	-	-	-	-	-	-
Citharichthys sordidus	Pacific sanddab (a)	-	-	-	-	-	-	1	6	0	-	-	-
Citharichthys stigmaeus	Speckled sanddab (j)	4	6	0	-	-	-	-	-	-	-	-	-
Citharichthys spp.	Sanddabs (j)	7	2	0	-	-	-	-	-	-	-	-	-
Carangidae													
Trachurus symmetricus	Jack mackerel (a)	-	-	-	6	12	0	7	1	0	4	12	0
Centrolophidae													
Icichthys lockingtoni	Medusafish (a)	-	-	-	2	0	3	-	-	-	10	2	0
Clupeidae													
Clupea pallasi	Pacific herring (a)	2	1	6	-	-	-	1	7	1	5	6	3
Sardinops sagax	Pacific sardine (a)	-	-	-	3	8	1	16	3	0	3	9	0
Cottidae													
Scorpeanichthys marmoratus	Cabezon (j)	3	4	0	-	-	-	-	-	-	-	-	-

Table continued on next page

Table 4.2 continued

Class, Family, and Species	Common Name	June 2000			August 2000			June 2002			August 2002		
		No HS (n=51)	HBHS (n=14)	CCHS (n=8)	No HS (n=39)	HBHS (n=19)	CCHS (n=9)	No HS (n=45)	HBHS (n=22)	CCHS (n=3)	No HS (n=49)	HBHS (n=28)	CCHS (n=3)
Engraulididae													
Engraulis mordax	Northern anchovy (j)	-	-	-	3	2	0	-	-	-	-	-	-
Engraulis mordax	Northern anchovy (a)	-	-	-	-	-	-	2	4	0	0	8	0
Gadidae													
Microgadus proximus	Pacific tomcod (j)	-	-	-	-	-	-	-	-	-	8	6	1
Hexagrammidae													
Ophiodon elongatus	Lingcod (j)	5	0	1	-	-	-	-	-	-	-	-	-
Icosteidae													
Icosteus aenigmaticus	Ragfish (j)	-	-	-	-	-	-	-	-	-	4	1	1
Osmeridae													
Hypomesus pretiosus	Surf smelt (a)	0	1	6	1	0	5	-	-	-	0	1	3
Osmeridae	Smelt (j)	2	1	1	3	1	0	4	1	0	-	-	-
Pleuronectidae													
Errex zachirus	Rex sole (j)	4	8	0	6	3	0	13	1	2	11	8	0
Salmonidae													
Oncorhynchus tshawytscha	Chinook salmon (a)	7	1	4	1	8	7	15	15	2	10	15	1
Oncorhynchus tshawytscha	Chinook salmon (j)	6	0	1	6	3	9	5	14	0	4	3	0
Oncorhynchus keta	Chum salmon (j)	-	-	-	-	-	-	1	6	0	-	-	-
Oncorhynchus kisutch	Coho salmon (a)	-	-	-	4	11	3	5	8	0	2	11	0
Oncorhynchus kisutch	Coho salmon (j)	11	0	1	3	9	3	6	13	0	3	12	0
Oncorhynchus clarki	Cutthroat trout (j)	-	-	-	-	-	-	-	-	-	1	5	0
Oncorhynchus mykiss	Steelhead trout (j)	4	0	2	5	1	5	2	2	1	4	1	0

Table continued on next page

Table 4.2 continued

Class, Family, and Species	Common Name	June 2000			August 2000			June 2002			August 2002		
		No HS (n=51)	HBHS (n=14)	CCHS (n=8)	No HS (n=39)	HBHS (n=19)	CCHS (n=9)	No HS (n=45)	HBHS (n=22)	CCHS (n=3)	No HS (n=49)	HBHS (n=28)	CCHS (n=3)
Scomberesocidae													
Cololabis saira	Pacific saury (a)	-	-	-	3	0	2	-	-	-	2	4	1
Scombridae													
Scomber japonicus	Chub mackerel (a)	-	-	-	1	4	0	-	-	-	-	-	-
Scorpaenidae													
Sebastes alutus	Pacific ocean perch (j)	-	-	-	-	-	-	6	2	0	-	-	-
Sebastes crameri	Darkblotched rockfish (j)	5	9	0	-	-	-	6	3	0	-	-	-
Sebastes flavidus	Yellowtail rockfish (j)	13	9	1	-	-	-	6	1	0	-	-	-
Sebastes melanops	Black rockfish (j)	-	-	-	-	-	-	5	3	0	-	-	-
Sebastes paucispinis	Bocaccio (j)	1	4	0	-	-	-	-	-	-	-	-	-
Sebastes pinniger	Canary rockfish (j)	2	3	0	-	-	-	4	2	0	-	-	-
Sebastes entomelas	Widow rockfish (j)	-	-	-	-	-	-	4	2	0	-	-	-
Sebastes spp.	Unidentified rockfish (j)	5	4	1	-	-	-	25	3	3	-	-	-

encountered. During June and August 2000, *C. fuscescens* was present in greater numbers close to shore and north of Cape Blanco. During the 2002 cruises, *C. fuscescens* was frequently encountered in the Heceta Bank (HB) hotspot region. During all cruises *Aurelia labiata* was consistently rare in the HB hotspot region in the north yet frequently encountered in the CC hotspot region in the south. The relatively small size of the CC hotspot region as determined from our cruise coverage results in a particularly low number of stations sampled in that region, especially during the 2002 cruises. Consequently, the low number of occurrences within the CC hotspot may reflect a large proportion of encounters within this region. During June 2000, *Phacellophora camtschatica* was only encountered at one station and was therefore not a dominant species during that cruise. During August 2000 and both of the 2002 cruises, *P. camtschatica* was most frequently encountered in the CC hotspot and non-hotspot regions.

Of the two species of cephalopods, market squid (*Loligo opalescens*) were most frequently encountered and were frequently encountered in both the HB and CC hotspot regions (Table 4.2). Proportionally, *L. opalescens* were relatively rare in the non-hotspot region. Pacific clubhook squid (*Onychoteuthis borealijaponicus*) was more abundant in the northern part of the study region and was encountered most frequently in the non-hotspot and HB hotspot regions. Although the frequency of occurrence of blue sharks (*Prionace glauca*) was relatively low, they were encountered most frequently in the HB hotspot and non-hotspot regions, and were absent from the CC hotspot stations. Spiny dogfish (*Squalus acanthias*), although only considered a dominant species during June 2002 were associated with the hotspot regions.

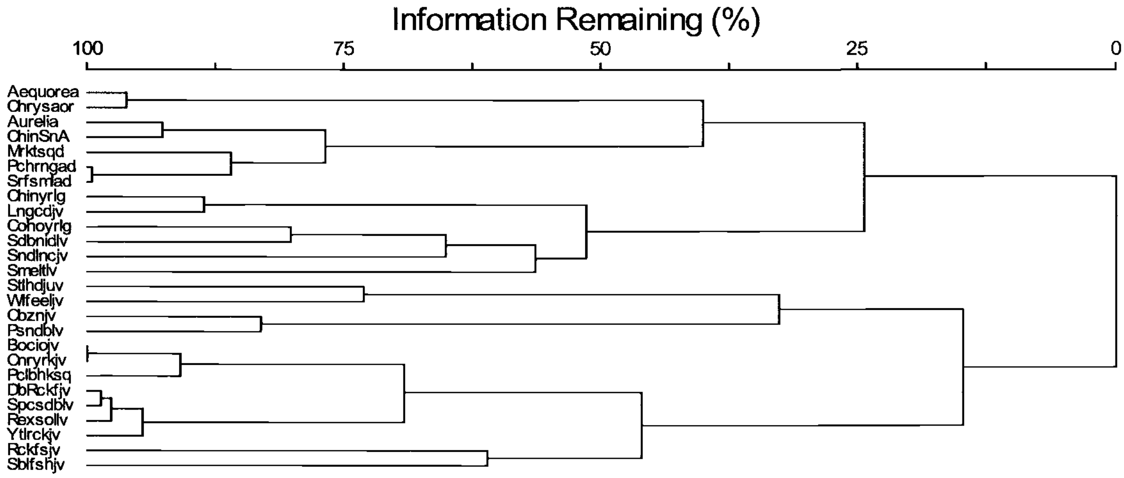
Of the teleosts, Chinook (*Oncorhynchus tshawytscha*) and coho (*O. kisutch*) salmon were among the most frequently occurring species (Table 4.2). Adult Chinook salmon were encountered most frequently at stations within the HB hotspot region and were more prevalent within both hotspots than in the non-hotspot region. Juvenile Chinook salmon tended to also be associated more with the hotspot regions than with the non-hotspot region. Adult coho salmon were most frequently encountered in the HB hotspot region. With the exception of June 2000, juvenile coho salmon were most frequently encountered in the HB hotspot as well. Juvenile steelhead trout (*O. mykiss*) proportionally were most frequently encountered in CC hotspot stations, with the exception of August 2002.

Jack mackerel (*Trachurus symmetricus*) were more frequently encountered in the HB hotspot region in August of 2000 and 2002 than in any other region. Pacific herring (*Clupea pallasi*) were encountered in greater proportions in both the HB and CC hotspot regions (Table 4.2). Pacific sardines (*Sardinops sagax*) were more frequently encountered in the HB hotspot region in the north, particularly during the August cruises, and rare in the CC hotspot region. Northern anchovies (*Engrulis mordax*) were more frequently associated with the HB hotspot in the north. Anchovies were rarely encountered in the non-hotspot region and never in the CC hotspot region. Surf smelt (*Hypomesus pretiosus*) were more frequently associated with the CC hotspot than any other region. Similarly, Pacific saury (*Cololabis saira*) were, proportionally, more frequently encountered in the CC hotspot region than in any other region.

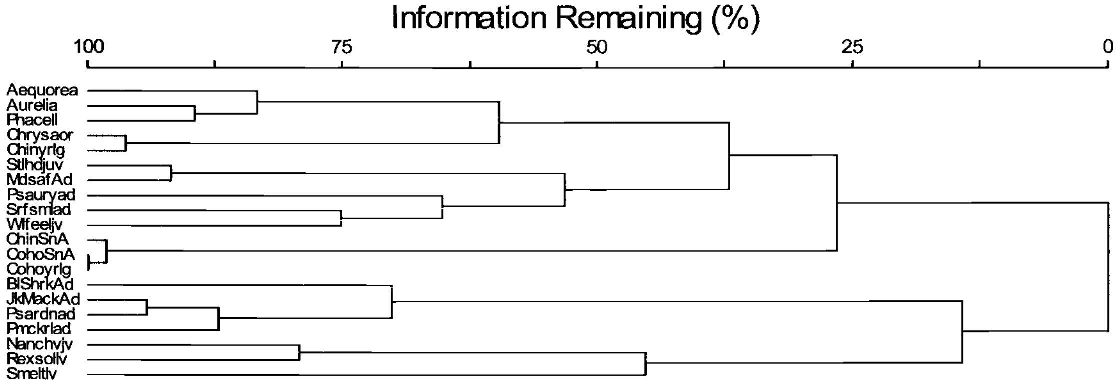
Juvenile rockfish species were also among the most dominant species encountered, however, they were only dominant during the June cruises when they are present in the surface waters (Table 4.2). During June 2000, darkblotched rockfish (*Sebastes crameri*), yellowtail rockfish (*S. flavidus*), bocaccio (*S. paucispinis*), canary rockfish (*S. pinniger*), and unidentified rockfish (*Sebastes* spp.) were frequently associated with the HB hotspot region. However, during June 2002, these same species, along with widow rockfish (*S. entomelas*), were encountered equally within the HB hotspot and non-hotspot regions. This is likely due to the shape of the HB hotspot during June 2002 given the relatively low number of sample stations within the region compared to the other cruises (Figure 4.3). The few stations sampled in this region were consequently weighted more heavily and therefore resulted in much of the region being classified as a non-hotspot region.

Species associations

Cluster analyses of species based on sample station assemblages identified species groups for each cruise (Figure 4.4; see Appendix 2 for coded species names). To classify groups, the cutoff levels were determined by balancing a low percentage of information remaining (approximately 30%) in the model while retaining biologically meaningful groups. For June 2000 and 2002 and August 2000, this cutoff resulted in four groups.

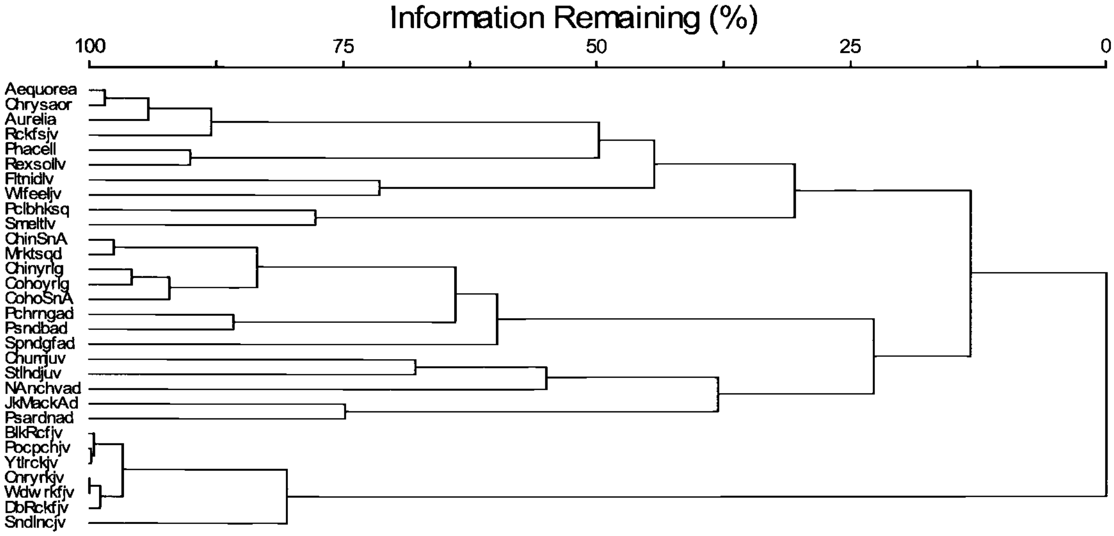


(a) June 2000

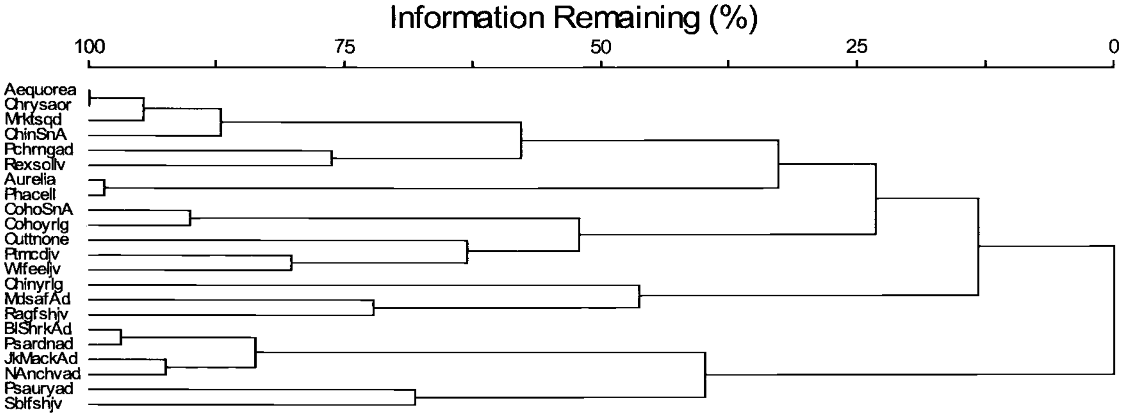


(b) August 2000

Figure 4.4. Cluster dendrograms of species associations for each cruise (a) June 2000, (b) August 2000, (c) June 2002, and (d) August 2002. *Continued on next page.*



(c) June 2002



(d) August 2002

Figure 4.4. Continued from previous page.

For August 2000, the cutoff was made at approximately 37% and resulted in five species groups.

During all cruises all large medusae clustered together, however the species with which they were associated varied by cruise. During June 2000, medusae were grouped with adult Chinook salmon, Pacific herring, surf smelt, and market squid (Figure 4.4). The remaining cluster groups consisted primarily of juvenile species. Cluster group two included juvenile Chinook and coho salmon which clustered with the following juvenile species: lingcod, unidentified sanddabs, sandlance, and smelt. A third group consisted of juvenile steelhead, and juvenile wolf-eels, juvenile cabezon, and juvenile Pacific sanddabs. The fourth group consisted of Pacific clubhook squid and primarily juvenile rockfish species.

For the August 2000 cruise, five cluster groups were formed. In the first cluster group large medusae were grouped with Chinook salmon juveniles (Figure 4.4). Steelhead grouped with adult medusafish, Pacific saury, surf smelt, and juvenile wolf-eels. The third grouping consisted of salmonids: adult Chinook and adult and juvenile coho salmon. A fourth group consisted primarily of adult pelagic species and the fifth group of juveniles.

During June 2002, four cluster groups were formed with the first group comprised of large medusae, several juvenile nekton species, and Pacific clubhook squid (Figure 4.4). The second group consisted primarily of predatory nekton including juvenile and adult Chinook and coho salmon and market squid. The third group was composed of juvenile chum salmon and several pelagic zooplanktivores and grazers including: adult jack mackerel, adult northern anchovies, and adult Pacific sardines. The fourth group consisted primarily of juvenile rockfish species.

For the August 2002 cruise, the four large medusae were grouped with market squid, adult Chinook salmon, adult Pacific herring, and juvenile rex sole (Figure 4.4). The second species grouping was composed of juvenile and adult coho salmon, cutthroat trout, and juvenile Pacific tomcod and wolf-eels. The third grouping consisted of juvenile Chinook salmon, medusafish, and juvenile ragfish. The fourth group was composed primarily of adult pelagic species including: blue sharks, jack mackerel, Pacific saury, Pacific sardines, and northern anchovies, as well as juvenile sablefish.

For all cruises, several dominant species, separated into age classes, were found to be strongly correlated (Spearman's rho, $p < 0.01$) (Figure 4.5). Nine positive and nine negative correlations were found between the large medusae and nekton species. Of the large medusae, *Chrysaora fuscescens*, the most abundant species, was positively correlated with *Aequorea* sp., and *Aurelia labiata* was positively correlated with *Phacellophora camtschatica*. *C. fuscescens* and *Aequorea* sp. were also positively correlated with market squid. Positive correlations with *C. fuscescens* were also found for whitebait smelt and adult and juvenile Chinook salmon. *C. fuscescens* was negatively correlated with five nekton species including: adult jack mackerel, juvenile yellowtail rockfish, juvenile darkblotched rockfish, Pacific clubhook squid, and Pacific saury. *Aequorea* sp. and *A. labiata* were also negatively correlated with adult jack mackerel. *A. labiata* was positively correlated with adult surf smelt, while negative correlations were

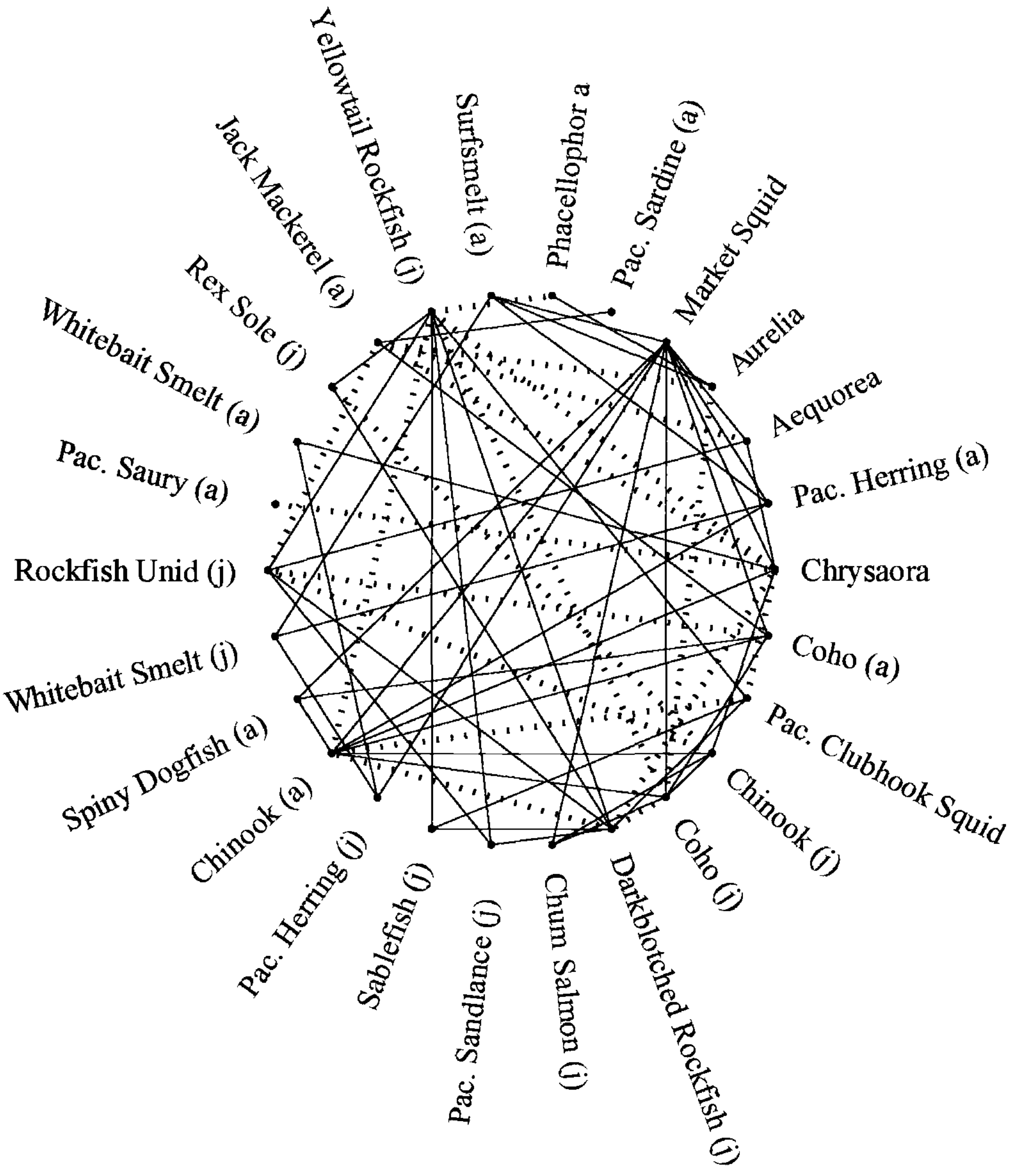


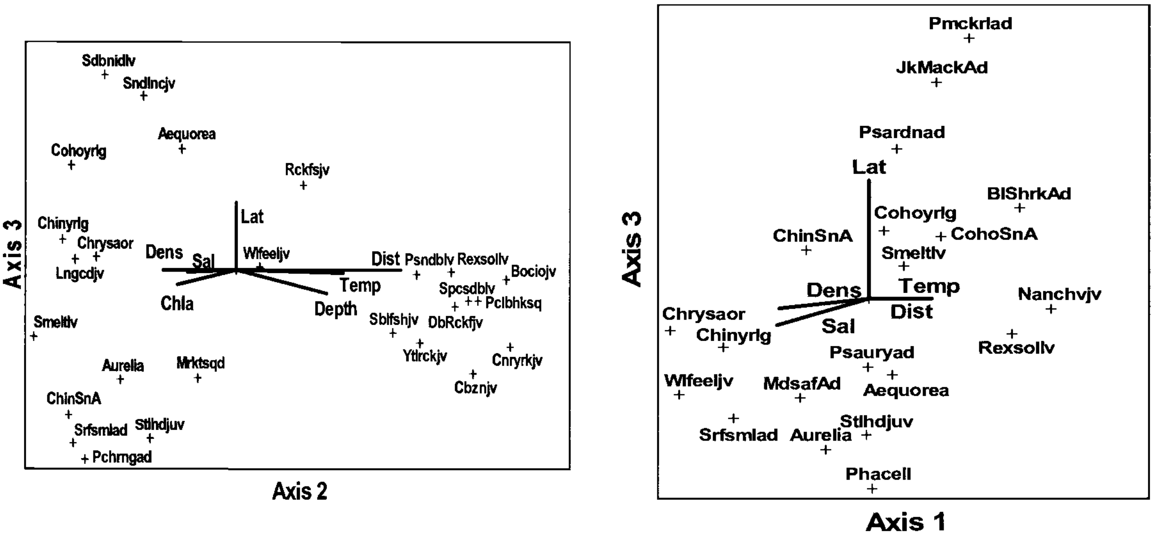
Figure 4.5. Correlation structure of the most abundant species and age classes for all cruises. Solid and dashed lines represent the most significant positive and negative correlations (p=0.01), respectively. Letters in parentheses denote either adults (a) or juveniles (j). Species and age classes are listed in order of overall abundance for the four cruises beginning with Chrysaora and continuing counter-clockwise.

found between *A. labiata* and juvenile coho, as well as between *P. camtschatica* and juvenile yellowtail rockfish.

Between the most abundant nekton species, 38 positive correlations and only 8negative correlations were found (Spearman's rho, $p < 0.01$) (Figure 4.5). Pacific herring, the most abundant nekton species, were positively correlated with market squid, adult surf smelt and Chinook salmon, and juvenile whitebait smelt. Market squid, juvenile yellowtail rockfish, and adult Chinook salmon were each correlated with 10 species. All 10 of the correlations with market squid were positive and tended to be with piscivores. Juvenile yellowtail rockfish were positively correlated with 6 species that tended to be zooplanktivorous and negatively correlated with 4 species that tended to be piscivorous. Adult Chinook salmon were positively correlated mostly with other piscivores (4 species) and negatively correlated with zooplanktivores (3 species). The majority of strong negative correlations were, in fact, between species that tend to be zooplanktivorous and those that are piscivorous or jellyfish (Figure 4.5).

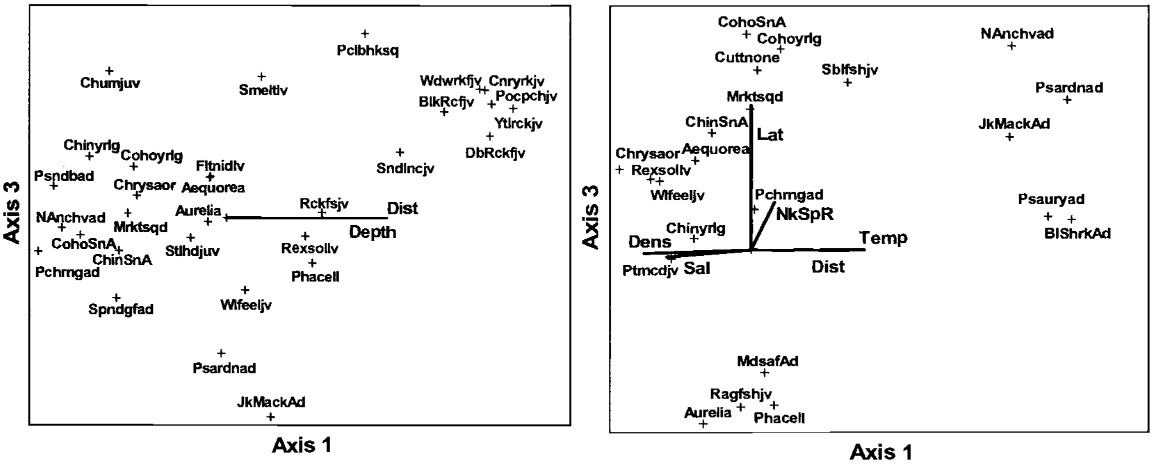
Species and environmental characteristics

Non-metric multidimensional scaling ordinations depicted dominant species associations and significant environmental correlates for each cruise (Figure 4.6). Species and age classes tended to group as determined by the cluster analyses (Figure 4.4). In June 2000, most of the variance was captured by two dimensions representing 42.7% and 25.7%, respectively, of the variance in the data (cumulative for 3-dimensional solution = 83.0%; stress = 14.96). Large medusae, market squid, adult Chinook salmon,



a) June 2000

b) August 2000



c) June 2002

d) August 2002

Figure 4.6. Nonmetric multidimensional scaling (NMS) ordination plots of species with environmental parameters from (a) June 2000, (b) August 2000, (c) June 2002, and (d) August 2002. The angles and lengths of the lines indicate the direction and strength of the relationships of the given parameters. Most significant vectors shown denote: chlorophyll concentration (Chla), density (Dens), depth (Depth), distance from shore (Dist), latitude (Lat), nekton species richness (NkSpR), salinity (Sal), and temperature (Temp).

Pacific herring, and surf smelt were all associated with lower temperatures, higher chlorophyll concentrations, higher salinities and densities, as are characteristics of nearshore, upwelling areas such as the Crescent City (CC) hotspot region (Figure 4.6; Table 4.1). In contrast, an offshore group at mid-latitudes within the range sampled, was composed primarily of rockfish species, and associated with warmer, offshore water that was less saline and had lower chlorophyll concentrations, characteristics associated with the Heceta Bank (HB) hotspot region (Table 4.1).

In August 2000, most of the variance was captured by two dimensions representing 16.5% and 42.9%, respectively, of the variance in the data (cumulative for 3-dimensional solution = 75.5%; stress = 16.84). In August 2000, there was a strong north-south component represented by axis 3 (r = 0.724) (Figure 4.6). Two of the cluster groups consisting of 1) large medusae and juvenile Chinook salmon and 2) juvenile steelhead and wolf-eels, and adult medusafish, Pacific saury, and surf smelt, were associated with cooler, higher salinity and density water that was closer to shore and in the southern part of the study area, characteristics of the CC hotspot region (Figure 4.6, Table 4.1). The salmonid cluster group was associated with mid-latitudes and at mid-depths. Blue sharks, adult mackerel and Pacific sardines were associated with warmer, offshore water in the northern part of the study area. Similarly, juvenile Northern anchovies, rex sole, and smelt were associated with warmer, offshore waters, however, at mid-latitudes.

During June 2002, most of the variance was captured by two dimensions representing 39.6% and 23.2%, respectively, of the variance in the data (cumulative for 3-dimensional solution = 84.1%; stress = 15.59). In June 2002, distance from shore and water depth were the only environmental parameters that explained the species distributions (Figure 4.6). Large medusae were all associated with shallower depths and were relatively closer to shore (Figure 4.6). Similarly, most of the predatory nekton were associated with shallower depths and closer to shore. In contrast, the rockfish cluster group was associated with deeper depths and further offshore.

In August 2002, most of the variance was captured by two dimensions representing 33.7% and 41.8%, respectively, of the variance in the data (cumulative for 3-dimensional solution = 84.1%; stress = 14.91). As in August 2000, there was again a strong north-south component represented by axis 3 ($r = 0.80$) (Figure 4.6). *Aequorea* sp., *Chrysaora fuscescens*, market squid, and adult Chinook salmon were associated with cooler, less saline water, closer to shore and at latitudes that were in the middle to northern part of the study region. *Aurelia labiata* and *Phacellophora camtschatica* were associated with similar environmental characteristics, however, in the southern part of the study region. Juvenile and adult coho salmon were associated with similar environmental conditions but in the north. Adult, pelagic species including blue sharks, Pacific sardines, jack mackerel, Northern anchovies, and Pacific saury were associated with warmer, offshore water with lower salinity and density, characteristic of the HB hotspot region (Figure 4.6, Table 4.1). In addition, this group tended to be associated with areas of increased nekton species richness.

Rare species distributions

The distributions of the omitted rare species were examined to identify regions with which they tended to more closely associate. During each cruise, the mean number of rare species at each station was lower in the non-hotspot regions than in either the Heceta Bank (HB) or Crescent City (CC) hotspot regions (Figure 4.7). Statistical tests were not performed given the large differences in sample sizes between the different regions. Nonetheless, more rare species were found within the HB hotspot region in both June and August 2000, however, more rare species were found within the CC hotspot region in August 2002. During June 2002, about equal numbers of rare species were found within the hotspot regions. In addition, during June 2002, more rare species were found in the non-hotspot region than during any other time period. In fact, during this cruise, the mean number of rare species in the non-hotspot region was greater than those found in the CC hotspot region during August 2000 or in the HB hotspot region during August 2002.

Discussion

The occurrence of contrasting environmental conditions between 2000 and 2002 off the West Coast of the United States provided an exceptional opportunity to examine community dynamics with respect to biological hotspots within the area. The distributions of several fish species and jellyfish overlap spatially and temporally, leading to the possibility of interactions, such as competition and predation. The primary goal of this paper was to identify associated species in relation to biological hotspots. Several surface dwelling species were found to associate within the study region. Moreover, both

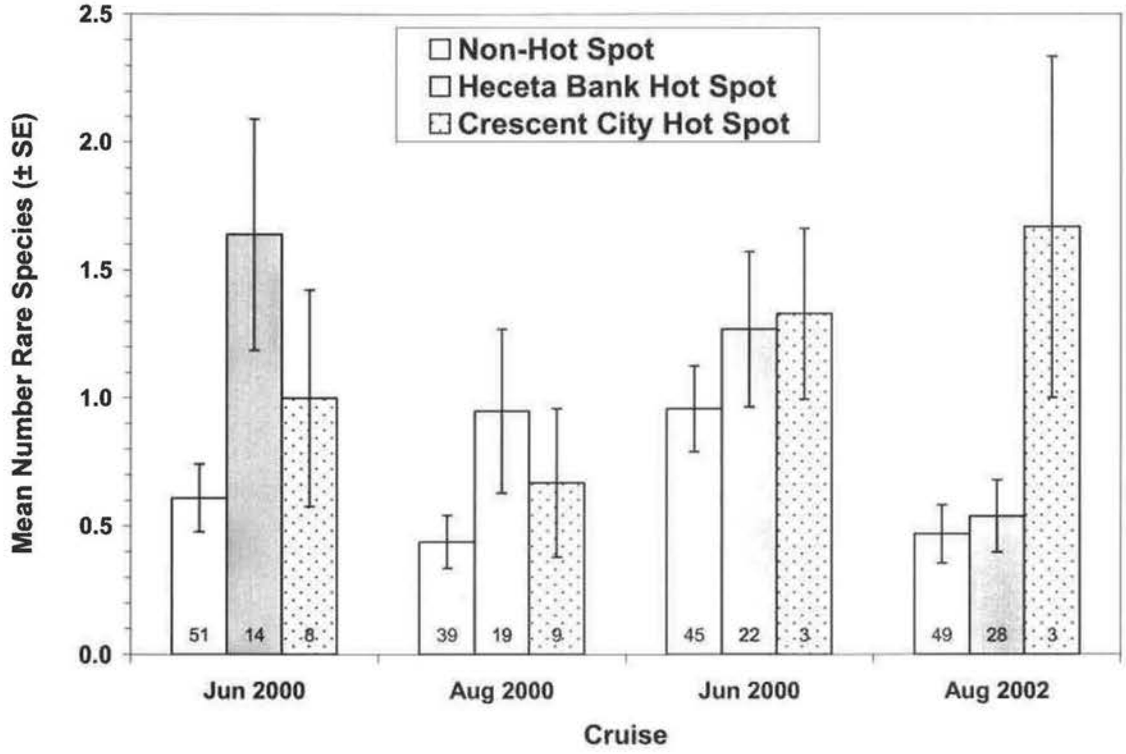


Figure 4.7. Mean number of rare species (± SE) at each sample station within each region. Numbers within the base represent the number of stations sampled within each region.

positive and negative associations were detected.

Considerable spatial and temporal variability with respect to environmental parameters were observed. Temperature, salinity, and density were among the most consistent parameters explaining the distribution of species in the study area, as well as characterizing the hotspot and non-hotspot regions. Temperatures were coldest in 2002, consistent with the anomalous intrusion of Subarctic Pacific water into the California Current system which resulted in increased nutrients and an increase in phytoplankton biomass within the region (Huyer, 2003; Wheeler et al., 2003). With respect to the biological hotspots, temperatures were coolest in the Crescent City (CC) hotspot and warmest in the Heceta Bank (HB) hotspot with intermediate values in the non-hotspot region. Salinity and density were highest during August cruises with highest values observed in the CC hotspot region to the south and lowest in the HB hotspot region in the north. These differences in environmental characteristics between the hotspots are due to the differences in the geographic locations and flow through the two areas. Flow through the region is generally towards the south during spring and summer with meanders and jets associated with topographical features, such as Heceta Bank and Cape Blanco (Barth, 2003; Barth et al., 2005). Two significant features are associated with the flow around Heceta Bank (Barth et al., 2005). The first is an onshore component to the flow around the southern flank of Heceta Bank at about 44° N and the second is a relatively weak flow inshore of the Bank. The resulting pattern of flow is the retention of water over the Bank (Barth et al., 2005). The CC hotspot region is located close to shore and is therefore greatly influenced by upwelling which brings cooler, higher salinity, nutrient-rich water to the surface. In the Pacific Northwest, the strength and duration of upwelling increases southward along the coast and therefore results in greater upwelling potential within this hotspot which is in the southern part of the study area (Hickey and Banas, 2003). In contrast, the HB hotspot is located further offshore, near the shelf-break and is thus influenced by warmer, offshore water. Also, since the HB hotspot is located in the northern part of the study area, it is influenced by lower salinity water associated with the Columbia River plume.

Coincident with the intrusion of Subarctic Pacific water during 2002 (Huyer, 2003; Wheeler et al., 2003) were the largest jellyfish densities. In addition, nekton species richness, density, and biomass also tended to be higher during 2002. Similarly, Brodeur et al. (2005) noted high species diversity during the same time period to the north off northern Oregon and Washington, yet overall nekton abundance was low. In particular, many common schooling pelagic forage fishes such as Pacific herring, Pacific sardine, smelts, and Northern anchovy were reported as absent or in low abundance in that study. In contrast, total nekton density was highest in the present study during June and August 2002. Moreover, Pacific herring was the dominant species caught during June 2002 representing approximately 92% of the total catch. During August 2002, abundances of Pacific herring, Pacific sardine, and surf smelt were also relatively high. This inverse relationship between forage fish from the two regions suggests the possibility that these fish were migrating out of the north to southern waters. Given the unusually high levels of primary production occurring throughout the region, these species may have been taking advantage of the anomalous conditions which resulted in high numbers of forage fish in the study area.

The four jellyfish species were found to overlap with the nekton biological hotspots during all cruises although the amount of overlap varied per cruise (Figure 4.3). Persistently high jellyfish densities were identified along the coast, particularly north of Cape Blanco and immediately to the south of the cape. Individual jellyfish species distributions can be found elsewhere in Suchman and Brodeur (2005). Although considerable overlap occurred during all cruises in the south within the CC hotspot, the HB hotspot was further offshore and tended to have less overlap with jellyfish except during August 2002. The greatest overlap occurred during both 2002 cruises, particularly during August when there was 46% overlap. During this cruise, jellyfish densities were particularly high and they were distributed further offshore than during the other cruises. The anomalous conditions that occurred during this cruise likely led to the increase in prey availability, such as euphausiid eggs, and thus supported the larger populations of jellyfish (Suchman et al., submitted). Nonetheless, the overlap with the HB hotspot was limited to the nearshore portion of the hotspot (Figure 4.3).

Just north of the current study, Brodeur et al. (2005) reported catches from central Oregon to northern Washington that were dominated by one species, northern anchovy, during June 2000. By September 2000, northern anchovy was rarely caught and dominance shifted to Pacific herring and Pacific sardines. In the present study, northern anchovy were rarely caught during any cruise and were not considered to be a dominant species. Nonetheless, Indicator Species Analysis indicated that there was a shift in the

Heceta Bank hotspot from one dominated by juvenile rockfish during June 2000 to one dominated by Pacific sardines, jack mackerel, and chub mackerel during August 2000. Pacific sardines were therefore abundant along much of the northern California Current.

Cluster analyses consistently grouped jellyfish species together (Figure 4.4). Individual jellyfish species were thus strongly correlated. In contrast, jellyfish species had many negative associations with nekton species (Figure 4.5). In general, the negative correlations were with nekton species that were typically encountered in the HB hotspot and thus further offshore beyond the peak distribution of the jellyfish. In contrast, the positive correlations with the jellyfish were with nekton species that were typically encountered closer to shore, especially with species associated with the CC hotspot such as market squid, whitebait smelt, and Chinook salmon. Ordinations of the species produced with nonmetric multidimensional scaling (NMS) suggest that the cluster groups and positive correlations among the species are related to the similarity in habitat preferences of the species (Figure 4.6).

Several species were determined previously to be significant indicators of either the HB or CC hotspots (Reese and Brodeur, 2006). Species correlated with these indicator species specify other species that may prefer similar habitats thus resulting in the positive correlations. Indeed, several species with positive correlations with these indicator species were identified within the two hotspots. For instance, adult Pacific herring, the most dominant nektonic species encountered, was previously determined to be a significant indicator species of the CC hotspot during two cruises: June 2000 and August 2002. Pacific herring was also found to be positively correlated with adult surf smelt (Figure 4.5). Surf smelt was found to be a significant indicator of the same hotspot region during the August 2000, June 2002, and August 2002 cruises. Since both of these species are zooplanktivores (T. Miller, Oregon State University, unpublished data), they occupy the same functional group yet, with the exception of August 2002, were dominant members within the same area during different times. NMS ordinations suggest that these species prefer habitats characterized by cooler, more saline water, closer to shore, in the southern part of the study area indicative of the nearshore upwelling area which is characteristic of the CC hotspot region. In addition, the mean densities of these two species varied yet strong positive correlations were found for each cruise except August 2000 when Pacific herring were absent. Within the CC hotspot, mean densities during June 2000 were comparable between the two species; however, Pacific herring were more faithful to the CC hotspot (as indicated by the ISA) whereas surf smelt were abundant outside the hotspot as well. During August 2000 and June 2002, Pacific herring were not found in high abundances within the CC hotspot yet surf smelt were. During August 2002, both species were in high abundance within the CC hotspot and were both determined to be indicator species for this area. In general, there appeared to be a flip in abundance within the CC hotspot such that an increase in abundance of one species corresponded with a decrease in abundance of the other species. Therefore, the potential for these two species to be complementary and redundant species exists since they occupy similar habitats, have overlapping distributions, and serve the same function within the ecosystem.

Similarly, adult Chinook and coho salmon typically clustered together, were positively correlated, and occupied similar habitats. Moreover, both were determined to be significant indicators of the HB hotspot yet during different cruises (coho salmon during August 2000 and Chinook salmon during June 2002). Diet analyses categorize both of these species within the same functional group, as secondary piscivores. Within the HB hotspot, mean densities of these two species varied by cruise yet strong positive correlations were found for the two cruises when these species were found to be significant indicators. Although the densities of these species remained positively correlated, there was a shift in abundance of these species within the hotspot such that Chinook salmon were more abundant during all cruises except August 2000 when coho salmon were determined to be more abundant and faithful to the HB hotspot and thus a significant indicator species within this area. Therefore, just as for the zooplanktivores, these two species have the potential to be complementary and redundant species.

The persistence of the Heceta Bank and Crescent City hotspots, despite changes in species composition and species dominance, suggests a possible resistance to change at the ecosystem level due to a complementarity of system function in that there may be a replacement of species by other species with similar function. This paper identifies potential complementary species in that many species tend to prefer similar habitats as determined by the NMS ordinations. In addition, rare species were consistently encountered more frequently in the hotspot regions than in the non-hotspot region (Figure 4.7). The function of rare species within an ecosystem is difficult to understand simply because they are rare (Lovejoy, 1988). Nevertheless, rare species may be important contributors to ecosystem function in their potential of replacing displaced members of a community which are lost due to changing environmental conditions or anthropogenic processes. The present study provides knowledge about species associations in the northern California Current and their potential for ecosystem stability within biological hotspots.

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DISTRIBUTION OF FUNCTIONAL GROUPS IN RELATION TO PERSISTENT BIOLOGICAL HOTSPOTS IN THE NORTHERN CALIFORNIA CURRENT ECOSYSTEM

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Abstract

The identification and function of marine, biological hotspots is a growing area of research and has broad implications for conservation, management, the design of marine protected areas, and monitoring purposes. The goals of this study are to: 1) determine if previously identified marine, biological hotspots persist over a decadal time period, and 2) compare the relative distributions of multiple functional groups over a broad geographic area in relation to the biological hotspots. Data from cruises during the 1980s regarding nekton species richness and abundance were compared to the distributions of biological hotspots determined from cruises during June and August 2000 and 2002. Nekton functional groups were defined in terms of trophic levels and consisted of grazers, zooplanktivores, primary piscivores, and secondary piscivores. A geostatistical approach was used to create surfaces in a Geographic Information System to determine the distributions of the functional groups relative to the locations of the biological hotspots. Results indicate that nekton biological hotspots in the northern California Current persisted across differing environmental and biological conditions, although upwelling-based hotspots may be more ephemeral and susceptible to climatic conditions than retention-based hotspots. In addition, the distributions of the functional groups are nonrandom and tend to occur within the hotspots indicating that the predominant biological activity is occurring within persistent, localized areas. The finding that large

regional areas are composed of smaller, localized hotspots where a predominant amount of biological activity is occurring, suggests that the evaluation of large marine ecosystems may lead to erroneous or misleading results if they do not consider the more localized biological hotspots.

Introduction

Biodiversity is distributed heterogeneously across the Earth often with peaks in localized areas (Gaston 2000). In terrestrial systems, persistent biodiversity hotspots are typically comprised of small-range specialists that are endemic to the hotspot areas (Stevens, 1989; Pagal et al., 1991; Smith et al., 1994; Blackburn and Gaston, 1996). The persistence of tropical terrestrial hotspots is believed to be due to the environmental predictability and stability in the regions which select for more specialized traits and thus result in more localized distributions of high species diversity (Stevens, 1989). The Central Indo-Pacific coral reef system, on the other hand, is one of the most distinctive and persistent regional hotspots on earth and is formed primarily from the combined contributions of numerous widespread species (Hughes et al., 2002). Central issues in ecological and environmental sciences over the past decade have been to understand the spatial patterns of biodiversity and to identify relationships between biodiversity and ecosystem function (Loreau et al., 2001).

The capacity of ecosystems to undergo extreme conditions is an important test of ecosystem function and is a measure of the fundamental ecosystem properties of resistance and resilience (Woodward, 1993). Moreover, ecosystem function and stability are related to increased biodiversity within the system (e.g., Tilman, 1996; McGrady-Steed et al., 1997; Naeem and Li, 1997; Petchey et al., 1999; Cardinale et al., 2002; Zavaleta and Hulvey, 2004). The enhancement is primarily due to the increased diversity associated with each functional group, suggesting that redundancy (multiple species per functional group) is a valuable trait (Naeem and Li, 1997).

Reese and Brodeur (2006) identified two temperate, marine biological hotspots based on surface nekton diversity, abundance, and/or biomass in the northern California Current. Both hotspots were found to persist seasonally and annually despite vastly different environmental conditions and community structure during those time periods. Further analyses of the communities associated with the hotspots found strong correlations in densities of species occupying similar trophic positions, as well as occupying similar habitats, suggesting that the persistence of these hotspots may be related to the redundancy within the system (Reese et al., 2006).

The California Current is a highly productive ecosystem, characterized by substantial spatial and temporal variability. In the past, this system has experienced dramatic shifts in both abundance and species composition at both the lower and higher trophic levels (Roemmich and McGowan, 1995; Emmett and Brodeur, 2000; Brodeur et al., 2003a; Peterson and Schwing, 2003). Strong seasonal variability within the California Current is due to the seasonal reversal in the alongshore winds north of 37° N, which are poleward in winter and equatorward in summer (Huyer, 2003). During summer with equatorward winds, the northern California Current experiences substantial wind-forced upwelling which results in high levels of primary production capable of supporting higher trophic levels (Barth et al., 2005). Interannual variability is typically associated with El Niño events (Chelton et al., 1982) and decadal variability appears to be related to large-scale regime shifts that change ocean characteristics over periods of decades (Mantua et al., 1997; Chavez et al., 2003). Recently, another form of variability was reported caused by the anomalous intrusion of cold, Subarctic Pacific waters into the California Current which greatly increased primary production in the pelagic ecosystem and led to anoxic events in the bottom water (Huyer, 2003; Wheeler et al., 2003; Granthan et al., 2004).

Communities are typically complex systems of many interacting species at various trophic levels, and one way to reduce this complexity is to group the species into categories, such as by their functional roles within the ecosystem (Krebs, 1985). To further elucidate spatial and temporal patterns of marine life and their potential roles in ecosystem function and stability, surface nekton species were grouped into four functional groups and their distributions analyzed with respect to known biological hotspots. The goals of this paper are to: 1) determine if previously identified marine biological hotspots persist over a decadal time period, and 2) compare the relative distributions of multiple functional groups over a broad geographic area in relation to the biological hotspots.

Methods

Study region and sampling design

Sampling was conducted at multiple stations as part of a mesoscale and fine-scale study within the U.S. GLOBEC Northeast Pacific Program (Batchelder et al., 2002). Four time periods were examined to identify seasonal and interannual patterns of community dynamics: during early summer (29 May to 11 June, 2000 and 1 June to 18 June, 2002: hereafter called June 2000 and June 2002 cruises, respectively) and during late summer (29 July to 12 August, 2000 and 1 August to 17 August, 2002: hereafter called August 2000 and August 2002 cruises, respectively). Sampling was conducted from chartered fishing vessels. The region of the California Current sampled extended from Newport, Oregon (44° 40' N) to Crescent City in northern California (approximately 42° N). Stations were sampled along five GLOBEC designated transects located 1, 5, 10, 15, 20, 25, and 30 nautical miles from shore and also at fine-scale sampling stations in areas of particular physical and/or biological interest (e.g., areas associated with fronts or eddies). Collections primarily took place during daytime but occasionally tows were made during twilight or nighttime (June 2000, n = 84; Aug 2000, n = 75; June 2002, n = 90; Aug 2002, n = 94). The analyses included in this paper were limited to collections made during daylight hours to avoid any changes in the day/night community structure.

Surface nekton were collected with a trawl towed in the surface layer (upper 18 m) at each station for 30 minutes at a speed of 6 km/hr with a Nordic 264 rope trawl (Nor'Eastern Trawl Systems, Inc., Bainbridge Island, WA) (see Brodeur et al. (2004) for additional sampling details). Nekton abundance was standardized for differences in effort between tows, based on the volume of water filtered per trawl.

Functional group classification

Nekton functional groups were determined based on the main component in the diet of collected animals (Brodeur et al., 1987; Brodeur and Pearcy, 1992, T. Miller, Oregon State University, unpublished data). Upon collection, individuals were immediately frozen and gut contents were later identified. Since organisms are known to alter their diets based on available food items and to feed on several different food items, the observed gut contents are representative of the diets of the species during the time periods encountered. The main component of the stomach contents was then determined to represent the diet of that particular species at the time of collection. The dominant component of the diet was then used to classify the species into one of the following functional groups: 1) grazer (feeding primarily on phytoplankton), 2) zooplanktivore (feeding primarily on zooplankton), 3) primary piscivore (feeding on grazers and zooplanktivorous fish), and 4) secondary piscivore (feeding on piscivorous fish). Because many of the nekton diets varied, the dominant component in the diet was used for classification. For instance, although sardines and anchovies were classified as grazers, they are omnivorous and also consumed euphausiids and other zooplankton. The classifications are meant to be general based on the main components in the diets of collected nekton. A total of 23 species were categorized into functional groups. In addition, multiple age classes of several species were included in the analysis (Table 5.1).

Spatial analysis

Table 5.1. List of species and age classes by functional group. Abbreviations indicate: sbyr = subyearling; yr = yearling; juv = juvenile; ad = adult.

Functional Group	Species	Common Name
Grazers	*Sardinops sagax*	Pacific sardine (ad)
	Engraulis mordax	Northern anchovy (ad)
Zooplanktivores	*Loligo opalescens*	Market squid (ad)
	Trachurus symmetricus	Jack mackerel (ad)
	Ophiodon elongatus	Lingcod (juv)
	Clupea pallasi	Pacific herring (ad)
	Cololabis saira	Pacific saury (ad)
	Merluccius productus	Pacific hake (ad)
	Ammodytes hexapterus	Pacific sandlance (juv)
	Anoplopoma fimbria	Sablefish (juv)
	Hypomesus pretiosus	Surf smelt (ad)
	Allosmerus elongatus	Whitebait smelt (ad)
	Sebastes pinniger	Canary rockfish (juv)
	Sebastes crameri	Darkblotched rockfish (juv)
	Sebastes flavidus	Yellowtail rockfish (juv)
	Sebastes entomelas	Widow rockfish (juv)
Primary Piscivores	*Oncorhynchus tshawytscha*	Chinook salmon (sbyr)
	Oncorhynchus tshawytscha	Chinook salmon (yr)
	Oncorhynchus kisutch	Coho salmon (juv)
	Oncorhynchus keta	Chum salmon (juv)
	Oncorhynchus clarki	Cutthroat (ad)
	Oncorhynchus mykiss	Steelhead (juv)
	Oncorhynchus mykiss	Steelhead (ad)
	Squalus acanthias	Spiny dogfish (ad)
Secondary Piscivores	*Prionace glauca*	Blue shark (ad)
	Oncorhynchus tshawytscha	Chinook salmon (ad)
	Oncorhynchus kisutch	Coho salmon (ad)

To identify the spatial patterns of nekton functional groups and thus identify relationships to nekton biological hotspot regions, geostatistical modeling techniques were employed and are discussed in detail in Reese and Brodeur (2006). Since the geostatistical methods employed in this paper for creating maps of the functional groups are the same as those used in Reese and Brodeur (2006) for identifying nekton biological hotspots, only a general description is presented here for illustrating the approach. Combined densities of the species belonging to each functional group were used to produce the density maps for each cruise.

Geostatistical analyses were completed by first calculating the empirical semivariogram. It was assumed that: (1) the spatial distribution of each variable was stable during the approximate 2 weeks of each cruise, and (2) the observed spatial patterns were the result of random processes (Johnston et al., 2001). Semivariance data clouds were used to examine the intrinsic stationarity assumption, such that the variance of the difference between two locations was the same between any two points at similar distances and direction (Johnston et al., 2001). Global trends and anisotropy were examined for each variable for their affect on surface predictions and these directional components were incorporated into the analyses when present (Johnston et al., 2001).

Large outlier values produce an increased nugget effect which consequently results in higher predicted values with greater uncertainty (Chiles and Delfiner, 1999). Thus, extreme outlier values were reduced to the value of the upper limit of the range not including the outlier, as suggested by Chiles and Delfiner (1999). The following equation given by Matheron (1971) was used to estimate the empirical semivariograms {γ(h)} by pooling pairs of observations:

$$\gamma(h) = \frac{\sum_{i=1}^{N_h} \{Z(x_i + h) - Z(x_i)\}^2}{2N(h)}$$

where $Z(x_i)$ is the value of the variable at location x_i, $Z(x_i + h)$ is the value separated from x_i by distance h (measured in meters), and $N(h)$ is the number of pairs of observations separated by distance h. To estimate the semivariogram values for each distance within the range of observations, exponential and spherical theoretical models were fit to the empirical semivariograms (Cressie, 1993). Kriging was then used to estimate the expected values of the variables for each cruise. Kriging uses weights, derived from the modeled semivariogram that characterizes the spatial structure of the data, to predict values at unsampled locations such that the nearest measured values have the most influence (Johnston et al., 2001). The predictor is then formed as the weighted sum of the data such that:

$$\hat{Z}(X_0) = \sum_{i=1}^{n} \lambda_i Z(X_i)$$

where, $Z(X_i)$ is the measured value at the ith location; λ_i is an unknown weight for the measured value at the ith location that minimizes prediction error (Cressie, 1993), and X_0 is the prediction location. The weighting factor, λ_i, therefore depends on three factors: 1) the semivariogram, 2) the distance to the prediction location, and 3) the spatial relationships among the sampled values around the prediction location. Cross-validation was used to evaluate model parameters and kriging results such that for each variable, multiple exponential and spherical models were evaluated and the best model was selected. ESRI's ArcGIS v8.3 with the geostatistical analyst extension was used in the spatial analyses (ESRI, Redlands, CA).

Although the data are not synoptic, the geostatistical method was used because it is ideal for identifying spatial patterns in a patchy environment. The maps are intended to elucidate broad-scale patterns in the distribution of surface nekton functional groups within the northern California Current. Geostatistically produced maps of sea surface temperature and chlorophyll closely resembled both satellite-derived maps and in situ sampling maps (Barth et al., 2005), thus supporting the assumption that the geostatistically produced maps are representative of ocean conditions during the four cruises (Reese et al., 2005).

Biological hotspots were previously described in Reese and Brodeur (2006) and were defined as areas with greater than average biological activity in terms of nekton species richness, nekton density, and/or nekton biomass. To identify the relationships of the functional groups with these biological hotspots, the geostatistically produced layers for the functional group densities and hotspots were combined and analyzed with ArcGIS v8.3 Spatial Analyst. From the geostatistically-produced layers, the mean or greater densities of each functional group were compared to the locations of the hotspots to identify the overlaps.

Historical data

Nekton data collected from June cruises in 1981, 1983, 1984, and 1985 (Brodeur and Pearcy, 1992; Brodeur et al., 2003b) were used to compare the locations of the biological hotspots as determined from cruises in June 2000 and 2002. Details of the sampling method are described in Pearcy and Fisher (1988, 1990) and Fisher and Pearcy (1994). Data from the 1980s were collected using purse seines with 32 mm mesh along a series of east-west transects off Oregon and Washington. In order to compare the historical data with data from 2000 and 2002, only historical data that spatially overlapped with the more recent surveys were used in the analyses.

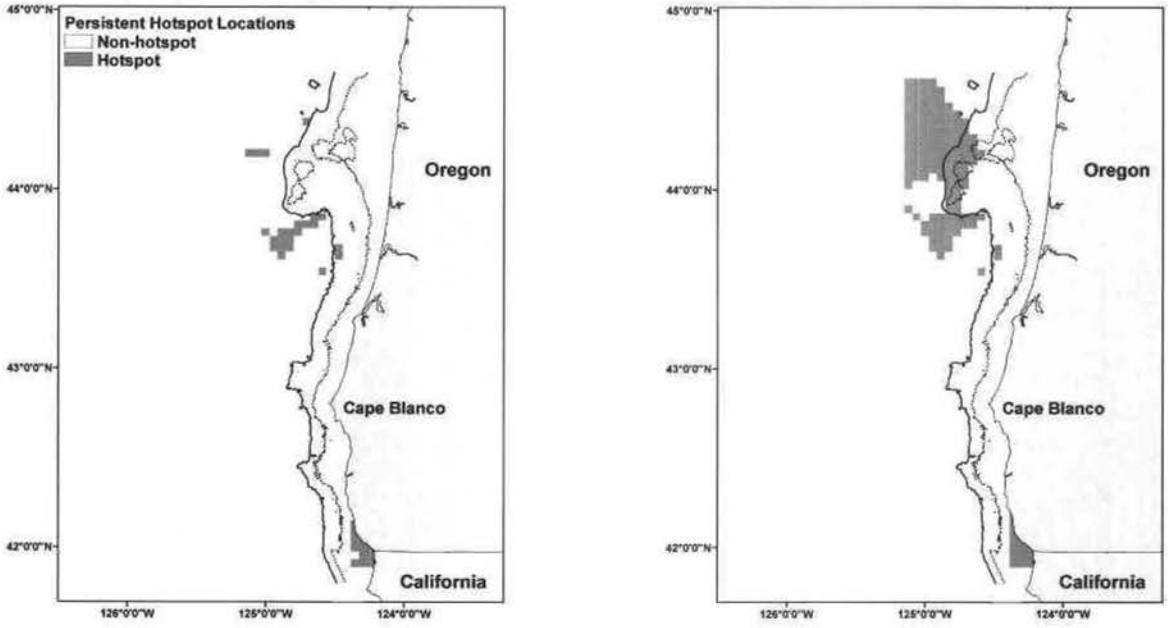
Because the biological hotspots were determined based on nekton species richness, densities, and/or biomass collected during 2000 and 2002, it was necessary to calculate species richness and total nekton abundance for each station during the 1980s. These values were then overlaid on the maps of the nekton biological hotspots determined from the 2000 and 2002 cruises for comparison. Because of the different collection methods, it is not suitable to compare species richness or abundance values between the two time periods. The purse seine used during the 1980s cruises sampled deeper water than the trawl used in the 2000 and 2002 cruises, therefore estimates of species richness and abundance are confounded by the inclusion of species found at deeper depths. Instead spatial patterns from each time period were treated separately and then the spatial patterns were compared. Reese and Brodeur (2006) found that although the general locations of the hotspots persisted, the sizes varied by season and year. Therefore, to maintain consistency, only June cruises from both time periods were used in the comparison. Since the sizes of the hotspots varied, the hotspot regions from June 2000 and 2002 were combined to depict the general location of the Heceta Bank hotspot to allow for comparison to the overlapping 1980s data.

Results

Persistence of biological hotspots

The persistence of the nekton hotspots through time was examined by combining the geostatistically produced spatial coverages of the hotspots for each 2000 and 2002 cruise (Figure 5.1; See also Reese and Brodeur, 2006). When hotspot locations are plotted for all four cruises, the two hotspot locations are evident in two locations: 1) near the shelf-break (200 m isobath) just south of Heceta Bank (~44° N) and 2) inshore near Crescent City, CA (~42° N). The same analysis was conducted after omitting the June 2002 cruise due to the poor sample coverage in the Heceta Bank region during that cruise. When the June 2002 cruise is omitted from the analysis, the size of the Heceta Bank (HB) hotspot becomes more apparent (Figure 5.1b). Coverage within the Crescent City (CC) hotspot region was comparable between cruises so this hotspot region is similar in both analyses.

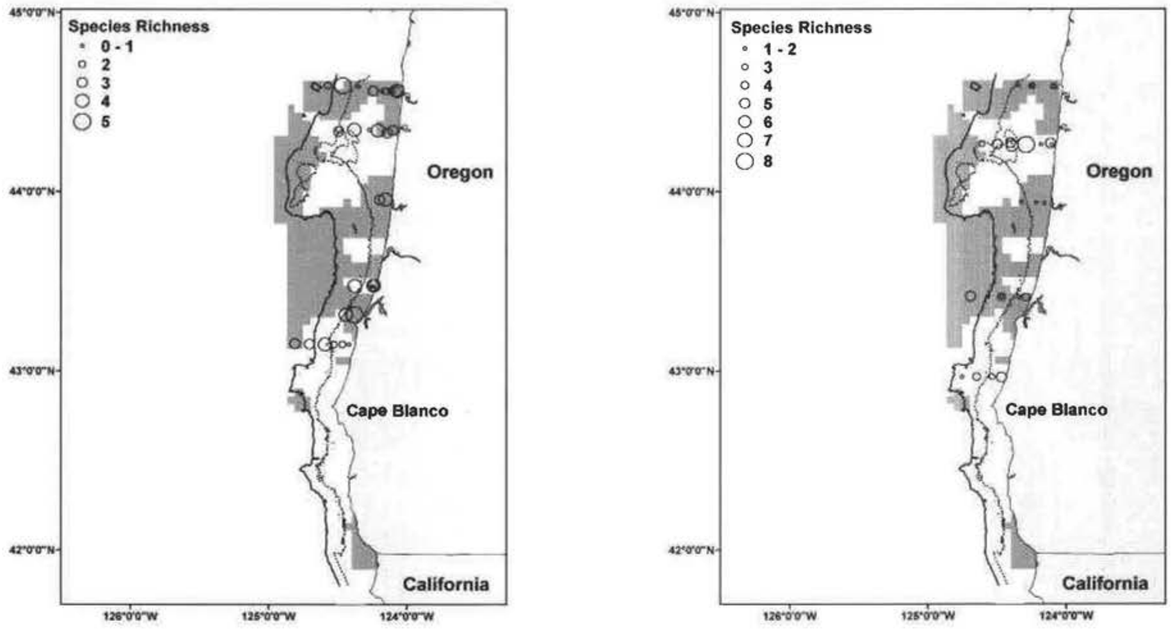
Nekton species richness and abundance observed during the 1980s were displayed over the hotspots determined from the 2000 and 2002 cruises to examine the decadal persistence of these hotspots (Figures 5.2 and 5.3, respectively). Although coverage was limited closer to shore during the 1980s cruises, species richness is generally higher in the HB hotspot region, especially during June 1981 and 1984 (Figure 5.2). The pattern is less clear during June 1983 when species richness was relatively high outside the hotspot regions. Nekton abundance was generally higher in the HB hotspot region and lowest outside the hotspot during all four cruises from the 1980s (Figure 5.3).



a) All Cruises

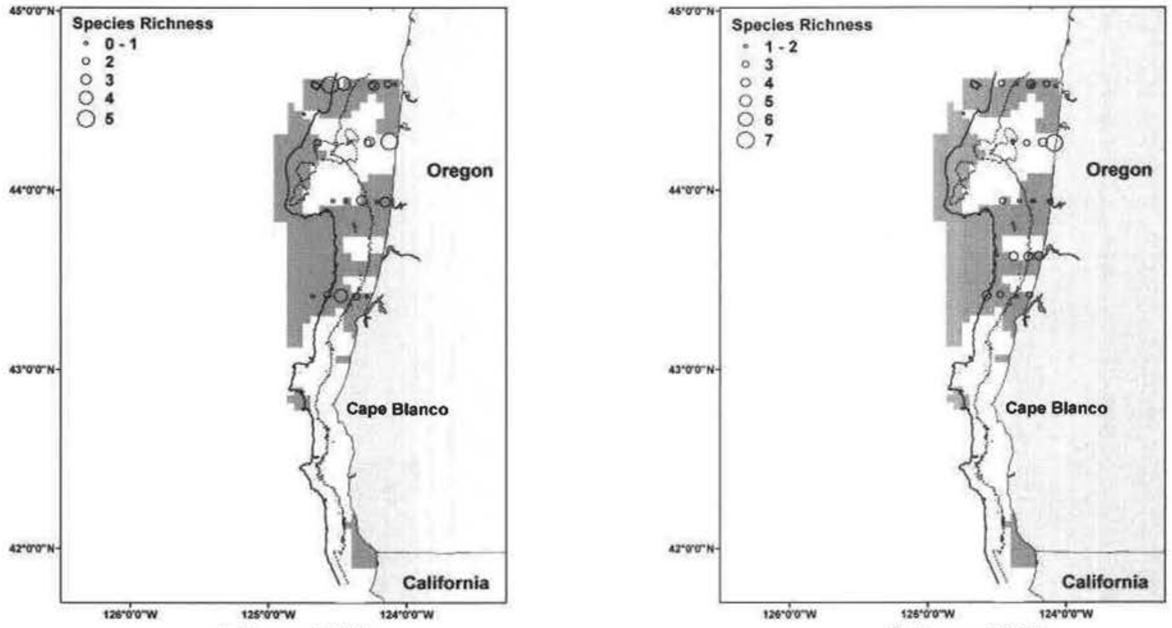
d) Omitting June 2002

Figure 5.1. Persistent nekton hotspots. Shaded areas indicate 5km grid cells that were determined to be hotspots during each of the four cruises. (a) Nekton hotspot locations that were present during all four cruises. (b) Hotspot locations present during the June 2000, August 2000, and August 2002 cruises. The June 2002 cruise was omitted due to the lack of sampling over the Heceta Bank area during that cruise. The solid contour represents the 200 m isobath and the hatched contour represents the 100 m isobath.



a) June 1981

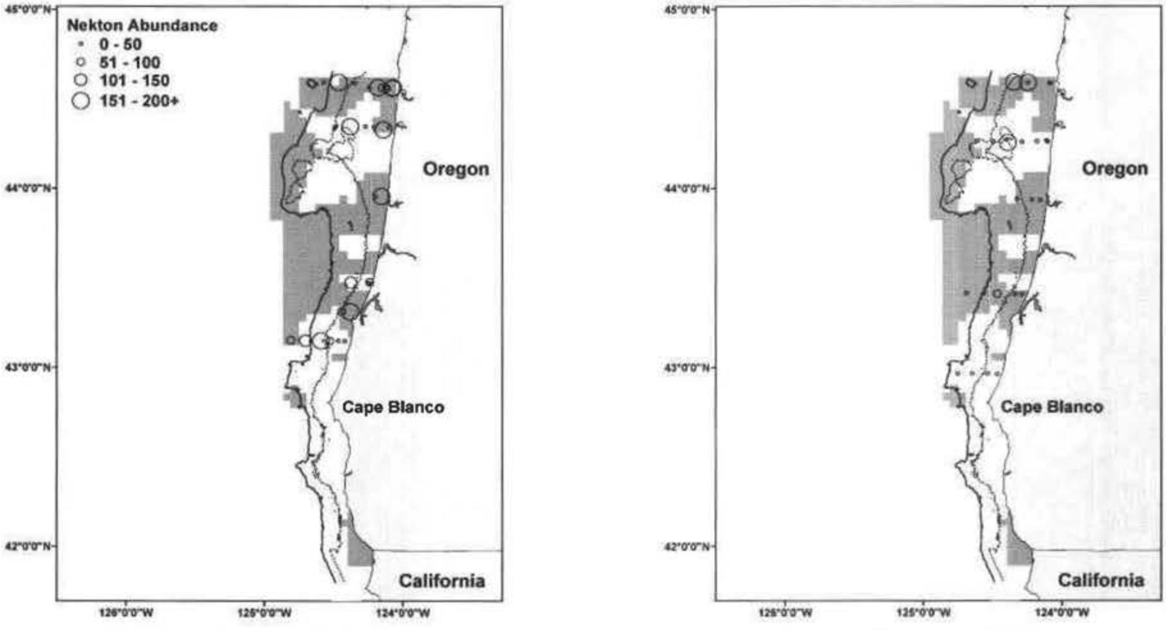
b) June 1983



c) June 1984

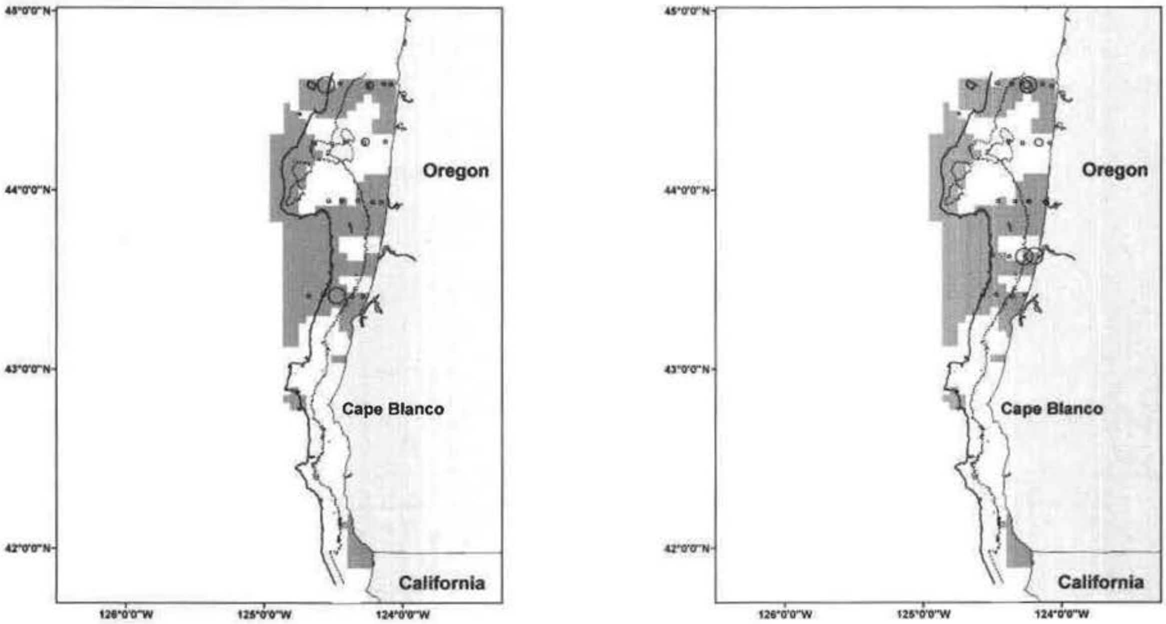
d) June 1985

Figure 5.2. Nekton species richness observed at stations during June cruises in the early to mid-1980s relative to biological hotspots determined from June 2000 and 2002. Data are from: (a) June 1981; (b) June 1983; (c) June 1984; and (d) June 1985. The solid contour represents the 200 m isobath and the hatched contour represents the 100 m isobath. Note different scales.



a) June 1981

b) June 1983



c) June 1984

d) June 1985

Figure 5.3. Nekton abundance observed at stations during June cruises in the early to mid-1980s relative to biological hotspots determined from June 2000 and 2002. Data are from: (a) June 1981; (b) June 1983; (c) June 1984; and (d) June 1985. The solid contour represents the 200 m isobath and the hatched contour represents the 100 m isobath.

Distribution of functional groups

The densities associated with the various functional groups varied between groups as well as seasonally and/or interannually within groups (Table 5.2). The most abundant group was zooplanktivores, which included the majority of species encountered compared to the other groups. Secondary piscivores were the least abundant group. Grazer and zooplanktivore densities varied seasonally. Grazers were much more abundant during August than during June in both 2000 and 2002. In contrast, zooplanktivorous nekton were more abundant during June than during August in each year. Primary piscivore densities fluctuated with relatively few encountered during June 2000 or August 2002 and higher densities in August 2000 and June 2002. Densities of secondary piscivores were relatively consistent between seasons and years with the exception of June 2000 when densities were particularly low.

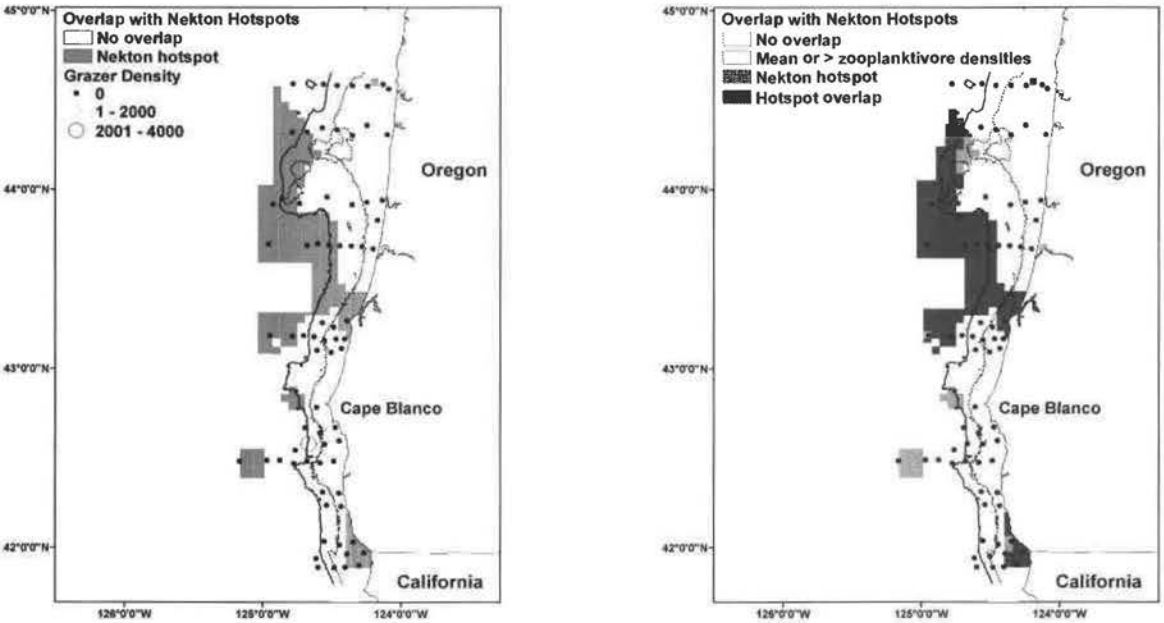
Different degrees of spatial correlation were fitted to grazer densities according to the cruises, with a spatially structured density component $[C/(C_0 + C)]$ ranging from 53 to 60% (Table 5.3). In June 2000, there were only two occurrences of grazers both of which occurred outside the two biological hotspot regions (Figure 5.4a). During August 2000 and 2002, the spatial correlation of grazer densities best fit anisotropic, exponential models with varying spatial dependences (Table 5.3). In August 2000 and 2002, directional influences were present with the direction of the major axis about 83° and 16° from north, respectively, and represents the directions over which spatial scales are longest, whereas the minor axis represents the direction of the strongest gradient. Therefore, during August 2000, the strongest gradient was observed in the north-south

Table 5.2. Mean (± SE) functional group densities (number/km^3) for each cruise.

	Cruise							
	June 2000 (n = 73)		**August 2000** (n = 70)		**June 2002** (n = 70)		**August 2002** (n = 84)	
Functional Group	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Grazers	59	43	86,018	84,457	982	362	20,656	16,298
Zooplanktivores	36,654	10,967	10,941	3,287	1,166,400	736,036	113,538	46,936
Primary Piscivores	702	189	2,926	1,174	8,514	4,919	520	128
Secondary Piscivores	235	82	1,025	236	1,351	262	1,171	255

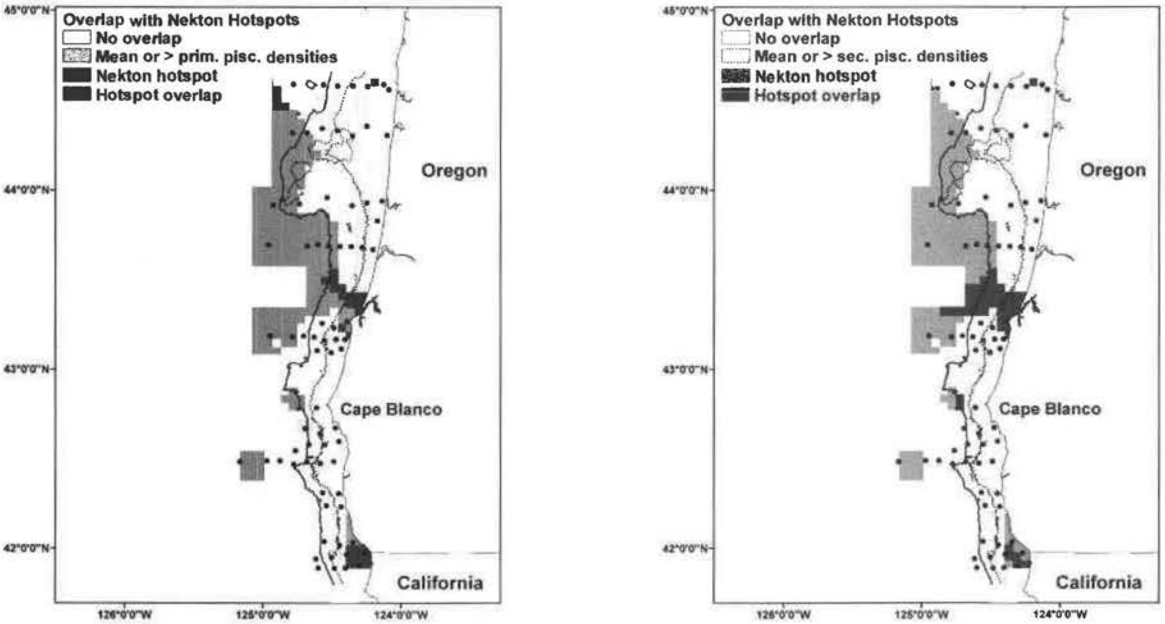
Table 5.3. Statistics and model parameters of the models fitted to the empirical semivariograms during the June and August 2000 and 2002 cruises for the observed functional groups. C_0 is the nugget effect or y-intercept of the model; C_0+C is the sill or model asymptote; $C/(C_0+C)$ is the spatially structured component; Major and Minor Ranges represent the range over which spatial dependence is apparent; Angle is the axis of rotation for the major axis for anisotropic models.

Spatial Process	**Month**	**Model**	**Nugget C_0**	**Sill C_0+C**	$C/(C_0+C)$	**Major Range**	**Minor Range**	**Major Angle**
Grazers	June 2000	-	-	-	-	-	-	-
	Aug 2000	Exponential	$4.20\text{x}10^{7}$	$1.06\text{x}10^{8}$	0.60	67 km	25 km	82.6°
	June 2002	IDW	-	-	-	-	-	-
	Aug 2002	Exponential	$5.02\text{x}10^{8}$	$1.08\text{x}10^{9}$	0.53	267 km	41 km	15.9°
Zooplanktivores	June 2000	Exponential	$2.02\text{x}10^{8}$	$1.26\text{x}10^{9}$	0.84	28 km	-	-
	Aug 2000	IDW	-	-	-	-	-	-
	June 2002	Exponential	$1.72\text{x}10^{9}$	$4.31\text{x}10^{9}$	0.60	24 km	-	-
	Aug 2002	Spherical	$1.45\text{x}10^{9}$	$3.90\text{x}10^{9}$	0.63	21 km	-	-
Primary Piscivores	June 2000	IDW	-	-	-	-	-	-
	Aug 2000	Spherical	$5.51\text{x}10^{6}$	$1.79\text{x}10^{7}$	0.69	256 km	71 km	16.7°
	June 2002	Exponential	$3.48\text{x}10^{7}$	$8.97\text{x}10^{7}$	0.61	254 km	-	-
	Aug 2002	Exponential	$1.82\text{x}10^{5}$	$1.27\text{x}10^{6}$	0.86	23 km	-	-
Secondary Piscivores	June 2000	IDW	-	-	-	-	-	-
	Aug 2000	Exponential	$1.47\text{x}10^{6}$	$3.46\text{x}10^{6}$	0.58	105 km	17 km	91.7°
	June 2002	Spherical	$1.48\text{x}10^{6}$	$5.07\text{x}10^{6}$	0.71	16 km	-	-
	Aug 2002	IDW	-	-	-	-	-	-



a) Grazers

b) Zooplanktivores



c) Primary Piscivores

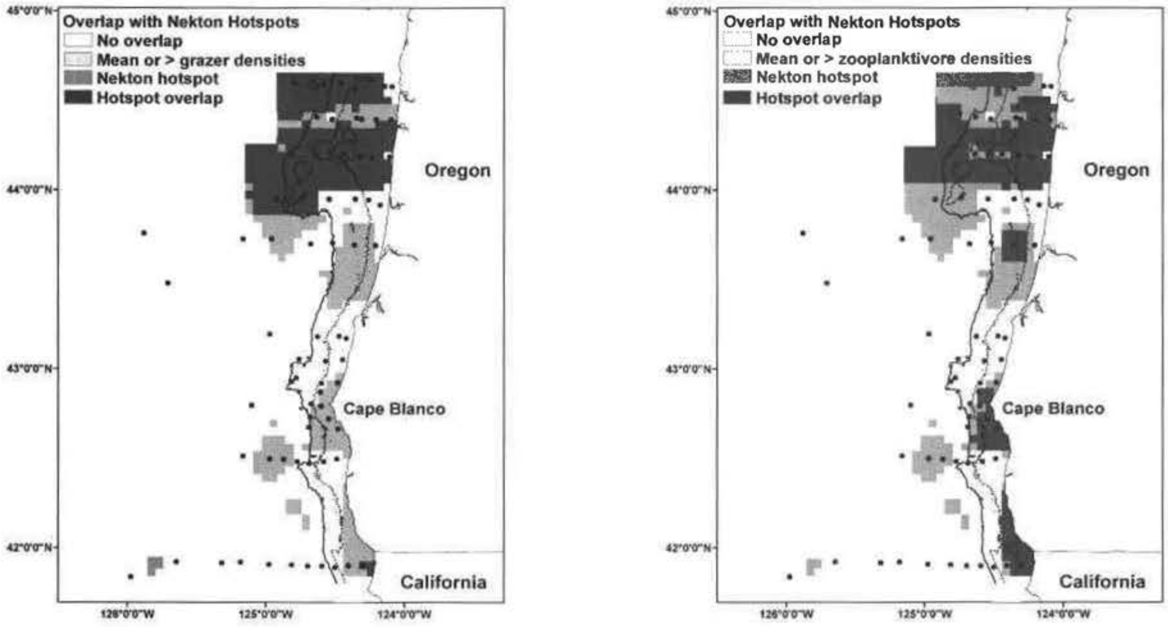
d) Secondary Piscivores

Figure 5.4. Spatial overlap of nekton hotspots and observed functional groups during June 2000: (a) grazers; (b) zooplanktivores; (c) primary piscivores; and (d) secondary piscivores. Shaded areas indicate 5km grid cells. Dots represent station locations. The solid contour represents the 200 m isobath and the hatched contour represents the 100 m isobath.

direction (or along shore), whereas during August 2002 was roughly in the onshore-offshore direction. During June 2002, there was an absence of spatial correlation and, therefore, Inverse Distance Weighting (IDW) was used to obtain the spatial coverage. During both August cruises, highest densities were observed around the Heceta Bank region, while in June 2002 high densities were also observed around Cape Blanco (Figures 5.4a-5.7a).

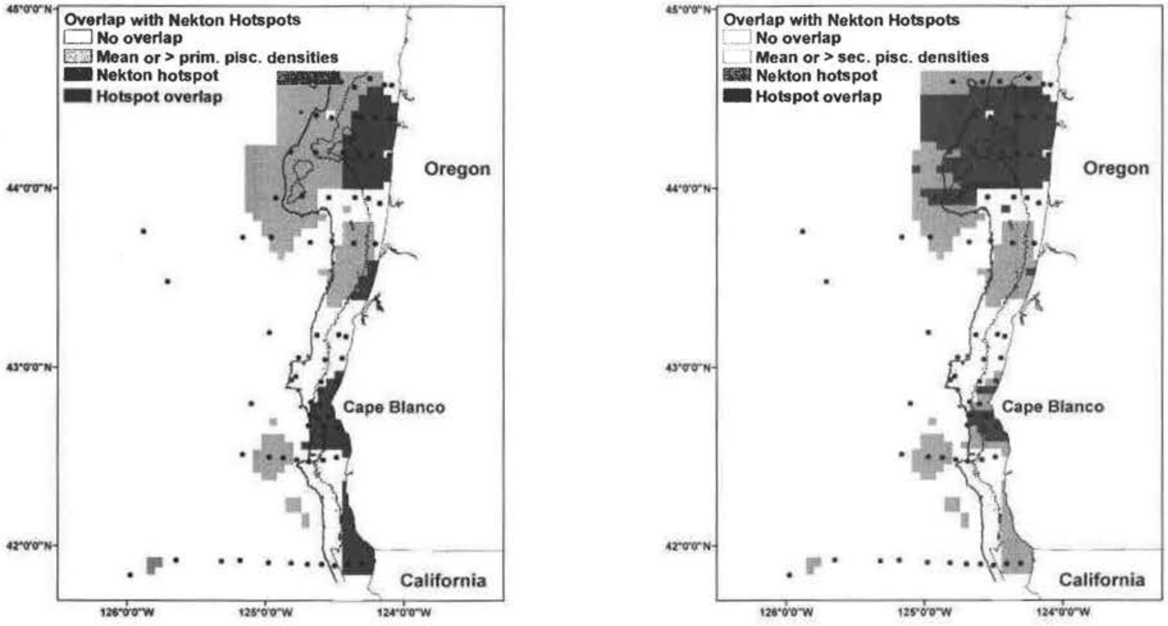
Locations of mean grazer densities greater than the cruise-wide mean were identified for each cruise and mapped relative to the nekton hotspots as identified in Reese and Brodeur (2006). The amount of overlap varied between seasons and years. The greatest overlap of grazer densities with the nekton hotspots occurred in August of both 2000 and 2002 and the smallest overlap during June 2002 (Table 5.4; Figures 5.4a-5.7a). The overlap occurred primarily with the Heceta Bank (HB) hotspot in the northern part of the study area. Since grazers were encountered at only two stations during June 2000, no overlaps were available for this cruise. Only during August 2000 was an overlap between grazers and the Crescent City (CC) hotspot observed.

The degree of spatial correlation fitted to zooplanktivore densities varied by cruise with a spatially structured density component ranging from 60 to 84% (Table 5.3). In June of both years the spatial correlations best fit isotropic, exponential models. In August 2000 there was an absence of spatial correlation, whereas in August 2002 the spatial correlation was best fit by an isotropic, spherical model. The ranges of spatial dependence were similar between these cruises. Highest densities were observed in three general areas throughout the study region: 1) near the Heceta Bank region and



a) Grazers

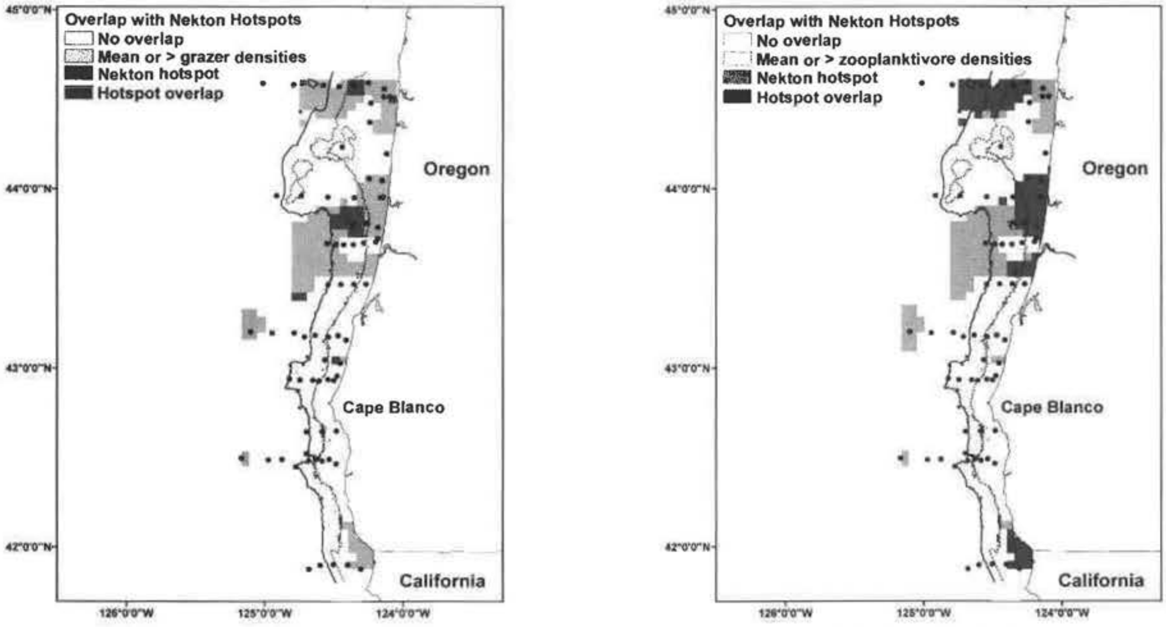
b) Zooplanktivores



c) Primary Piscivores

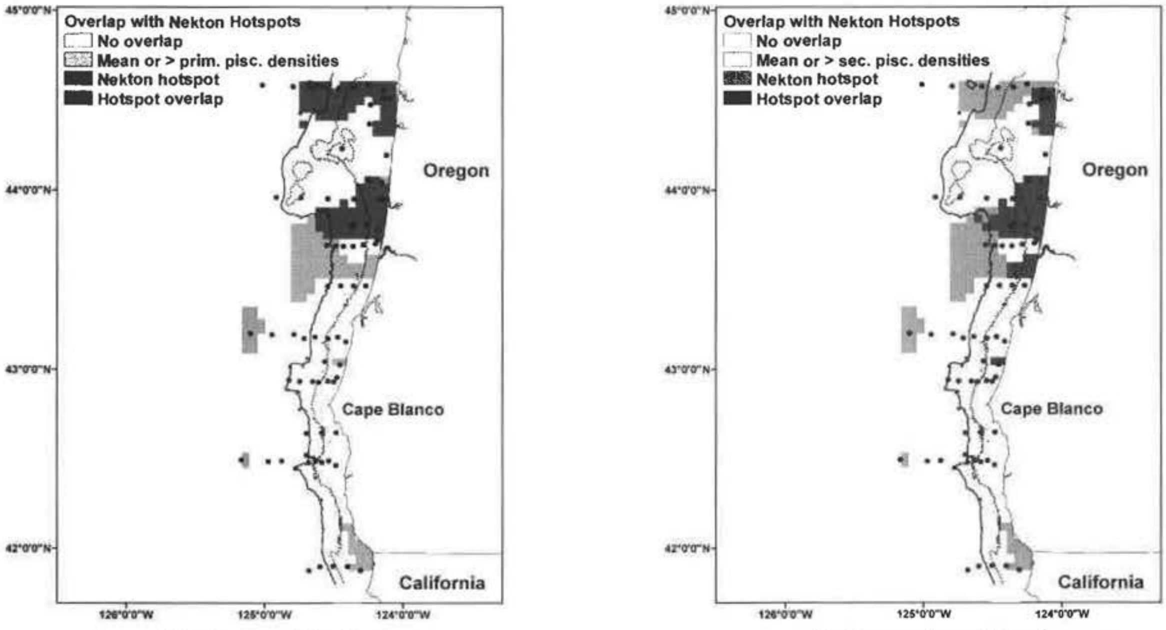
d) Secondary Piscivores

Figure 5.5. Spatial overlap of nekton hotspots and observed functional groups during August 2000: (a) grazers; (b) zooplanktivores; (c) primary piscivores; and (d) secondary piscivores. Shaded areas indicate 5km grid cells. Dots represent station locations. The solid contour represents the 200 m isobath and the hatched contour represents the 100 m isobath.



a) Grazers

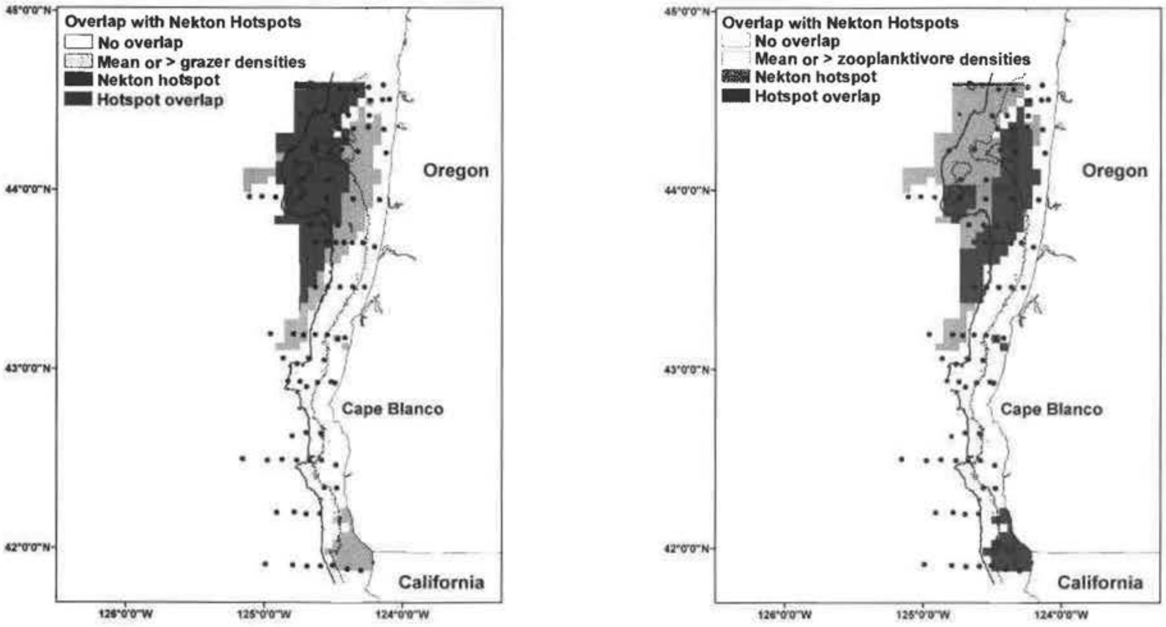
b) Zooplanktivores



c) Primary Piscivores

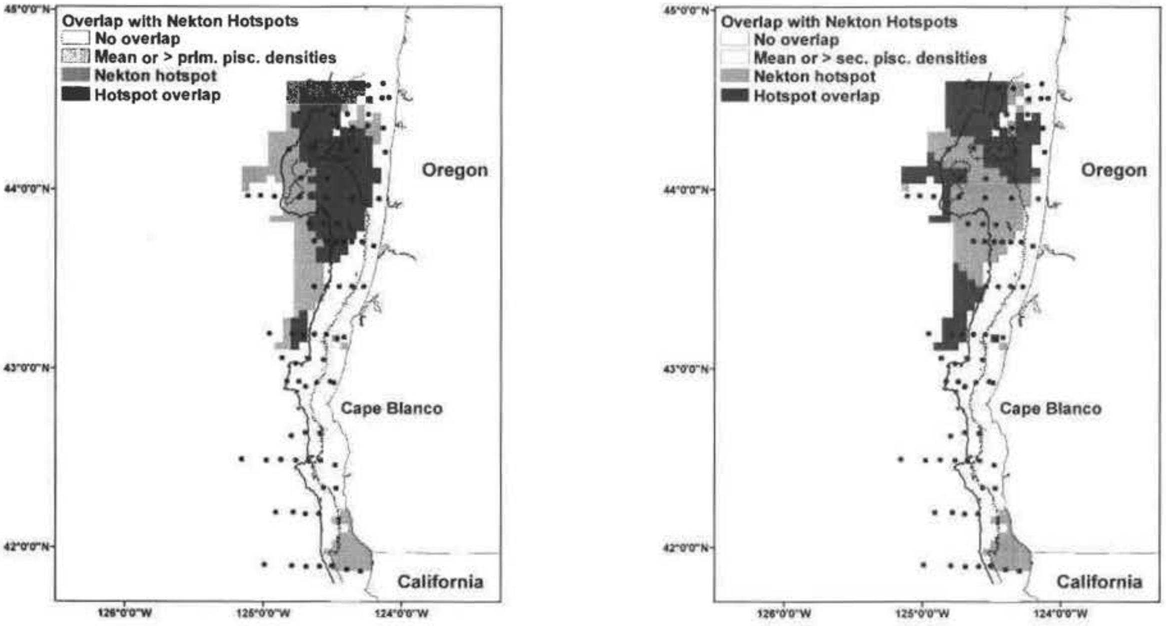
d) Secondary Piscivores

Figure 5.6. Spatial overlap of nekton hotspots and observed functional groups during June 2002: (a) grazers; (b) zooplanktivores; (c) primary piscivores; and (d) secondary piscivores. Shaded areas indicate 5km grid cells. Dots represent station locations. The solid contour represents the 200 m isobath and the hatched contour represents the 100 m isobath.



a) Grazers

b) Zooplanktivores



c) Primary Piscivores

d) Secondary Piscivores

Figure 5.7. Spatial overlap of nekton hotspots and observed functional groups during August 2002: (a) grazers; (b) zooplanktivores; (c) primary piscivores; and (d) secondary piscivores. Shaded areas indicate 5km grid cells. Dots represent station locations. The solid contour represents the 200 m isobath and the hatched contour represents the 100 m isobath.

Table 5.4. Percentage of the mean or greater densities of each functional group within hotspots. Percentages were based on values within 5 km^2 grid cells throughout the study area.

	Cruise			
Functional Group	**June 2000**	**August 2000**	**June 2002**	**August 2002**
Grazers	-	95%	12%	97%
Zooplanktivores	75%	94%	39%	53%
Primary Piscivores	25%	58%	55%	72%
Secondary Piscivores	29%	89%	46%	70%

immediately inshore, 2) nearshore around Cape Blanco, and 3) nearshore around Crescent City, CA in the south extending northward into southern Oregon (Figures 5.4b-5.7b).

The amount of overlap between zooplanktivores and hotspots fluctuated annually with greater overlap during both 2000 cruises (Table 5.4). In contrast to the grazer distributions, zooplanktivores were distributed such that overlap occurred with both the HB and CC hotspots during each cruise. Within the HB hotspot region, high densities of zooplanktivores were encountered across the shelf and beyond the shelf-break.

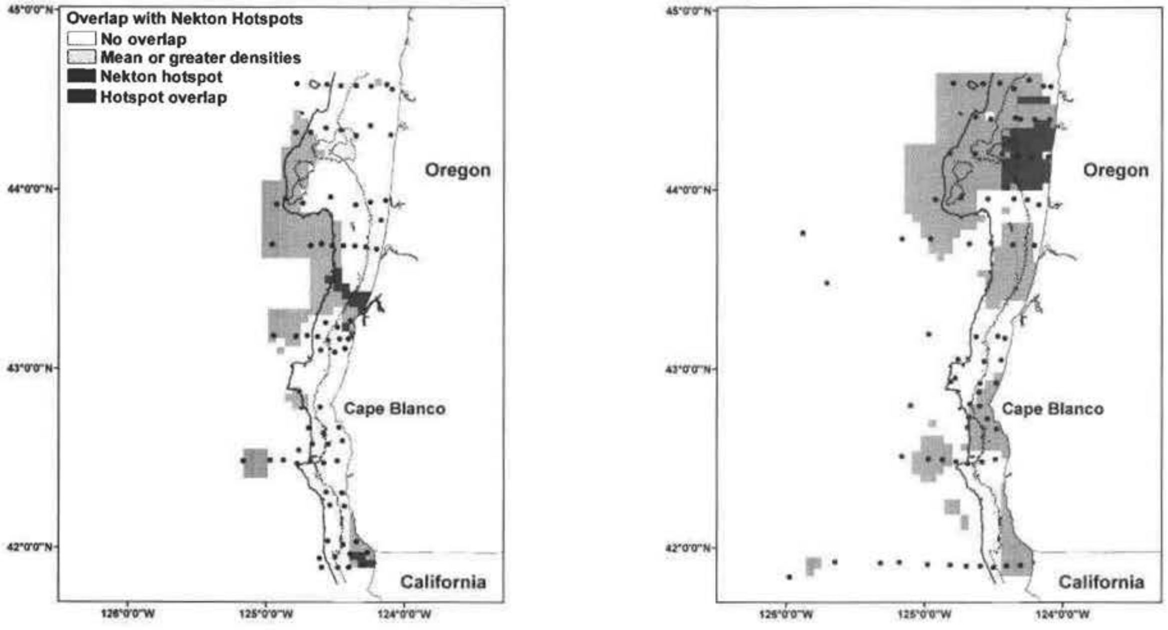
The degree of spatial correlation fitted to primary piscivore densities ranged from 61 to 86% (Table 5.3). During June 2000, there was an absence of spatial correlation, however in August 2000 the spatial correlation best fit anisotropic, spherical model. In August 2000 directional influences were present with the direction of the major axis about 17° from north indicating the strongest gradient in primary piscivore densities occurred in the inshore-offshore direction with densities fairly uniform along the shore (Figure 5.5c). During both June and August 2002, spatial correlations best fit isotropic, exponential models. The ranges of spatial dependence varied between these cruises with the largest distances observed in 2000. Highest primary piscivore densities were typically observed along the coast over much of the study range extending beyond the shelf-break in the HB hotspot region during both June and August 2002 (Figures 5.4c-5.7c). During June and August 2000, relatively high densities of primary piscivores were encountered in the CC hotspot region, however, high densities were not encountered within this region during the 2002 cruises. During August 2000, primary piscivore densities were also high around Cape Blanco out to the shelf-break.

The amount of overlap between primary piscivores and hotspots was higher during August cruises during each year (Table 5.4). Only during the 2000 cruises did overlap occur between high densities of primary piscivores and the CC hotspot (Figures 5.4c-5.7c). In addition, the distribution of the high densities of primary piscivores was limited to the nearshore portion of the HB hotspot during the 2000 cruises. In contrast, during the 2002 cruises no overlap was found within the CC hotspot, and high densities were encountered further offshore within the HB hotspot region.

During June 2000 and August 2002, there was an absence of spatial correlation for secondary piscivores. In August 2000, the spatial correlation best fit an anisotropic, exponential model, whereas in June 2002 the best fit was with an isotropic, spherical model (Table 5.3). In August 2000 directional influences were present with the direction of the major axis about 92° from north indicating the strongest gradient in secondary piscivore densities occurred in the north-south direction with densities fairly uniform across the shelf (Figure 5.5d). During all cruises, highest densities were observed nearshore typically north of Cape Blanco (Figures 5.4d-5.7d). High densities were encountered furthest south during June 2000 and were present in the CC hotspot region only during this cruise. During both August cruises, high densities were also further offshore near the shelf-break particularly within the HB hotspot region.

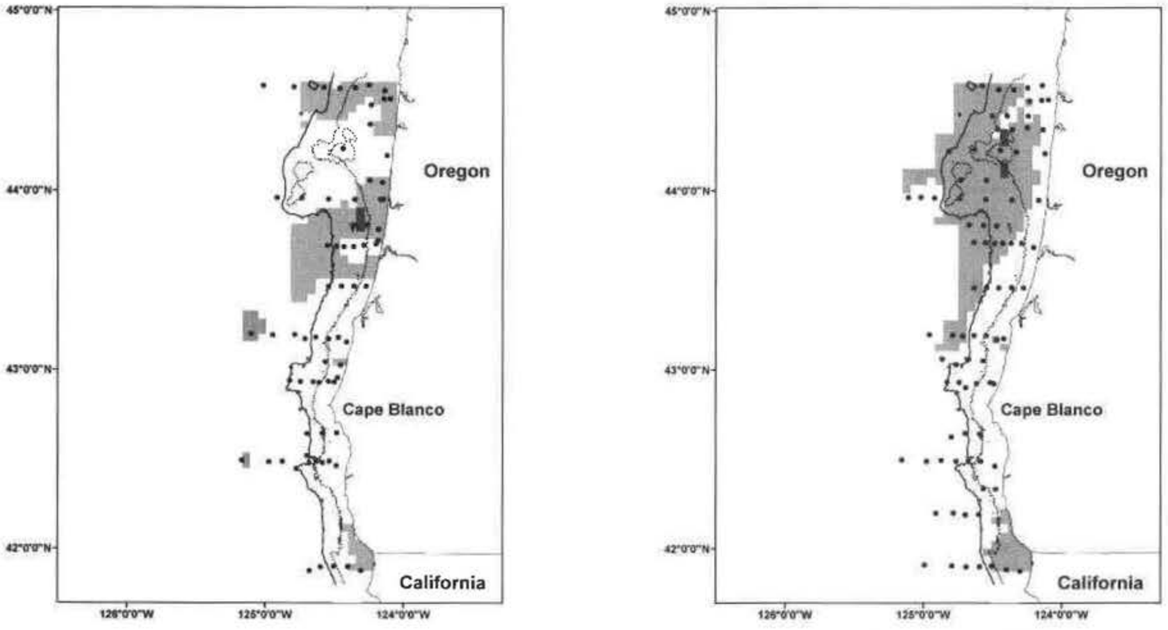
The amount of overlap between secondary piscivores and hotspots varied considerably between seasons and years (Table 5.4). The greatest overlap of secondary piscivore densities with the nekton hotspots occurred during both August cruises and the smallest overlap during June 2000 (Table 5.4; Figures 5.4d-5.7d). The overlap occurred primarily within the HB hotspot in the northern part of the study area with overlap with the CC hotspot occurring only during June 2000. During both August cruises, secondary piscivores were distributed such that the overlap with the HB hotspot extended from nearshore to beyond the shelf-break. In contrast, during both June cruises the overlap was primarily limited to the nearshore portion of the HB hotspot.

The spatial distributions of the largest densities (mean or greater) from each functional group were combined to identify the locations with the greatest potential for encounters between functional groups (Figure 5.8). During each of the four cruises, the locations in which the combined high densities of each functional group overlapped occurred primarily within the HB hotspot region. Very little overlap of all functional groups occurred outside the hotspot regions during June 2000, only one of the combined 5 km^2 grid cells was outside a hotspot region in August 2000, and none were outside during either cruise in 2002. During June and August 2000, the amount of area in which all functional groups were present in high densities was greater than during either 2002 cruise. Only in June 2000 were the three functional groups (zooplanktivores, primary and secondary piscivores) present in relatively large numbers in the CC hotspot region in the southern part of the study area. During no other cruises were high densities of all functional groups present within the CC hotspot region. Very little overlap between high densities of the functional groups occurred during either 2002 cruise indicating that



a) June 2000

b) August 2000



c) June 2002

d) August 2002

Figure 5.8. Spatial overlap of nekton hotspots and all functional groups for the four cruises: (a) June 2000; (b) August 2000; (c) June 2002; and (d) August 2002. Shaded areas indicate 5km grid cells. Dots represent station locations. The solid contour represents the 200 m isobath and the hatched contour represents the 100 m isobath. Note: June 2000 does not include grazers.

during these cruises the distributions of the highest densities of the individual functional groups differed.

Discussion

Areas with high species diversity are important components of ecosystems because they possess the conditions necessary to maintain large numbers of potentially competing species in sympatry. Furthermore, the ability to understand the biogeography associated with a system is important in marine conservation efforts, as well as in terrestrial systems, because policy decisions typically depend on the determination of where biological processes occur (Norse, 1993). Since the ocean is a heterogeneous environment with marine resources spatially uneven (Steele, 1976; Mackas and Boyd, 1979), abundances of marine organisms tend to be higher in localized areas. Consequently, the identification of these marine, biological hotspots is a necessary and expanding area of research (Malakoff, 2004; Worm et al., 2005).

One of the goals of this study was to examine nekton data collected along the Oregon and Washington coasts during the early to mid 1980s to identify the spatial distributions of nekton species richness and abundance. The distributions were then compared to the hotspot locations determined from sampling conducted during 2000 and 2002. Sampling during the June 1980s cruises was limited to the region north of Cape Blanco and therefore did not include samples within the Crescent City (CC) hotspot. Overlapping the maps of the hotspots and 1980s data suggest that at least the Heceta Bank (HB) hotspot was present in the 1980s. Reese and Brodeur (2006) noted that although the general location of the hotspots persisted on a seasonal and annual basis, the sizes of the hotspots varied. Therefore, although the HB hotspot appears to be present across decades under vastly different environmental conditions, conclusions based on the 1980s data should be taken with caution because, if the hotspots were indeed present, the sizes of the hotspots would likely be different between the years and decades. Moreover, sampling did not occur as far offshore during the 1980s and therefore overlap with the HB hotspot was limited to the nearshore portion of the hotspot. Nevertheless, it appears as though the HB hotspot was present during the 1980s. This is rather remarkable given the different environmental conditions that were present during the different time periods.

Reese and Brodeur (2006) determined that the hotspots persisted through highly variable seasonal and interannual conditions, including the anomalous Subarctic influence that occurred in 2002. On a multidecadal scale, the California Current and the Gulf of Alaska ecosystems are known to alternate between anomalously warm and cool states, known as regimes (Peterson and Schwing, 2003). During 1977, a regime shift occurred in the North Pacific from a cold regime to a warm regime along the coast, which led to a seven-fold decrease in zooplankton biomass in the California Current (Roemmich and McGowan, 1995) and a decline in salmonid survival and production (Pearcy, 1992). Following a strong El Niño event in 1997-98, the California Current system again shifted to a cool regime (Peterson and Schwing, 2003). This led to the strengthening of upwelling-favorable winds within the California Current, zooplankton biomass in the northern California Current doubled and switched from warm to cold-water species, and fish stocks began to increase (Peterson and Schwing, 2003). Therefore, the persistence of the HB hotspot through both the warm and cold regimes indicates stability within the system. In fact, it may well be that it is the persistence of the hotspots through vastly different environmental and ecological conditions that provides the stability to the function of the ecosystem.

The two biological hotspots differ with respect to the physical and biological characteristics associated with each (Reese and Brodeur, 2006). The HB hotspot typically had lower chlorophyll concentrations and surface zooplankton biovolume than the CC hotspot (Reese and Brodeur, 2006), yet higher levels compared to non-hotspot regions, and was characterized as a retention zone (Barth et al., 2005, Ressler et al., 2005). Barth et al. (2005) identified northward flow inshore of Heceta Bank which results from the flow of the upwelling jet turning cyclonically back toward the coast on the southern part of the Bank. Moreover, the inshore waters of Heceta Bank have low-flow velocities resulting in slower offshore advection. The result of this low-flow region inshore of Heceta Bank, coupled with the higher velocity flow around the southern flank of Heceta Bank, create a retention area responsible for the increased chlorophyll concentrations. This flow regime has been described as the retention mechanism which supports higher trophic levels as well. Ressler et al. (2005) reported high concentrations of euphausiids within this area which were correlated with near-surface chlorophyll concentrations. Even members of higher trophic levels, such as marine mammals (Tynan et al., 2005), seabirds (Ainley et al., 2005), and nekton (Reese and Brodeur, 2006) are found in greater abundance within this area, presumably supported by the high abundances of phytoplankton and zooplankton over Heceta Bank (Barth et al., 2005).

Chlorophyll concentrations vary with seasonal upwelling activity as upwelled water brings cooler, nutrient-rich water to the well-lit surface area, which then stimulates primary production (Landry et al., 1989). In the Pacific Northwest, the strength and duration of upwelling increases southward along the coast (Hickey and Banas, 2003). The characteristics within the CC hotspot and the proximity of this hotspot near the coast in the south indicate that this hotspot is highly associated with upwelling activity. Since upwelling-favorable winds were diminished during the warm regime after 1977 (Peterson and Schwing, 2003), it would be interesting to see if the CC hotspot was present during this time period. Data collected during July 1984, the only cruise in which sampling was conducted south of Cape Blanco, had three stations near the California-Oregon border. During July 1984, both nekton species richness and abundance were high within the HB hotspot area, however, values were very low around the CC hotspot. Although it is not possible to draw conclusions based on only three data points collected during one time period, this observation suggests that the persistence of upwelling-driven hotspots, such as the CC hotspot, may be more dependent on climatic conditions.

Because biological communities are complex systems with many interacting species at various trophic levels, it is difficult to study ecosystem-level processes by considering each species separately (Krebs, 1985; Walker, 1992). Although every organism contributes to the function of ecosystems, individual contributions vary considerably (i.e., keystone species). In addition, it is not often possible to determine the relative contributions of individual species to ecosystem processes. In fact, most ecosystem processes are driven by the combined biological activities of many species which form functional groups. Furthermore, the stability of such systems appears to be related to species richness. For instance, in a laboratory study, McGrady-Steed and Morin (2000) found an inverse relationship between the temporal variation of functional groups composed of multiple species and species richness. Increasing species richness resulted in a decrease in temporal variation thus providing stability to the system. However, the stability of individual populations was not predicted by that of functional groups. With controlled laboratory studies, it is not necessary to examine the distributions of various functional groups because they are simply present or absent from the treatments. In a natural system, however, it is of utmost importance to identify their relative distributions to gain insight into how natural ecosystems function and persist.

The northern California Current system is a highly dynamic and complex system. The nekton communities that exist there are highly complex and variable. For instance, Reese and Brodeur (2006) noted that nekton community composition within the hotspots varied between seasons and years. Using species diversity as a community characteristic, however, implies the assumption that all species are equal in the community. To reduce the complexity associated with the communities, species were grouped into broad functional groups according to the dominant components in their diets.

The distributions of the four functional groups were not random. Instead, all functional groups examined were found to overlap considerably with the hotspot areas, however, the amount of overlap varied within and between groups, as well as temporally. Reese and Brodeur (2006) defined the biological hotspots as locations that were characterized as having greater than average species richness, abundance, and/or biomass for a particular cruise. Therefore, one might reasonably expect that a particularly abundant group might dictate the locations of the hotspots, especially a group that contained a lot of species, such as zooplanktivores. This appeared to be the case during June 2000 when relatively few grazers or secondary piscivores were encountered. Sampling in June 2002 was limited in the Heceta Bank region and, due to the reliance on very few sample stations in that area, resulted in a reduced size of the HB hotspot (Reese and Brodeur, 2006). Therefore, it is not surprising that overlap for grazers and zooplanktivores was lowest during June 2002. Nonetheless, zooplanktivores were the only group consistently found in high abundances within both the HB and CC hotspots. Although the zooplanktivore group contained the most species and tended to be the most abundant group, the other three functional groups were also found to overlap with the hotspots. Grazers were more abundant during the August cruises than during the June cruises and consequently had more overlap with the hotspots during August.

The group with the lowest overlap during 2000 was the primary piscivores which was composed of species that are typically found closer to shore. This was evident in the fact that primary piscivores overlapped nearly completely with the nearshore CC hotspot in the southern part of the study, and also predominantly with the nearshore side of the HB hotspot. The secondary piscivore group tended to be distributed further offshore than the primary piscivores and consequently had greater overlap with the offshore portion of the HB hotspot. Secondary piscivores were rarely a dominant component of the CC hotspot.

Spatial patterns of all groups were combined for each cruise to identify areas where all functional groups were present which is important for understanding potential interactions between the groups. During all cruises, the vast majority of the overlap between all functional groups occurred within the HB hotspot (Figure 5.8). During June and August of both years, the overlap occurred in the nearshore to midshelf portion of the hotspot. The locations of the overlaps differed seasonally, however. During June of both years the overlap of all functional groups and hotspots occurred south and shoreward of Heceta Bank, yet during August of both years the overlap occurred inshore and north of Heceta Bank. This suggests that these portions of the HB hotspot may be particularly biologically active locations. Very little overlap of the combined distributions of the functional groups occurred during the 2002 cruises. One explanation for the lower overlap during June 2002 is likely due to the low sampling in the Heceta Bank region and smaller hotspot size. Another explanation is due to the much different environmental conditions present during the 2002 cruises as a result of the anomalous input of Subarctic Pacific water (Huyer, 2003; Wheeler et al., 2003). This input resulted in increased nutrients and at least a doubling of phytoplankton biomass along the Oregon coast. Offshore, maximum chlorophyll levels were 2-4 times greater in the subsurface layer in 2002 compared with 2000 (Wheeler et al., 2003). Within the HB hotspot in June 2002, mean chlorophyll concentration was approximately 6 times higher than in June 2000 and highest chlorophyll concentrations were observed in August 2002, presumably as the upwelled water was displaced further offshore (Reese and Brodeur, 2006). Since the anomalous input led to increased primary production all along the coast, this likely led to the diffusion of functional groups given the ubiquity of food resources.

Localized biological hotspots would be most advantageous to marine life if their locations were predictable in time and space. Organisms searching for food in a patchy environment would conceivably utilize less energy if food items were distributed in a persistent, thus predictable, location. There has been an increasing awareness of the need for protecting pelagic zones of predictable high productivity, since these areas may serve as critical feeding locations for higher trophic level predators. One such way of protection is by setting up systems of marine protected areas (MPAs). MPAs have become increasingly popular tools to counter threats to marine ecosystems (Bohnsack, 1993; Sobel, 1993; Agardy, 1994; Carr, 2000; Gladstone, 2002; Sala et al., 2002). Determining persistence is difficult in the marine environment, however. It involves long-term sampling programs with consistent protocols, which are exceedingly rare in marine studies given the high costs of sampling in the marine environment.

Complex food webs, those with not only multiple trophic levels but also with multiple species per level, tend to be more stable given the redundancy in these systems. If the abundance of one species decreases in a given area, the abundance of a complementary species may increase to maintain the function of the system. Therefore, areas characterized by having multiple trophic levels would presumably be more stable. This would appear to be the case within the northern California Current system. Nekton biological hotspots were found to persist across much different environmental and biological conditions, yet nekton community structure varied. Although inconclusive, these data suggest that the persistence of upwelling-based hotspots, such as the CC hotspot, may be more ephemeral and susceptible to climatic variability than topographically-linked, retention-based hotspots, such as the HB hotspot. Analyses of the distribution of the functional groups within the region indicate that the predominant biological activity is spatially nonrandom and occurs within persistent, localized areas. Such findings are very important to understanding the biological importance of specific geographic locations and have broad implications for the preservation of ecosystems and in the creation of marine protected areas. Furthermore, the evaluation of large marine ecosystems as a whole unit may lead to erroneous or oversimplified results if they are indeed composed of multiple biological hotspots. Results from this study indicate that large regional areas, such as the northern California Current, are composed of smaller, localized areas where a substantial amount of biological activity is occurring. These localized hotspots should be considered when evaluating large marine ecosystems.

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CONCLUSIONS

The complexity associated with marine ecosystems makes understanding processes that provide structure and function difficult. The spatial and temporal variability associated with the physical and biological characteristics within upwelling regions are particularly challenging. Despite such intrinsic variability, stability has been found within the California Current system (Rebstock, 2003). This stability is generally described for small pelagic fishes and one proposed mechanism is that the stability is due to the shifting locations of these pelagic populations in response to changing environmental conditions (Rebstock, 2003). The goals of the present study were to provide insight into the distributions of zooplankton and nekton community characteristics and, therefore, further our knowledge regarding this stability and address potential mechanisms for how it arises and persists.

Individual populations of nektonic species are known to fluctuate over time. From a community perspective, these fluctuations may result in the replacement of some dominant species and thus causing a change in ecosystem function. One of the issues in community ecology is to understand species associations and how some species may be redundant, where the redundancy is due to complementary species within each functional group. In fact, many studies have shown that increased biodiversity leads to enhanced ecosystem stability and function (e.g., Tilman, 1996; McGrady-Steed et al., 1997; Naeem and Li, 1997; Petchey et al., 1999; Cardinale et al., 2002; Zavaleta and Hulvey, 2004), and this enhancement is typically attributed to the redundancy of species within each functional group (Naeem and Li, 1997).

Given the high variability inherent with individual populations of nektonic species, the present study employed grouping strategies to temper the variability. Essentially, this is equivalent to the "portfolio effect" in that the sum of multiple varying species typically deviates less than that observed for individual species (Doak et al., 1998). The name derives from the analogy to the stock market in that financial consultants suggest customers diversify their stock holdings rather than investing in a single company, because, on average, the total of the stocks will be less variable over time. This approach allows for the identification of spatial patterns that may otherwise be obscured by the high variability. This strategy involved grouping species at various levels. All surface nekton species were originally grouped to identify patterns of distribution related to species richness, abundance, and biomass. Another level of grouping involved the analysis of the distribution and abundances associated with nekton functional groups.

To understand the spatial patterns of nektonic communities, it is important to understand the habitats with which they are associated. Chapter two focused on how near-surface zooplankton are distributed in the northern California Current, not only in space and time but also with reference to species assemblages, habitat characteristics, and environmental factors. The spatial patterns of zooplankton species richness varied temporally. During June 2000, species richness was determined to be spatially patchy, whereas in August 2000, species richness was more uniformly distributed throughout the study area. Highest values were observed during June in localized areas along the coast with lowest values observed further offshore. During August, species richness was highest nearshore south of Cape Blanco, yet in the north, higher values extended offshore over the Heceta Bank region presumably as upwelled water was displaced offshore. A similar pattern to what was observed within the Heceta Bank region during August was observed by Gibbons and Hutchings (1996) in the Benguela upwelling system of South Africa where lower species diversity was observed closer to shore with a general increase in species richness offshore. A different pattern of species richness was observed near Cape Blanco during August, however, such that species richness was higher adjacent to the shore and associated with a localized area of high upwelling activity indicated by much cooler temperatures and high levels of primary production. Overall surface-zooplankton concentrations were low in this area, but species richness was high indicating that multiple species were taking advantage of the increased primary production. This was a rather atypical finding since, in general, diversity tends to be lower in newly upwelled water during strong upwelling events (Brodeur and Pearcy, 1992; Gibbons and Hutchings, 1996). A possible explanation for this observed pattern is that the species within the upwelling center were all taking advantage of the increased primary production and that time had not permitted the dominance by a few select species. Nonetheless, a cross-shelf zonation pattern of zooplankton was generally observed, with sea surface temperature the most consistent environmental parameter explaining the distributions.

One of the most frequently used attributes of communities used in ecosystem-based studies is that of biodiversity. An important aspect of these studies is to identify the spatial patterns of biodiversity thereby identifying which portions of a region have the highest biodiversity (Walker, 1992). Because marine resources are patchily distributed, abundances of marine organisms tend to be higher in localized areas (Steele, 1976; Mackas and Boyd, 1979). Identifying such marine, biological hotspots is a growing area of research and was a main goal of this study (Malakoff, 2004).

In chapter three, biological hotspots were defined in terms of nekton community characteristics such as species richness, abundance, and biomass and were examined in relation to habitat characteristics. From this analysis, two biological hotspots were identified and determined to persist in space and time over the course of the study, yet differed with respect to biological and physical features and in the amount of area covered. The hotspots were associated with the offshore Heceta Bank region in the northern part of the study area and with the nearshore region around Crescent City, California in the south.

Indicator species analyses (ISA) and nonmetric multidimensional scaling (NMS) were used to explore patterns in community structure related to the hotspot and non-hotspot regions. Results indicated that although the general locations of the biological hotspots persisted over the course of the study, the habitat characteristics and nekton community composition within each hotspot varied over time. The most consistent environmental parameters explaining the distributions were sea-surface temperature, salinity, and density, indicating the likely structuring mechanism of the hotspots is related to the flow through the region and differing patterns of circulation associated with each hotspot.

Since individual populations vary dramatically in abundance over time and space, the identification of such spatial patterns would likely not have been possible by examining the distributions of individual species. Large aggregations in localized areas of higher trophic level species, such as schooling pelagic fish, are common in the marine environment and has been documented in the Benguela upwelling system as well (Coetzee et al., 2001). Coetzee et al. (2001), however, only had one 10-day survey so could not examine the persistence of these larger aggregations. They were primarily interested in identifying the spatial variation associated with high density schools of fish such as to improve acoustic surveys. Nevertheless, in the present study, these two hotspot regions are clearly important regions since, despite the highly variable nature of this system, they appear to be stable over the study period. In fact, it may be that it is the persistence of such hotspots through vastly different environmental and ecological conditions that provide the stability described by Rebstock (2003). Rebstock (2003) reported evidence that the California Current system is simultaneously variable and stable. Significant changes in populations from many different trophic levels were found to be related to increases in water temperature, thermocline depth, and stratification of the water column. Nonetheless, some pelagic populations and assemblages were found to persist over time. One of the possible mechanisms proposed to explain this stability was that these pelagic populations or communities shift location in response to changing environmental conditions. Results from the present study suggest, at least for nekton, that specific, localized areas may in fact persist and be important areas where much biological activity is occurring. This is supported by the fact that the persistent hotspots were defined as being areas of above average species richness, abundance, and/or biomass.

Interrelations among organisms are known factors that limit local distributions and abundances of species. Evaluating the associations among species is one means to help explain the observed spatial patterns and distributions. One mechanism for the persistence of these biological hotspots in the northern California Current may be the redundancy present in these biologically diverse hotspot communities. Frost et al. (1995) examined species compensation and functional complementarity in ecosystem function in a lake system and found that biomass of zooplankton remained at high levels despite the loss of component species from each functional group. Compensatory increases by other taxa were determined to be responsible for the complementarity of function. A key factor increasing the degree of compensation among species in response to environmental change was the functional similarity of associated species (Frost et al., 1995). Species redundancy, as reflected in more biologically diverse areas, may therefore preserve ecosystem functioning despite changes in the environment (Naeem, 1996). Therefore, the persistence of the biological hotspots in the northern California Current system may be related to species complementarity.

In chapter four, the primary goal was to identify species associations in relation to biological hotspots. Identifying which species are indicators of specific habitats and which species associate with them are important in understanding ecosystem structure.

Several nekton species within the northern California Current were found to be positively associated. Positive associations between species whose dominance fluctuates may facilitate the complementary functioning of species within a system such that if one species becomes limited in abundance another associated, and functionally similar, species may replace it thus preserving ecosystem function. Dominant species from the hotspots varied seasonally and annually. However, there appeared to be some replacement of species dominance by other similar species with respect to functional group and preferred habitat. This finding supports the idea that the persistence of these hotspots is related to species redundancy and is an important attribute contributing to the persistence of ecosystem function in this system. The Heceta Bank and Crescent City hotspots, despite changes in species composition and species dominance, may be resistant to change at the ecosystem level due to a complementarity of system function in that there may be a replacement of species by others with similar ecological niches.

To further understand the distribution of nekton and how this pertains to the functioning of the system relative to the persistent biological hotspots, in chapter five nekton were grouped according to functional groups and their distributions examined. The distributions of the functional groups were found to be spatially nonrandom and tended to occur within the hotspots indicating that the predominant biological activity occurred within persistent, localized areas. Systems with not only multiple trophic levels but also with multiple species per level, tend to be more stable given the redundancy in these systems (Naeem, 1996). This stability appears to be related to the compensatory increase in abundance of one species as another, complementary species decreases.

Therefore, localized areas with multiple trophic levels and multiple species per level should be more stable. This would appear to be the case within the northern California Current system in that these localized hotspots persisted over the time period of the study.

The persistence of the hotspots was examined further in chapter five by comparing observations from the early to mid 1980s relative to the hotspots determined from the 2000 and 2002 cruises. Sampling during the June 1980s cruises was limited to the region north of Cape Blanco and therefore did not include samples within the Crescent City hotspot. However, comparisons of the maps of the hotspots and 1980s data suggest that at least the Heceta Bank hotspot was present in the 1980s. This is rather remarkable given the vastly different environmental conditions that were present during the different time periods.

The two biological hotspots were found to differ with respect to the physical and biological characteristics associated with each. The Heceta Bank hotspot typically had lower chlorophyll concentrations and surface zooplankton biovolume than the Crescent City hotspot, and the Heceta Bank region has been characterized as a retention zone (Barth et al., 2005). Chlorophyll concentrations vary with seasonal upwelling activity as upwelled water brings cooler, nutrient-rich water to the well-lit surface area which stimulates primary production (Landry et al., 1989). In the Pacific Northwest, the strength and duration of upwelling increases southward along the coast (Hickey and Banas, 2003). The characteristics within the Crescent City hotspot and the proximity of this hotspot near the coast in the southern part of the study area indicate that this hotspot is highly associated with upwelling activity. During the warm regime after 1977, upwelling-favorable winds were diminished (Peterson and Schwing, 2003). Therefore, to determine the possible persistence of the Crescent City hotspot, data from July 1984 were compared to the hotspots. Only during July 1984 was the region south of Cape Blanco sampled. During July 1984, both nekton species richness and abundance were high within the Heceta Bank hotspot area, however, values were very low around the Crescent City hotspot. Since there were only three stations sampled within the Crescent City area and this occurred during only one time period it is not possible to draw conclusions. However, this observation suggests that perhaps the persistence of upwelling-driven hotspots, such as the Crescent City hotspot, may be more dependent on climatic conditions, which affect upwelling intensity, whereas hotspots characterized as retention-based systems are not.

In the present study, nekton biological hotspots were found to persist across much different environmental and biological conditions, yet nekton community structure varied. The identification and function of marine, biological hotspots is an expanding area of research and has broad implications for conservation, management, the design of marine protected areas, and monitoring purposes. The capacity of ecosystems to undergo extreme conditions is an important test of ecosystem function and is a measure of the fundamental ecosystem properties of resistance and resilience (Woodward, 1993). This study shows that despite widely varying environmental characteristics, nekton biological hotspots persisted. The functional groups examined were found to be considerably associated with these hotspots. Analyses of species associations' suggest a moderate degree of redundancy and the presence of such complementary species within functional groups may confer the stability observed within these systems. Additional studies with greater sampling within the biological hotspot areas will likely provide greater insight into the redundancy of species and further our knowledge of the stability associated with marine hotspot regions. Results from this study indicate that large regional areas, such as the northern California Current, are composed of smaller, localized areas where a predominant amount of biological activity is occurring, and suggests that the evaluation of large marine ecosystems may lead to erroneous or misleading results if they do not consider the more localized biological hotspots.

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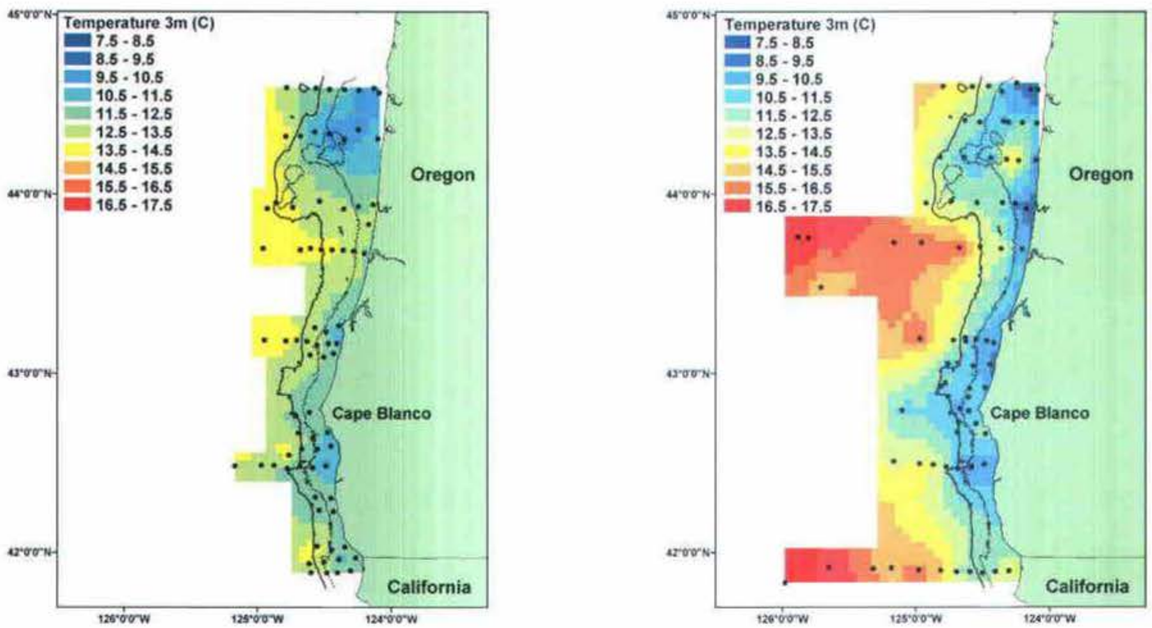
APPENDIX 1



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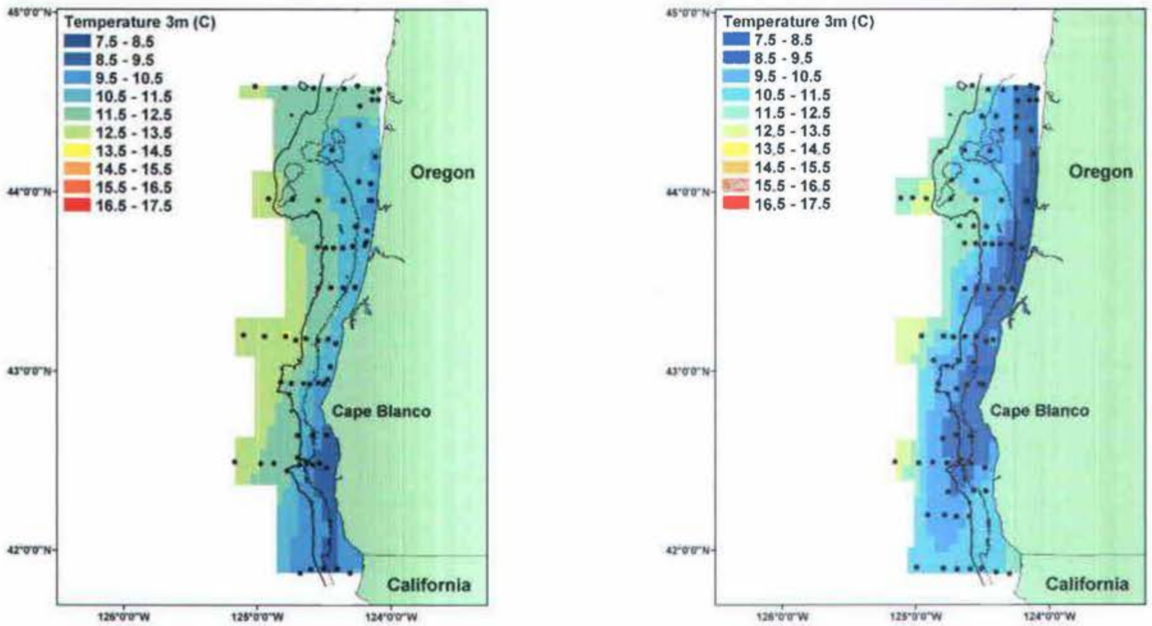

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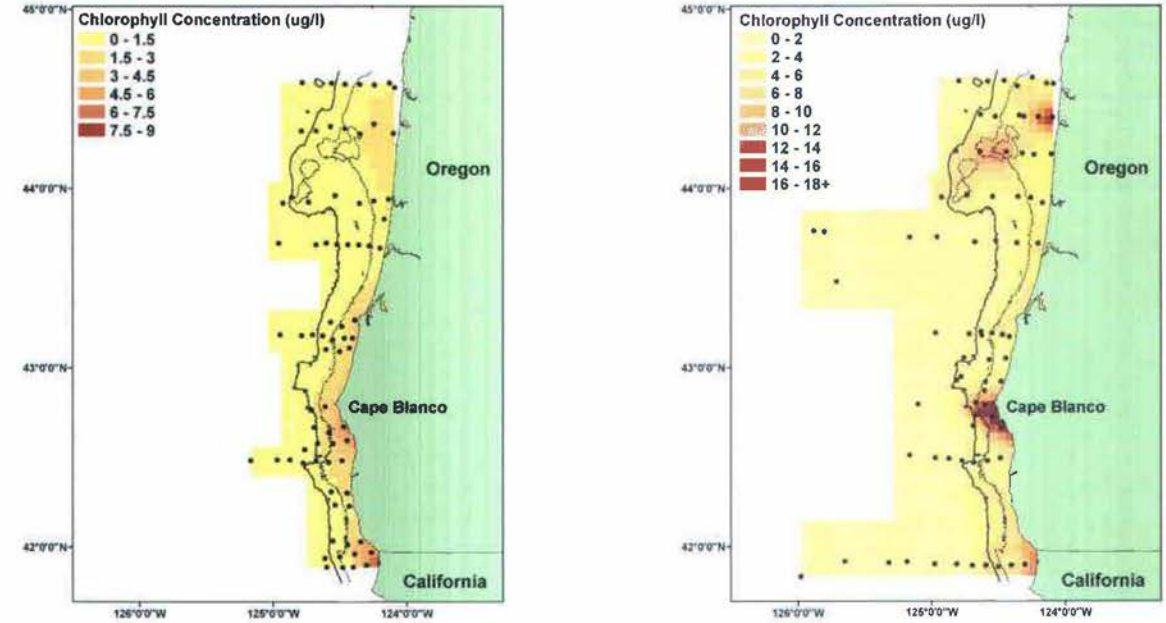
d) August 2002

Figure 8.1. Kriging maps of sea surface temperature (°C) at 3 m during: (a) June 2000; (b) August 2000; (c) June 2002; and (d) August 2002. The solid contour represents the 200 m isobath and the hatched contour represents the 100 m isobath. Grid cells are 5 km^2.



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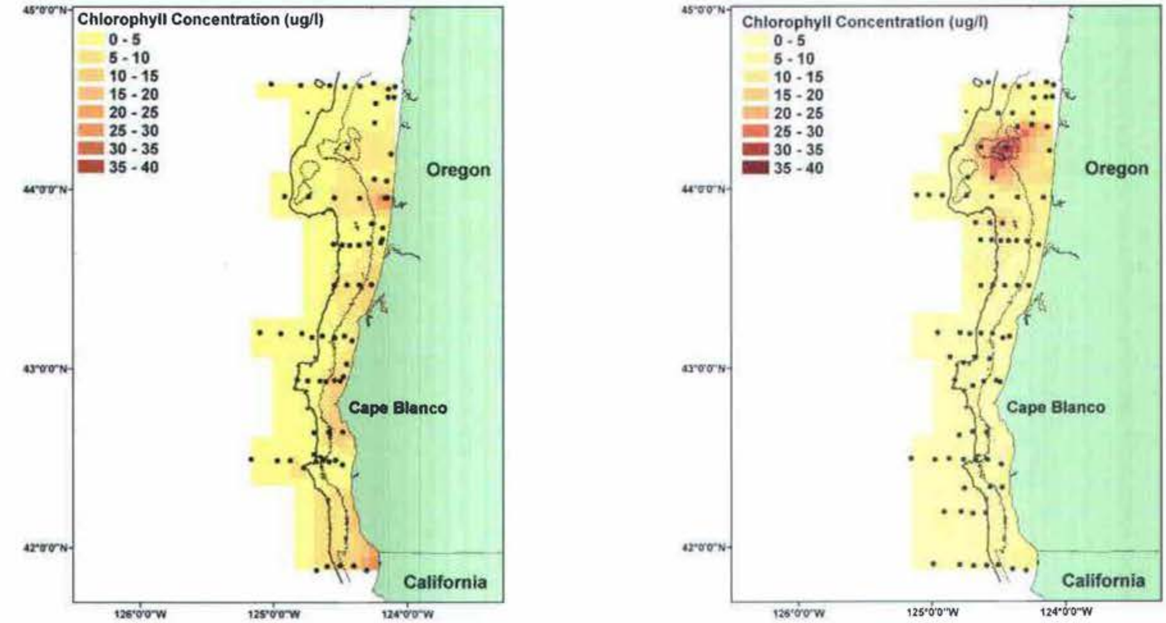

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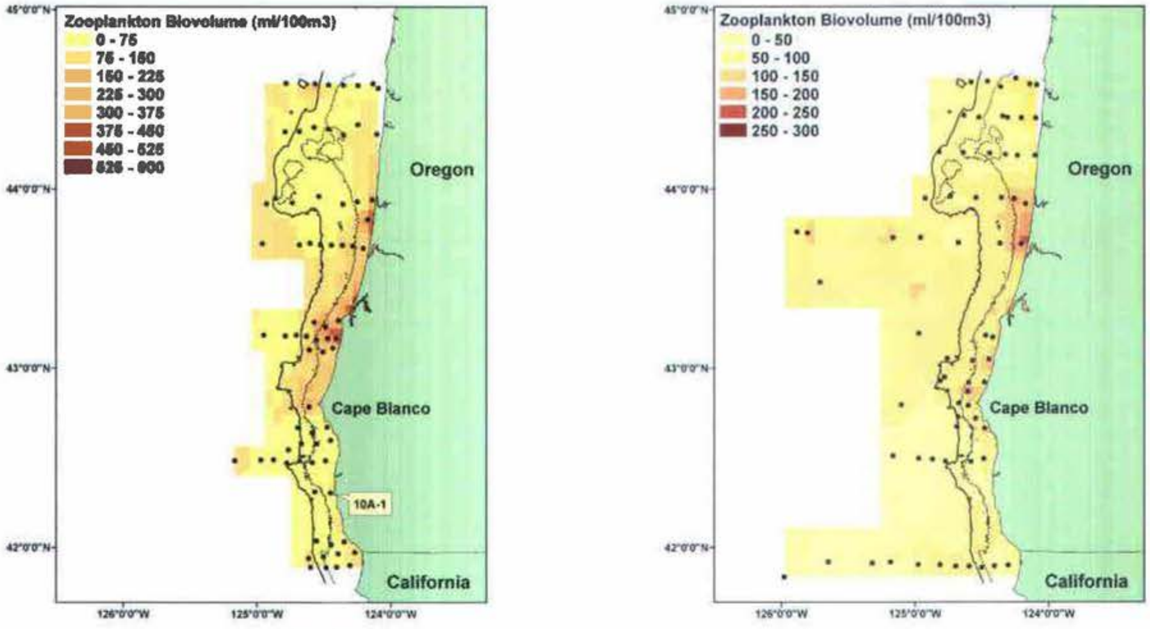
Figure 8.2. Kriging maps of chlorophyll concentration (μg/l) at 3 m during: (a) June 2000; (b) August 2000; (c) June 2002; and (d) August 2002. The solid contour represents the 200 m isobath and the hatched contour represents the 100 m isobath. Grid cells are 5 km^2. Note: different scales used.



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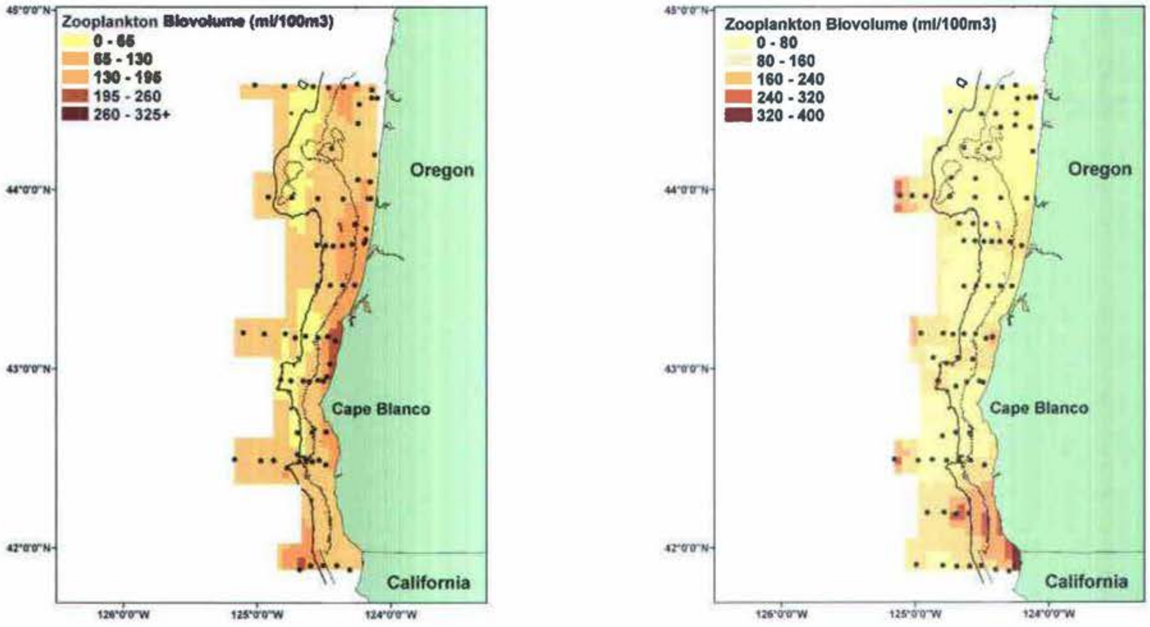

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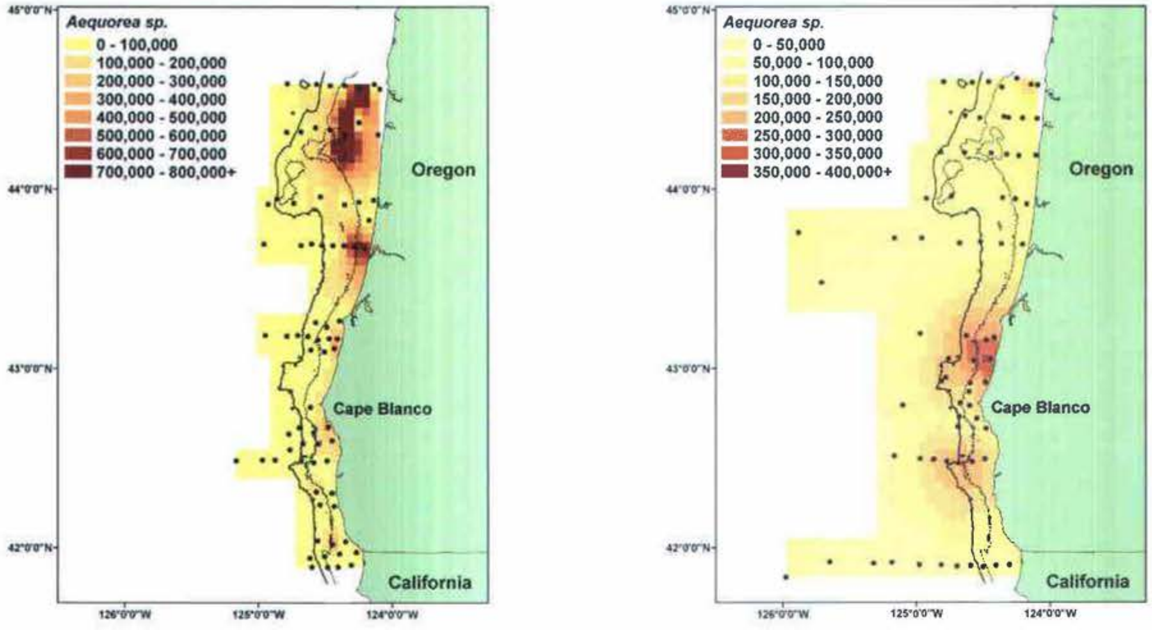
Figure 8.3. Kriging maps of surface zooplankton biovolume (ml/100m^3) during: (a) June 2000; (b) August 2000; (c) June 2002; and (d) August 2002. The solid contour represents the 200 m isobath and the hatched contour represents the 100 m isobath. Grid cells are 5 km^2. Note: different scales used.



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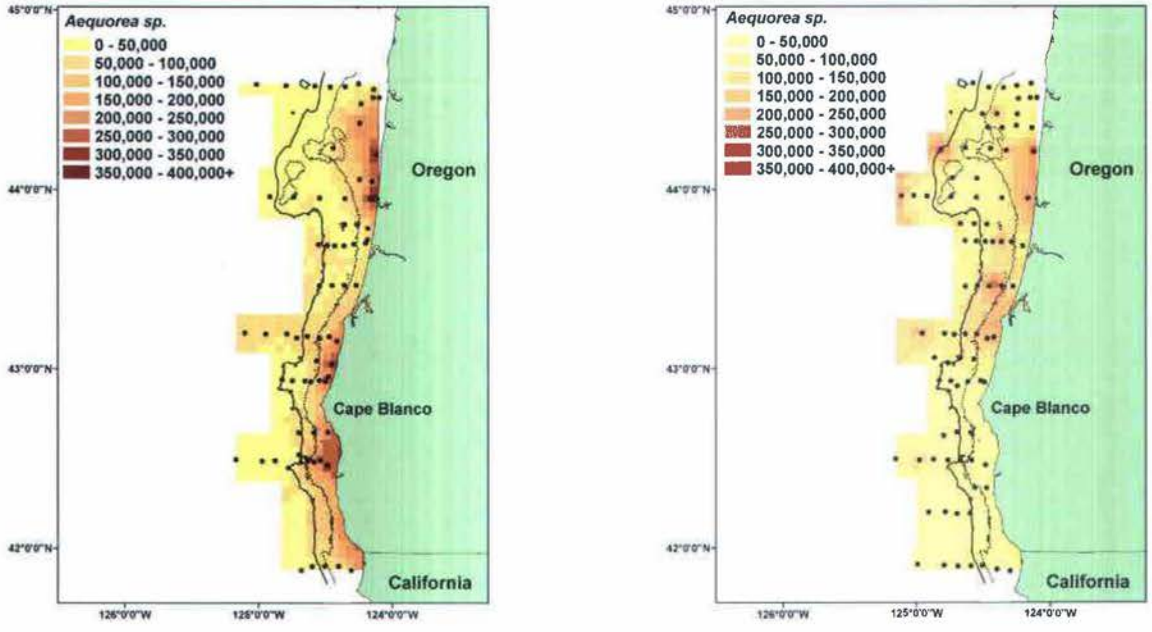

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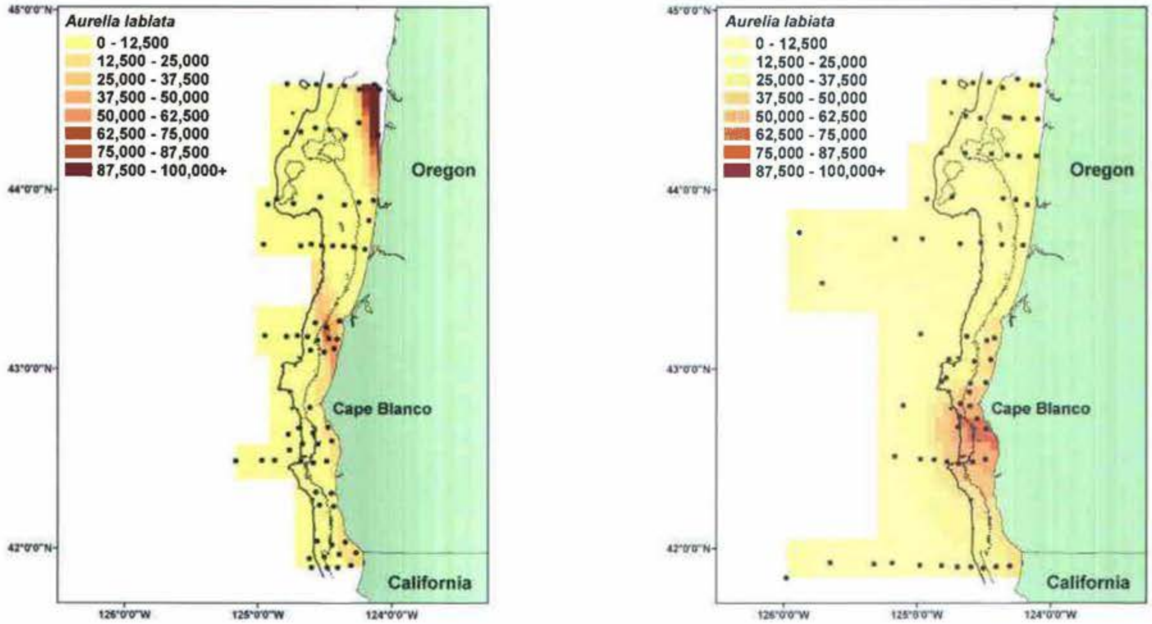
Figure 8.4. Jelly hydromedusa, *Aequorea* sp., distributions (#/km^3) during: (a) June 2000; (b) August 2000; (c) June 2002; and (d) August 2002. The solid contour represents the 200 m isobath and the hatched contour represents the 100 m isobath. Grid cells are 5 km^2. Note: different scales used.



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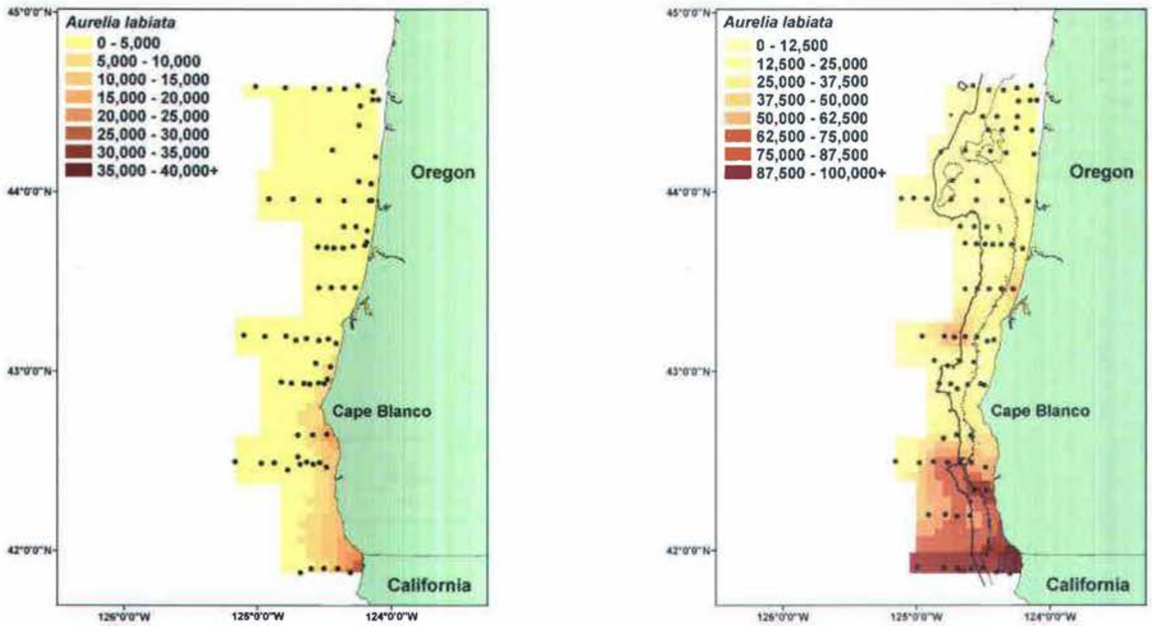

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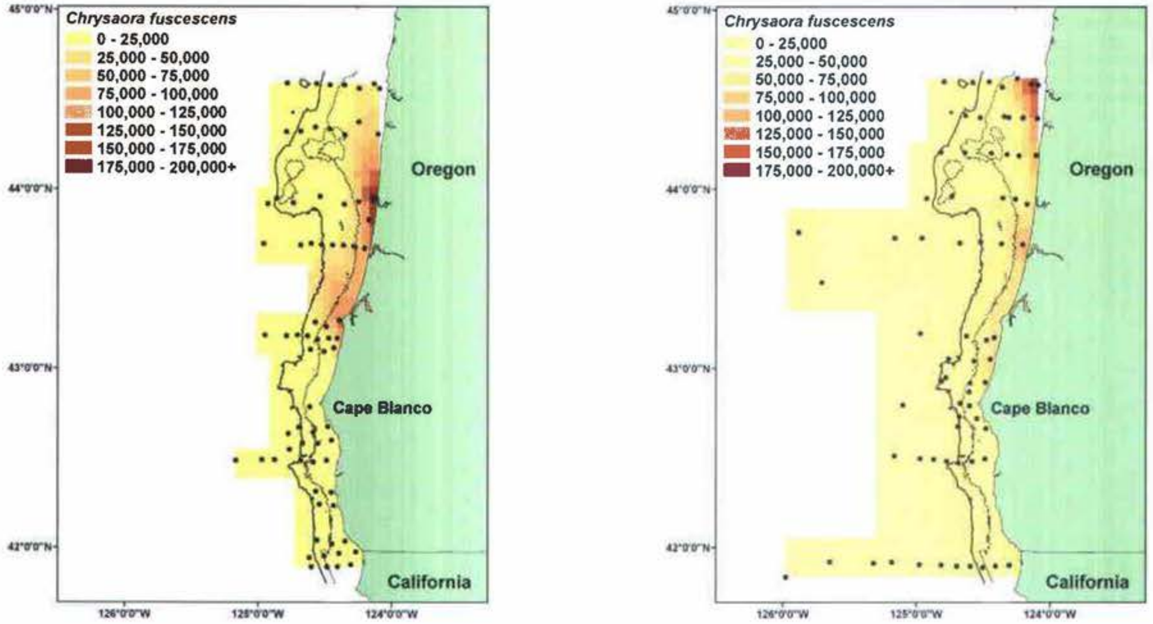
Figure 8.5. Moon jelly, *Aurelia labiata*, distributions (#/km^3) during: (a) June 2000; (b) August 2000; (c) June 2002; and (d) August 2002. The solid contour represents the 200 m isobath and the hatched contour represents the 100 m isobath. Grid cells are 5 km^2. Note: different scales used.



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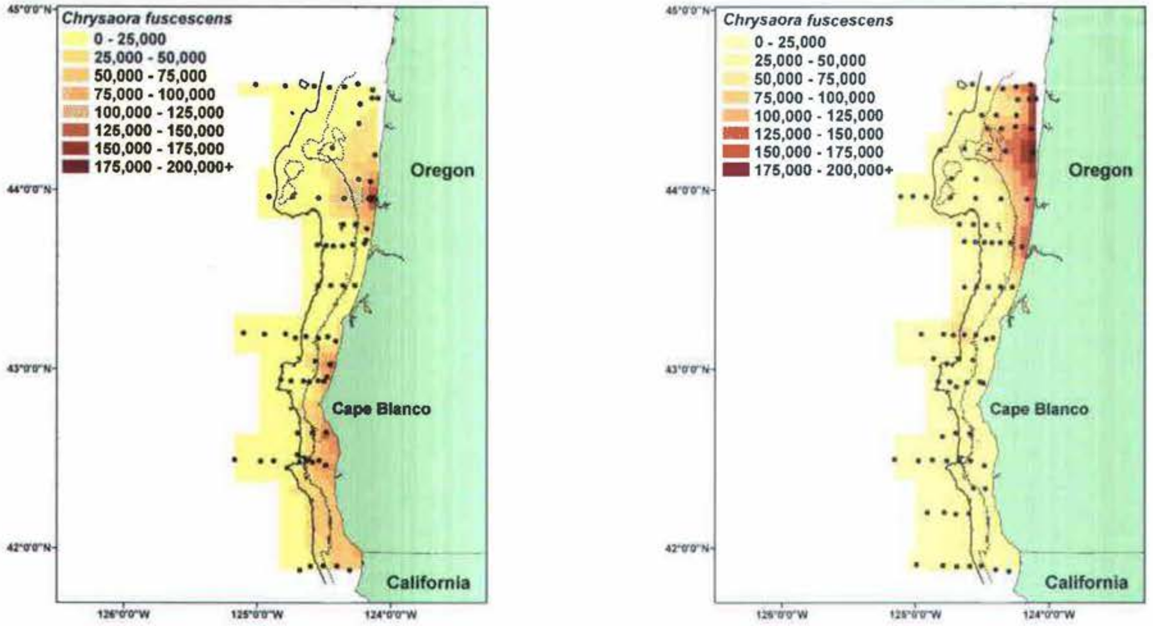

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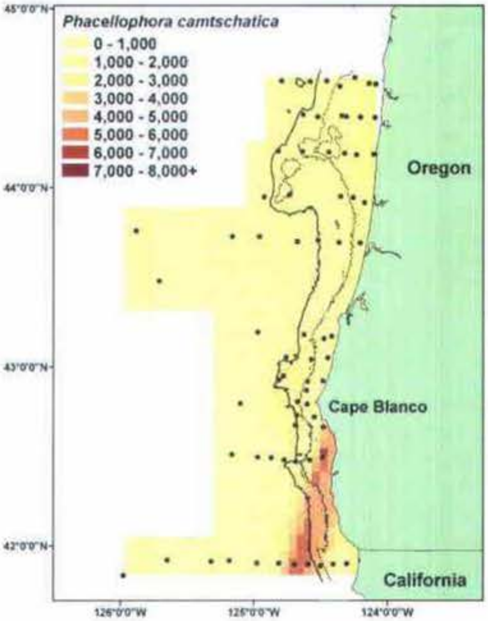
Figure 8.6. Sea nettle, *Chrysaora fuscescens*, distributions (#/km^3) during: (a) June 2000; (b) August 2000; (c) June 2002; and (d) August 2002. The solid contour represents the 200 m isobath and the hatched contour represents the 100 m isobath. Grid cells are 5 km^2.

N/A



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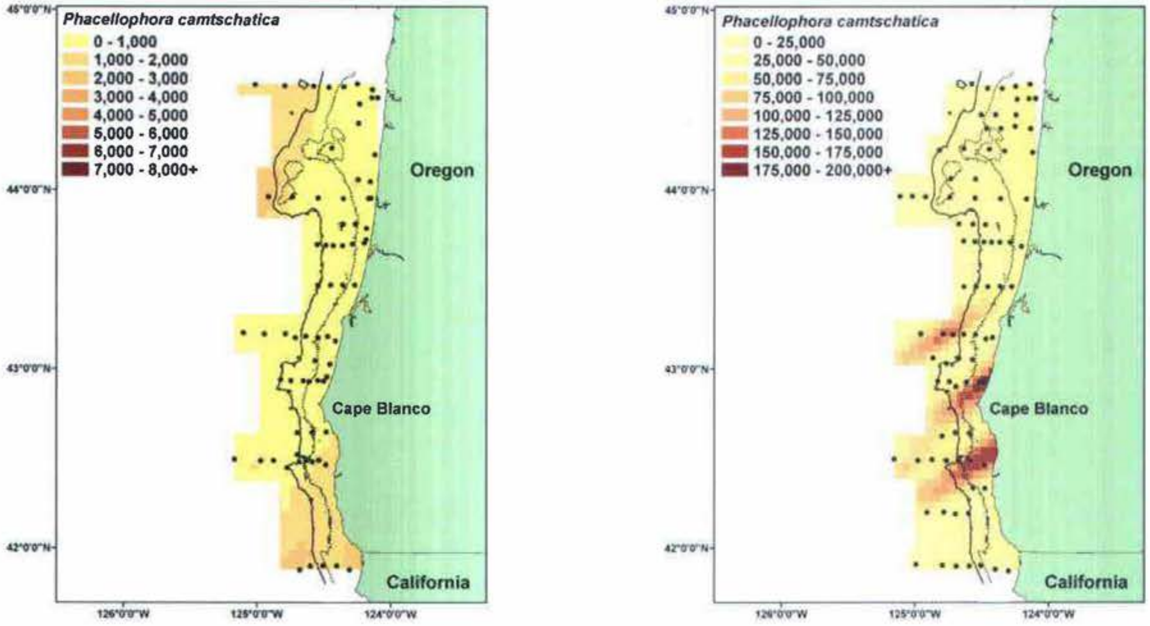

c) June 2002

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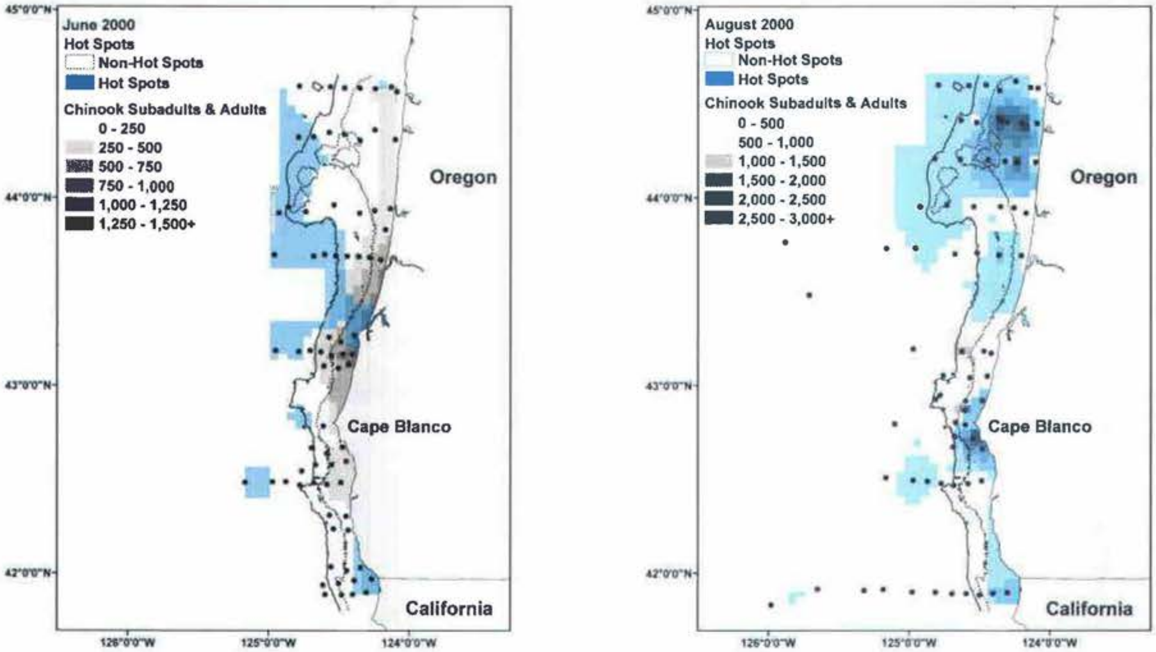
Figure 8.7. Egg-yolk jelly, *Phacellophora camtschatica*, distributions (#/km^3) during: (a) June 2000; (b) August 2000; (c) June 2002; and (d) August 2002. The solid contour represents the 200 m isobath and the hatched contour represents the 100 m isobath. Grid cells are 5 km^2. Too few encountered in June 2000. Note: different scales used.



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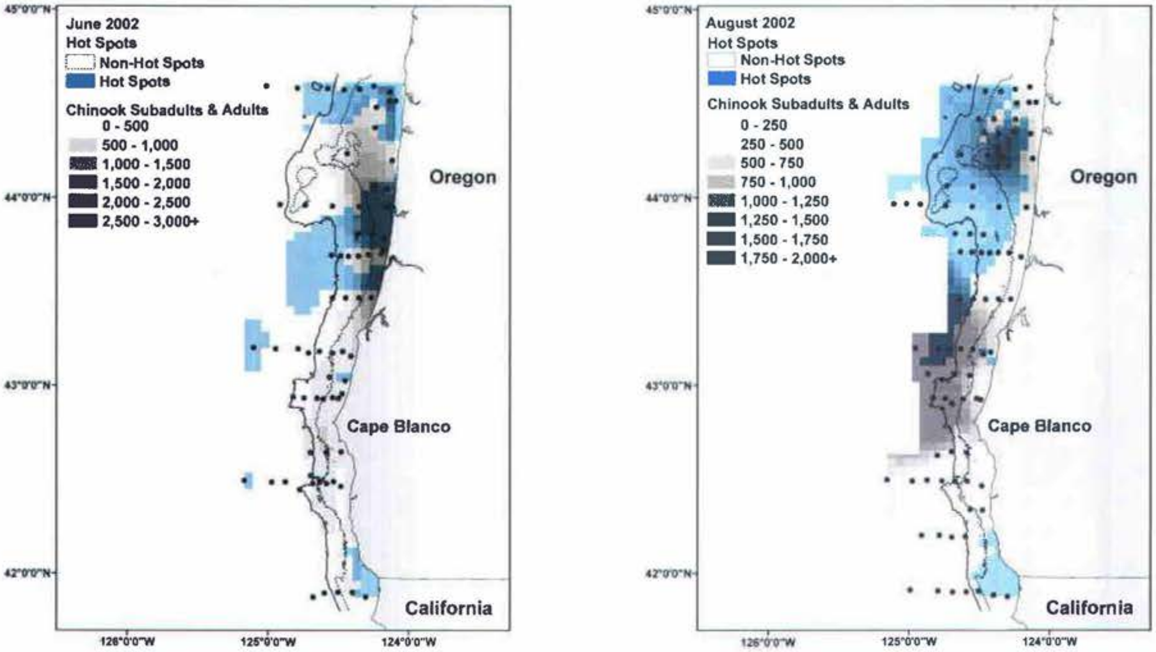
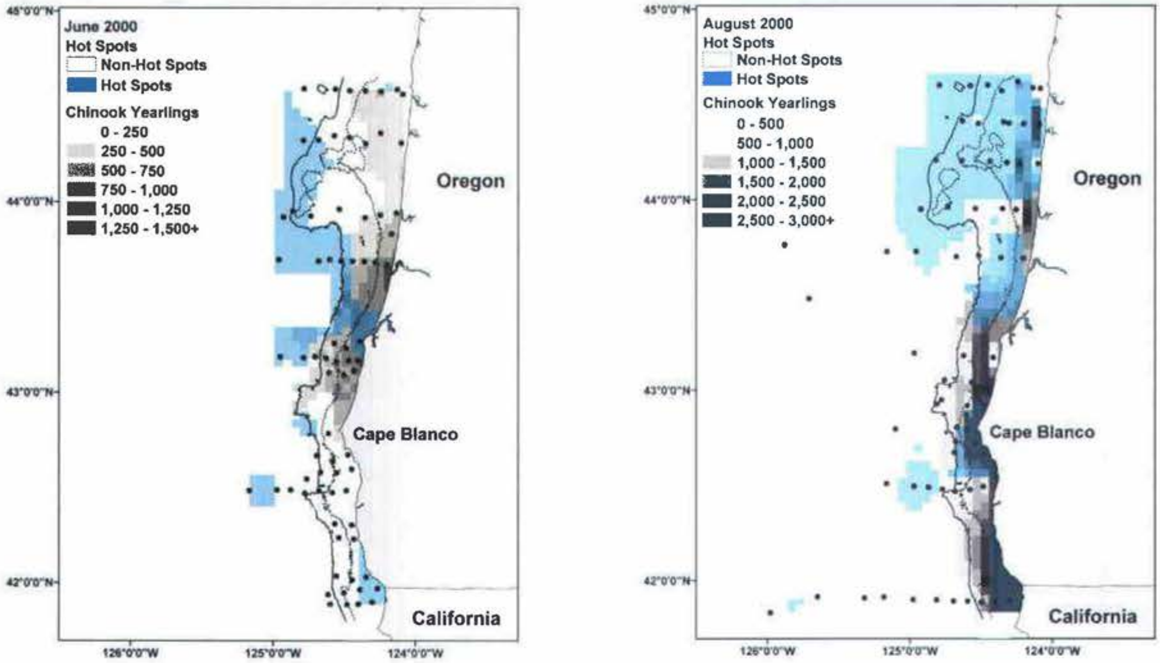


c) June 2002 d) August 2002

Figure 8.8. Chinook salmon, *Oncorhynchus tshawytscha*, adult and subadult distributions (#/km^3) relative to biological hotspots during: (a) June 2000; (b) August 2000; (c) June 2002; and (d) August 2002. The solid contour represents the 200 m isobath and the hatched contour represents the 100 m isobath. Grid cells are 5 km^2. Note: different scales.



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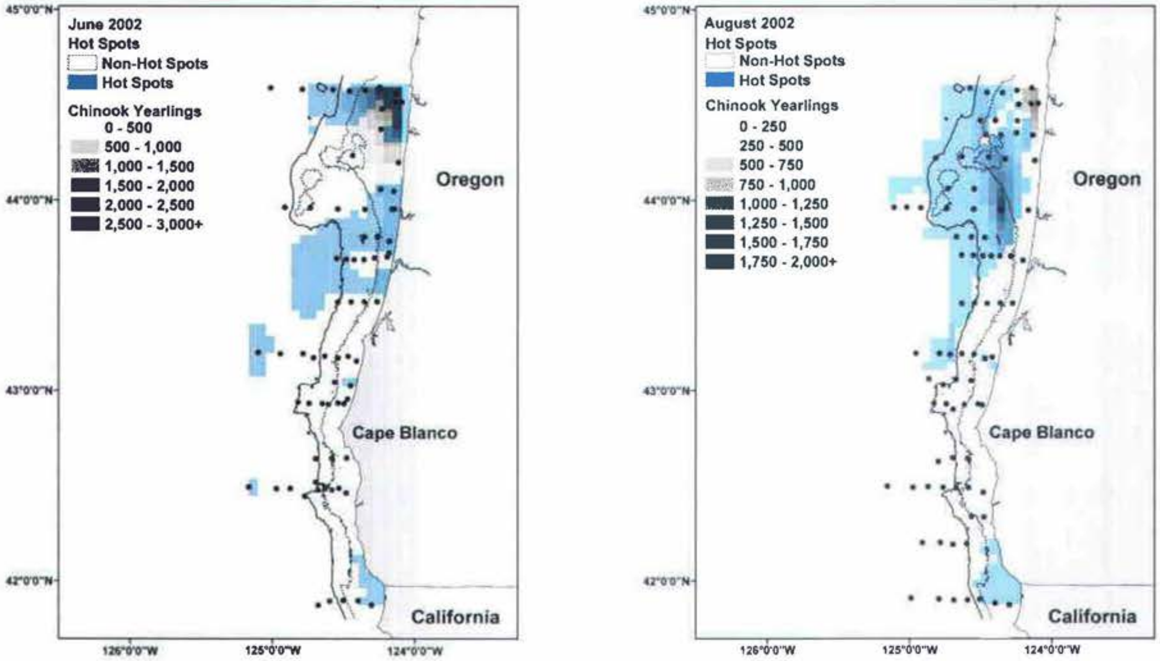

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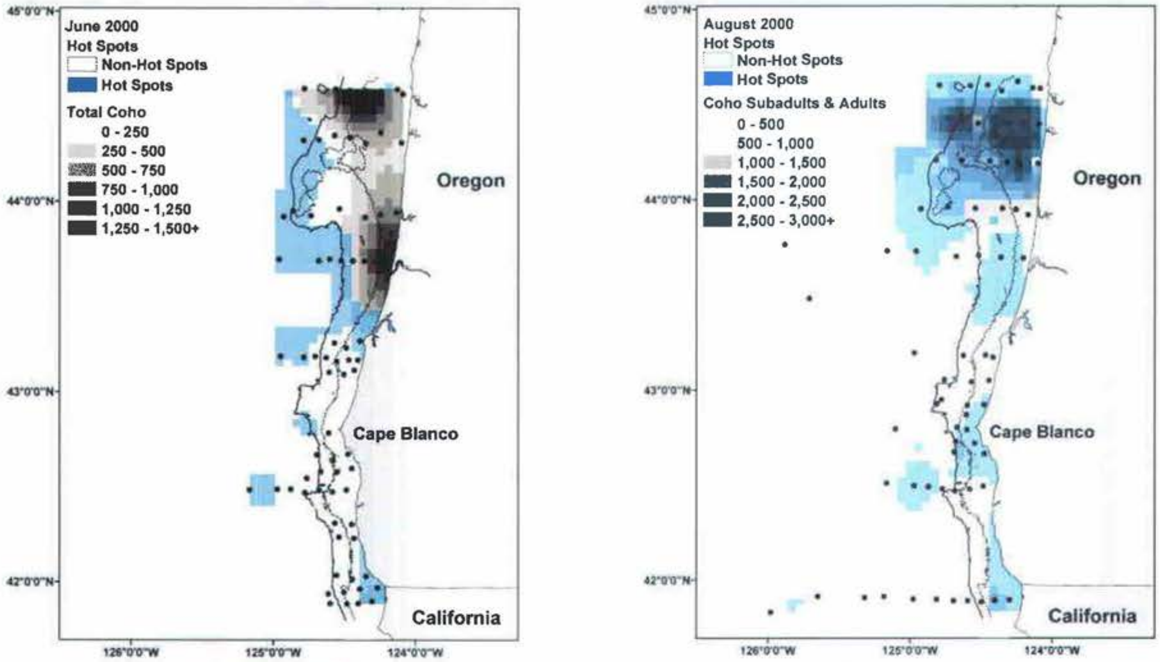
Figure 8.9. Chinook salmon, *Oncorhynchus tshawytscha*, yearling distributions (#/km^3) relative to biological hotspots during: (a) June 2000; (b) August 2000; (c) June 2002; and (d) August 2002. The solid contour represents the 200 m isobath and the hatched contour represents the 100 m isobath. Grid cells are 5 km^2. Note: different scales.



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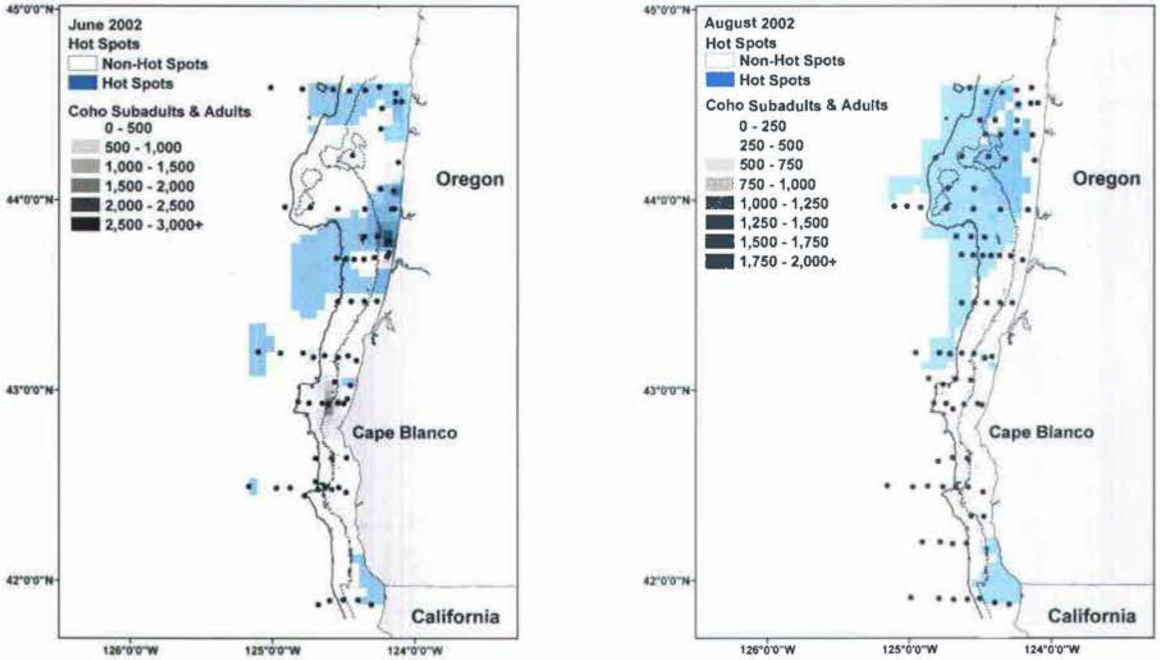
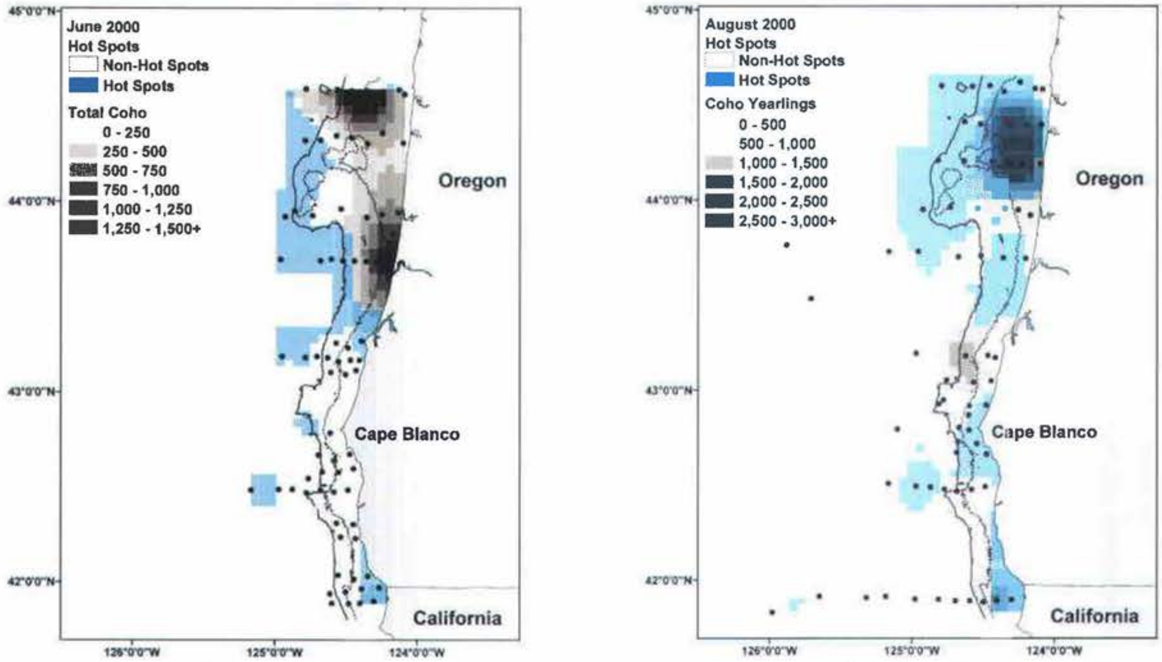


c) June 2002 d) August 2002

Figure 8.10. Coho salmon, *Oncorhynchus kisutch*, adult distributions (#/km^3) relative to biological hotspots during: (a) June 2000; (b) August 2000; (c) June 2002; and (d) August 2002. The solid contour represents the 200 m isobath and the hatched contour represents the 100 m isobath. Grid cells are 5 km^2. Note: different scales and June 2000 is combination of all age classes of Coho due to low numbers.



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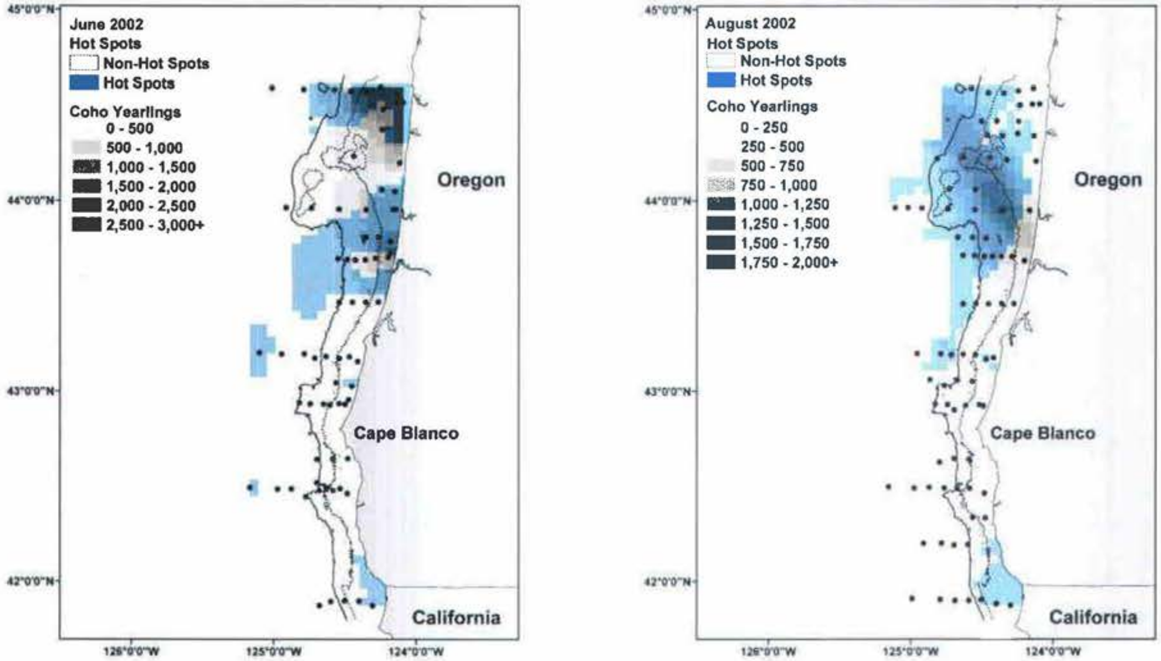

c) June 2002 d) August 2002

Figure 8.11. Coho salmon, *Oncorhynchus kisutch*, yearling distributions (#/km^3) relative to biological hotspots during: (a) June 2000; (b) August 2000; (c) June 2002; and (d) August 2002. The solid contour represents the 200 m isobath and the hatched contour represents the 100 m isobath. Grid cells are 5 km^2. Note: different scales and June 2000 is combination of all age classes of Coho due to low numbers.

APPENDIX 2

Table 9.1. List of nektonic species labels and common names used throughout text.

Species Label	Common Species Name
BgSktAd	Big skate adult
BlkRcfAd	Black rockfish adult
BlkRcfjv	Black rockfish juvenile
BlRckfjv	Blue rockfish juvenile
BlShrkAd	Blue shark adult
BnkRfjuv	Bank rockfish juvenile
Bociojv	Bocaccio juvenile
BtrSolAd	Butter sole adult
BtrSolLv	Butter sole larval
Cbznjv	Cabezon juvenile
ChinSnA	Chinook salmon subadult/adult
Chinyrlg	Chinook salmon yearling
ChmSnA	Chum salmon subadult/adult
ChnSbyl	Chinook salmon subyearling
Chumjuv	Chum salmon juvenile
Clpdlarv	Clupeid larval
Cnryrkjv	Canary rockfish juvenile
CohoSnA	Coho salmon subadult/adult
Cohoyrlg	Coho salmon yearling
CrfnSlLv	Curlfin sole larval
Cuttnone	Cutthroat trout none
Dallsprp	Dall's porpoise
DbRckfjv	Darkblotched rockfish juvenile
DvrSlLv	Dover sole larval
EngSolAd	English sole adult
Fltnidlv	Flatfish (unidentified) larval
Gddnidjv	Gadid (unidentified) juvenile
Hbrprpad	Harbor porpoise adult
HibCstjv	Highbrow crestfish juvenile
IrsLrdjv	Irish lord juvenile
Jacksmlt	Jacksmelt
JkMackAd	Jack mackerel adult
KgoSlmjv	King-of-the-salmon juvenile
Lngcdjv	Lingcod juvenile
Lptocslv	Leptocephalus larval (eel)
Mctpduid	Myctophid (unidentified)
MdsafAd	Medusafish adult
Mdsafjv	Medusafish juvenile
Mrktsqd	Market squid

Table continued on next page

Table 9.1 continued

Species Label	Common Species Name
NAnchvad	Northern anchovy adult
Nanchvjv	Northern anchovy juvenile
NFlyngsq	Neon flying squid
Nlmpfsad	Northern lampfish adult
Ocsunfsh	Ocean sunfish
Paccodjv	Pacific cod juvenile
Pachakad	Pacific hake adult
Pchrngad	Pacific herring adult
Pchrngjv	Pacific herring juvenile
Pchrsjv	Poachers juvenile
Pclbhksq	Pacific clubhook squid
Pclmpry	Pacific lamprey
PinkSnA	Pink salmon subadult/adult
Plrnctlv	Psettichthys Pleuronectid larval
Pmckrlad	Pacific mackerel adult
Pocpchjv	Pacific ocean perch juvenile
PpWdrfjv	Pacific ocean perch/Widow rockfish juvenile
Prlctdlv	Paralichthyid larval
Prwfsh	Prowfish
Psardnad	Pacific sardine adult
Psauryad	Pacific saury adult
Psndbad	Pacific sanddab adult
Psndblv	Pacific sanddab larval
Psndfhad	Pacific sandfish adult
Pspnylmp	Pacific spiny lumpsucker
PSrckfjv	Puget Sound rockfish juvenile
Pstghrns	Pacific staghorn sculpin
Ptmcdjv	Pacific tomcod juvenile
Ragfshjv	Ragfish juvenile
Rckfsjv	Rockfish (unidentified) juvenile
Rexsollv	Rex sole larval
Sblfshjv	Sablefish juvenile
Sdbnidlv	Sanddabs (unidentified) larval
ShadAdlt	American shad adult
Shblrfjv	Shortbelly rockfish juvenile
Smeltjuv	Smelt juvenile
Smeltlv	Smelt larval
Sndlncjv	Pacific sandlance juvenile
Sndsollv	Sand sole larval
SockSnA	Sockeye salmon subadult/adult

Table continued on next page

Table 9.1 continued

Species Label	**Common Species Name**
Spcsdblv	Speckled sanddab larval
Spfnshad	Soupfin shark adult
Spndgfad	Spiny dogfish adult
Srfsmlad	Surf smelt adult
Srfsmljv	Surf smelt juvenile
Stgnprjv	Sturgeon poacher juvenile
Stlhdjuv	Steelhead trout juvenile
StlhdSnA	Steelhead trout subadult/adult
StRckfjv	Stripetail rockfish juvenile
Strflnad	Starry flounder adult
Turbotlv	Turbot larval
Wdwrkfjv	Widow rockfish juvenile
Wlfeeljv	Wolf eel juvenile
Wtsmltad	Whitebait smelt adult
Wtsmltjv	Whitebait smelt juvenile
Ylwrngoc	Yellow-ringed octopus
Ytlrckjv	Yellowtail rockfish juvenile