LOCAL AND REGIONAL PATTERNS OF TRANSPORT, DISPERSAL, AND EXCHANGE IN COASTAL FISHES

by

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A DISSERTATION

Presented to the Department of Biology
and the Graduate School of the University of Oregon
in partial fulfillment of the requirements
for the degree of
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Ocean transport processes affect larval dispersal and influence survival and exchange among populations. Cross-shelf and alongshore transport are known to be important but it is not understood which mechanisms are dominant or whether similar mechanisms regulate transport to and between coastal and estuarine areas. Time series, chemical, and genetic analyses were used to provide information on transport, dispersal, and exchange in coastal fishes. Time series analyses of high frequency (every 1–2 d), short–term (4 mos) light trap collections were completed to compare species' abundances, examine potential transport mechanisms, and document exchange between the coastal ocean and an adjacent estuary. Peak abundances of juvenile fish in the estuary occurred 0 to 4 d after peaks at the outer coast, which indicate that estuarine ingress was a two-stage process. Next, a long–term (3 ¾ yr) time series of light trap collections within Coos Bay, Oregon was analyzed. Thirty-eight taxa of larval and juvenile fishes were collected. Within

the estuary, fish were most abundant during downwelling but there was little evidence for wind-driven transport. Tidal periodicities in fish abundances were observed in the estuary and at the outer coast, which indicate shoreward transport and estuarine ingress may have occurred via selective stream tidal transport and/or internal tides and bores. Thirdly, the otolith elemental composition of black rockfish (*Sebastes melanops*), collected at sites 120–420 km apart, was examined at various positions along the otolith growth axis to estimate relative extents of larval dispersal and adult movement. Geochemical otolith signatures accurately classified 67% to 81% of individuals to collection location throughout their life. A probable explanation is that individuals from geographically distinct locations never mixed and possibly did not disperse long distances as larvae, which may contribute to population divergence. DNA microsatellite analysis identified significant genetic differences ($F_{ST} = 0.018 \pm 0.004$) between adults from Oregon and Washington, providing corroborative evidence for limited larval dispersal. Lastly, spatial and temporal variation in otolith elemental composition of staghorn sculpin (*Leptocottus armatus*), collected in Oregon and California estuaries, was examined to further evaluate the utility of otolith microchemistry in determining movements of individual fish.

This dissertation includes both my previously published and my co-authored materials.

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Chapter I

Introduction

It has been recognized for nearly a century that population abundances of marine fishes can be highly variable over time and often appear erratic (Hjort 1914). Furthermore, Hjort (1914) noted that cycles in abundance could be coherent over relatively wide spatial scales both within and among species. At that time, he suggested that the size "of a year class is apparently determined at a very early stage." He offered two possible mechanisms for such patterns; 1) starvation and/or 2) the transport of larvae away from adequate rearing and/or settlement habitats. Since Hjort's proposal, numerous studies have attempted to support or refute his hypotheses (Cushing 1990; Lasker 1974; Peterman et al. 1988; Peterman 1987; Sinclair 1988). Cushing (1975, 1990) expanded Hjort's "critical period" hypothesis to include development through metamorphoses (typically defined as settlement for benthic species or the acquisition of a full complement of adult characters) and proposed his "match-mismatch" hypothesis, which predicts the timing of larval release should coincide with peaks in prey production cycles. Although evidence that supports starvation as a primary determinant of recruitment is equivocal, recruitment success in numerous species has been related to physical environmental factors (Dixon 1999; Higgins et al. 1997; Koslow 1984; Sinclair et al.

1985; Ware 1991). Therefore, numerous research efforts have focused on the transport and dispersal of marine fish eggs and larvae.

Various physical features, such as fronts (Shanks et al. 2000), gyres (Flierl and Wroblewski 1984), and wind-driven circulation (Epifanio and Garvine 2001; Shanks 1995), often in conjunction with individual behaviors (Forward and Tankersley 2001; Kingsford et al. 2002), can affect the transport and dispersal of marine fish during their early life history. Furthermore, species of fish that reside in coastal areas as adults must either return to or maintain positions in nearshore or estuarine areas upon completion of the larval or juvenile period. Both cross-shelf and alongshore transport affect larval dispersal and, therefore, influence survival and exchange among populations. However, it is not understood which physical mechanisms are primarily responsible for transport or whether similar mechanisms regulate transport to and between coastal areas and estuaries. Furthermore, the alongshore extent of larval dispersal is not known for most species of coastal fish.

The west coast of the United States lies within the California Current system. Oregon's coastal region is characterized by seasonal, wind-driven upwelling (during late spring and summer) and downwelling (during late fall and winter) due to Ekman transport of surface waters (Huyer 1976). During upwelling, northwest winds result in the offshore movement of a shallow surface layer and the establishment of a front where low density off-shore waters meet high density, recently upwelled waters (Mooers 1976). At this time, the predominant alongshore surface current over the continental shelf is equatorward. There is a seasonal reversal during late fall through winter when southwest

winds promote downwelling, or the shoreward movement of surface waters. At this time, the predominant alongshore surface current over the continental shelf is poleward (i.e. the Davidson or Inshore Counter Current). This dynamic coastal system presents challenges for the successful transport and recruitment of marine larvae.

Assumptions regarding larval dispersal in marine populations include that 1) dispersal is primarily passive, 2) dispersal distances are typically long, 3) recruitment into a population comes from outside sources, and, therefore, 4) populations are primarily open (Cowen et al. 2000). Sinclair (1988) challenged the notion that planktonic larval stages are predominantly for dispersal of propagules and suggests, alternatively, that reproductive strategies of marine fish have evolved to maintain larvae in geographically stable retention areas. The number of geographically stable retention areas thereby determines the number and size of sub-populations (Iles and Sinclair 1982). Sinclair (1988) presented evidence primarily on pelagic fish stocks but an apparent lack of offshore, and possibly alongshore, dispersal has also been documented in tropical (Jones et al. 1999; Swearer et al. 2002; Taylor and Hellberg 2003) and rocky intertidal (Marliave 1986) fishes. Other researchers suggest that large-scale larval dispersal in marine organisms may be a "byproduct of an ontogenetic migration into the water column that is favored for other reasons" (Strathmann et al. 2002).

Studies on larval dispersal have been hampered by inadequate analytical techniques. Individual tagging studies are expensive, logistically difficult, and typically not feasible for larval stages, during which mortality often exceeds 90% (but see Jones et al. 1999). Although genetic techniques can underestimate the extent of population

structure and offer only indirect information on larval sources and dispersal distances, they do provide some indication of exchange among populations (Kinlan and Gaines 2003; Palumbi 2003). However, recent management efforts, such as the establishment of marine protected areas (MPAs) for both the maintenance of biodiversity and population recovery efforts, are hampered by the "current paucity of information regarding meroplanktonic larval transport processes" (Lockwood et al. 2002).

The elemental composition of teleost (bony fish) otoliths may serve as a natural tag with which to track larvae (Campana 1999). Briefly, otoliths are crystalline structures, comprised primarily of calcium carbonate, located in the inner ear and function as balance organs. Teleost otoliths grow by continuous deposition of calcium carbonate with no evidence of resorption. At the time of deposition, certain trace elements can accumulate within otoliths in proportion to seawater concentrations (Bath et al. 2000; Campana 1999). Therefore, otolith elemental composition can reflect ambient water conditions at the time of deposition.

In this dissertation, I addressed questions related to local and regional patterns of transport, dispersal, and exchange in coastal fishes. I designed a number of studies to provide new information on 1) the cross-shelf and estuarine transport of coastal fishes, 2) the extent of ocean-estuary coupling, and 3) the movement patterns of larval and juvenile coastal fishes, specifically black rockfish (*Sebastes melanops*) and staghorn sculpin (*Leptocottus armatus*).

Chapter II, "The abundance and distribution of larval and juvenile fish in the Coos Bay estuary, Oregon: a time-series analysis based on light-trap collections," presents the

results of a long-term estuarine time series. The objectives of this study were to use a long-term time series (3¾ years) of high-frequency (every 1 to 2 days) light-trap collections in Coos Bay, a temperate estuary, to: 1) document fish species diversity (i.e. richness and abundance); 2) document inter- and intra-annual species abundance patterns; 3) make relative comparisons of species distributions based on collections from different sample locations; and 4) examine potential transport mechanisms, specifically wind-driven and tidal transport, for species collected in adequate numbers for time-series analysis.

Chapter III, "Ocean-estuary coupling in the Oregon upwelling region: abundance and transport of juvenile fish and of crab megalopae," presents a comparison between an outer coastal and estuarine location. Here I also used high-frequency light-trap collections to collect juvenile fish and crab megalopae at the two sites. The time series of juvenile fish and crab megalopae were statistically compared with physical variables indicative of wind and tidal conditions to identify potential transport mechanisms and to provide information on transport mechanisms and the exchange of organisms between the coastal ocean and an adjacent estuary. This chapter, authored by myself and A. L. Shanks, is published in *Marine Ecology Progress Series*.

Chapter IV, "Evidence for limited larval dispersal in black rockfish (*Sebastes melanops*): implications for population structure and marine reserve design," presents a study on the otolith microchemistry of juvenile black rockfish. In this study, I used otolith elemental composition as a relative indicator of larval and juvenile movement. I did not attempt to identify specific larval sources. Rather, I used the otolith elemental

composition of black rockfish (*Sebastes melanops*), a northeast Pacific species with an extended (3 to 6 months) pelagic larval and juvenile period, in conjunction with otolith microstructure analyses, to determine if I could generate relative estimates of alongshore dispersal distance. To do this, I compared otolith geochemical signatures at three discrete positions along the otolith growth axis throughout the early life history of fish collected from different geographic locations along the Washington and Oregon coast. This chapter, authored by myself and A. L. Shanks, is published in the *Canadian Journal of Fisheries and Aquatic Sciences.*

Chapter V, "Population structure in black rockfish (*Sebastes melanops*): a comparison between otolith microchemistry and DNA microsatellites," compares two relatively new techniques. I examined both otolith microchemistry and DNA microsatellites in adult black rockfish to determine if there was evidence of population structure along the Oregon/Washington coast. DNA microsatellite markers, due to their high level of genetic variation, have a promising advantage over previous genetic techniques for detecting population structure (Banks et al. 2000). The primary questions were: 1) Are there unique geochemical signatures in adult otoliths? 2) Do those geochemical signatures vary ontogenetically, i.e. at the otolith core vs. otolith edge? 3) Do otolith elemental signatures provide discriminatory power to predict the collection location of *S. melanops* along the Oregon/Washington coast? 4) Do DNA microsatellites provide evidence for genetic population structure in *S. melanops* collected along the Oregon/Washington coast? 5) Do DNA microsatellite data provide discriminatory power to predict the collection location of *S. melanops* along the Oregon/Washington coast? 6)

Are data generated with otolith microchemistry and DNA microsatellite data complementary and corroborative?

Chapter VI, "Spatial and temporal variation in the otolith microchemistry of staghorn sculpin (*Leptocottus armatus*)," takes a detailed look at the scales of variation in the otolith microchemistry of a marine species often found within estuaries during its early life history. In order to quantify spatial and temporal variation in otolith microchemistry, I examined staghorn sculpin collected within three estuaries, including the Columbia River estuary and Coos Bay, Oregon and Humboldt Bay, California. I addressed a number of questions: 1) Are there significant differences in the otolith chemistry of *L. armatus* collected from different estuaries and from different sites within those estuaries? 2) At what spatial scales are such differences detectable? 3) Does otolith elemental composition, whether due to intrinsic or extrinsic factors, vary throughout ontogeny? 4) Is there interannual variation in otolith elemental composition? And, if so, how large is that variation and how does it compare to spatial and intra-annual variation? 5) Which, if any, elements provide discriminatory information regarding collection location among and within bays?

Finally, Chapter VII presents a brief summary of my major findings and presents some overall conclusions.

Chapter II

Abundance and distribution of larval and juvenile fish in Coos Bay, Oregon: a time-series analysis based on light-trap collections

Introduction

Numerous species of marine fish spend a portion of their lives, often as larvae or juveniles, within estuaries (Beck et al. 2001; Elliott and Hemingway 2002). Some estuarine habitats, such as salt marsh and seagrass, are often said to play a vital role in the early life history of many marine fish species. Although the presence of many marine fish species in estuaries is well documented, the specific role estuaries play in species persistence is less certain. In an attempt to more precisely define the role of estuaries as nurseries, Beck et al. (2001) state "a habitat is a nursery for juveniles of a particular species if its contribution per unit area to the production of individuals that recruit to adult populations is greater, on average, than production from other habitats in which the juveniles occur." They call on researchers to refine both their definition of "nursery habitat" and the experiments used to test the nursery function of estuaries. Specifically, they see a need to quantify estuarine use in terms of density, growth, survival, and movement to adult habitats. This effort is, in part, motivated by the current need for precise descriptions of "essential fish habitat" as prescribed in the 1996 Magnuson-Stevens Fishery Conservation and Management Act (Public Law 94-265). Essential fish

habitat is defined as "those waters and substrates necessary to fish for spawning, breeding, feeding, or growth to maturity."

Along the west coast of the United States, estuaries have often been considered less important in the early life history of marine species than in other geographic regions, such as the Gulf of Mexico and the southeastern United States (Boehlert and Mundy 1987; Haedrich 1983; Pearcy and Myers 1973). However, numerous fish species (i.e. > 20) are found in Pacific Northwest estuaries (Haertel and Osterberg 1967; Mistano 1977; Monaco et al. 1992). Conclusions regarding estuarine use appear, in part, to be influenced by the method of collection. For example, Pearcy and Myers (1973) concluded, after completing a planktonic survey that identified 45 types of larval fish in Yaquina Bay, Oregon, that the estuary appeared to function as a nursery only for Pacific herring (*Clupea harengus pallasi*) and a variety of small cottids (sculpins), gobies (gobies), and stichaeids (pricklebacks). However, they note that their planktonic survey was not adequate to fully assess the estuary as a nursery due to their sample bias toward weakly swimming organisms in the water column. Strong swimmers, such as the Embiotocids (surf perches), or benthic juveniles, such as the starry flounder (*Platyichthys stellatus*) and English sole (*Parophrys vetulus*), are not adequately sampled with plankton nets. Other earlier research in the Pacific Northwest on fish use of estuaries includes surveys that targeted larval and post-larval planktonic fishes (Mistano 1977) or benthic fishes (Bottom et al. 1987; Haertel and Osterberg 1967). However, since the 1970s, most research on fishes in Pacific Northwest estuaries has focused primarily on a few commercially important species, notably Pacific salmon (*Oncorhynchus* spp.) (Fisher and

Pearcy 1990; Healey 1982; Miller and Sadro 2003) and English sole (*Parophrys vetulus*) (Boehlert and Mundy 1987).

Oregon's numerous and relatively small estuaries are strongly influenced by the coastal ocean (Roegner et al. 2003; Roegner and Shanks 2001). Therefore, it is logical that marine fish in this region would not be as dependent on the relatively small estuarine area available compared with regions that have more diverse and expansive estuaries, such as the Gulf of Mexico and the southeastern United States. However, there has been very little research on the use of estuaries by larval and juvenile fishes, other than that noted above, in Oregon's estuaries since the 1970s. This lack of information inhibits efforts to identify changes in species composition, abundance, or habitat use.

Numerous species of marine fish are transient estuarine residents, often present only during their early life history. Later in life, individuals move out of estuaries to settle in adult habitats and/or reproduce. Even if a species is not classically estuarine dependent (i.e. a period of estuarine residence is necessary for successful recruitment to the adult population), individuals that resided within estuaries may contribute substantially to adult populations. Furthermore, juvenile survival rates can be habitat-specific. The relative contributions of new recruits that reared in separate habitats, e.g. the lower estuary vs. coastal waters, may vary considerably under different environmental conditions (i.e. the contingent hypothesis). A contingent represents a group of fish that, due to distinct migration patterns, use different habitat areas than other individuals or groups in their cohort, or year-class (Secor 1999; Secor et al. 2001). Potentially, for species that enter

estuaries during their early life history, a portion of their larvae and juveniles remain in coastal waters where they may experience differential growth and survival.

Larval and juvenile fish exhibit a diversity of swimming abilities and depth distributions that vary among species and over the course of development. These factors present considerable challenges to adequately sample larval and juvenile fishes. Light traps hold promise for determining the distribution and relative abundance of the larvae and juveniles of some species (Doherty 1987; Hickford and Schiel 1999). Although there are few published reports of light traps being used in the Northeast Pacific (Miller and Shanks 2004; Roegner et al. 2003), they have been used to collect larval and juvenile fish in tropical (Doherty 1987; Kingsford and Battershill 1998; Thorrold 1992) and temperate (Hickford and Schiel 1999) regions. In 1998, 21 species representing 14 families were collected over 130 d in a single light trap in Coos Bay, Oregon. Three species, the penpoint gunnel (*Apodicthys flavidus*), rosylip sculpin (*Ascelichthys rhodorus*), and northern anchovy (*Engraulis mordax*), were dominant, comprising over 80% of the total catch. For these species, relatively little is known about the timing of their arrival in Oregon estuaries, their abundance, or the length of their residence.

The family Cottidae (the sculpins) is a major component of the Northeast Pacific fish fauna, represented by over 100 species in 45 genera, and commonly found in nearshore and intertidal areas (Matarese et al. 1989). The family Pholidae (gunnels) is comprised of eel-like fishes with nine species in three genera in the Northeast Pacific. Early life histories of most Cottid and Pholid species are not well known. The family

Engraulidae is a widespread taxa, found in the Indian, Atlantic, and Pacific Oceans, with 139 species in 16 genera.

The northern anchovy (*Engraulis mordax*) is the sole representative of the family in Oregon waters and is an ecologically and, at times, economically important species. There are three sub-populations of *E. mordax*, including northern (British Columbia to northern California), central (off southern California and northern Baja California), and southern (off central and southern Baja California) populations (Kucas 1986). There is little known about the movements of juvenile *E. mordax* and even less about the northern sub-population in general. It is reported that juveniles and adults move offshore in winter and return shoreward in the spring (Kucas 1986).

The coastal environment off Oregon is characterized by seasonal upwelling, when deeper, colder waters move toward the surface along the coast. During spring and summer, northwest winds result in persistent upwelling and the establishment of an upwelling front where low density off-shore waters meet high density, recently upwelled waters (Mooers et al. 1976). Late fall through early spring, winds are from the southwest and promote downwelling. Additionally, the predominant alongshore surface current over the continental shelf is equatorward during the upwelling period and reverses seasonally when the Davidson, or Inshore Counter Current, moves shoreward and toward the surface. The apparent potential for larval loss in such a system due to advection away from adequate rearing and/or settlement areas contributed to Parrish et al.'s (1981) hypothesis that pelagic species should spawn primarily during downwelling to minimize larval loss. However, some pelagic species reproduce and have eggs and larvae in the

coastal waters during summer upwelling (e.g. peak spawning for the northern sub-population of northern anchovy is July and August) (Richardson 1981).

The larvae of coastal fishes that enter estuaries during their early life history need to locate, enter, and, potentially, remain in such environments (Boehlert and Mundy 1988). Research has shown that various mechanisms, including forms of wind-driven and tidal transport, can promote the shoreward transport (Epifanio and Garvine 2001; Forward and Tankersley 2001; Pineda 1991; Pineda 1994; Shanks 1983; Shanks 1995) and estuarine ingress (Boehlert and Mundy 1988; Goodrich et al. 1989; Munch and Conover 2000) of organisms. For example, estuarine ingress may be associated with onshore, or downwelling, winds that force coastal waters into the estuary (Goodrich et al. 1989; Munch and Conover 2000). Additionally, non-linear internal tides and bores and tidal-stream transport through vertical migration can promote shoreward transport and estuarine ingress of organisms. Internal tides are generated at the shelf break or over other topographic features on the seafloor and typically occur on diurnal and semi-diurnal frequencies (Inall et al. 2000; Kropfli et al. 1999). Numerous studies have documented increased concentrations of larval fish and invertebrates (Pineda 1991; Pineda 1994; Shanks 1983; Shanks 1988; Shanks 1995; Shanks 1998), juvenile fish (Kingsford and Choat 1986), and small adult fish (Rogachev et al. 1996) in slicks associated with internal waves and bores. Some of these studies (Shanks 1983; Shanks 1998) directly observed the shoreward transport of material concentrated in slicks associated with internal waves and/or identified tidal frequencies in the nearshore abundance of larval invertebrates and fish (Shanks 1983, 1988; Pineda 1991, 1994; Shanks 1998; Johnson & Shanks 2002).

Finally, modeling efforts have demonstrated the potential for net horizontal transport to occur in organisms that undergo diel vertical migration in oscillatory tidal currents over the continental shelf (Hill 1998).

The objectives of this study were to use a long term time series (3¾ years) of high-frequency (every 1 to 2 d) light-trap collections in Coos Bay, a temperate estuary, to: 1) document fish species diversity (i.e. richness and abundance); 2) document inter- and intra-annual patterns in species abundance; 3) make relative comparisons of species distributions based on collections from different sample locations; and 4) examine potential transport mechanisms, specifically wind-driven and tidal transport, for species collected in adequate numbers for time-series analysis. This study did not aim to comprehensively document larval and juvenile fish use of Coos Bay. Rather, the intention was to document seasonal and interannual fish use at selected locations in the lower estuary with a method relatively new to temperate waters.

Methods

Study site

The Coos Bay estuary is located on Oregon's south coast (Fig. II.1). A drowned river valley, Coos Bay, at approximately 54 km^2, is the second largest estuary in Oregon. Tides are mixed, semi-diurnal with a mean amplitude of 2.0 m. The long term (30 year) average annual precipitation is 161.3 cm, nearly half of which falls from November through January. A two layer, stratified water column typically occurs during periods of high freshwater flow while a less stratified, more marine dominated system is observed during summer and fall.

Biological sampling

Light traps were used to collect larval and juvenile fish. Traps consisted of a 10 L polycarbonate (clear) carboy with ten circular funnel openings (1 to 1.25 cm in diameter) and an 8 W fluorescent light in a sealed tube powered either by shore power or with a 12.0 volt, 12.0 AH rechargeable Pb-Acid battery controlled with a photocell (Fig. II.2). One light trap was deployed at the Outer Boat Basin, Charleston, Oregon (43°20'36"N, 124°19'17"W) from 1 April 1998 to 31 December 2001 (Fig. II.1). Hereafter, this site is

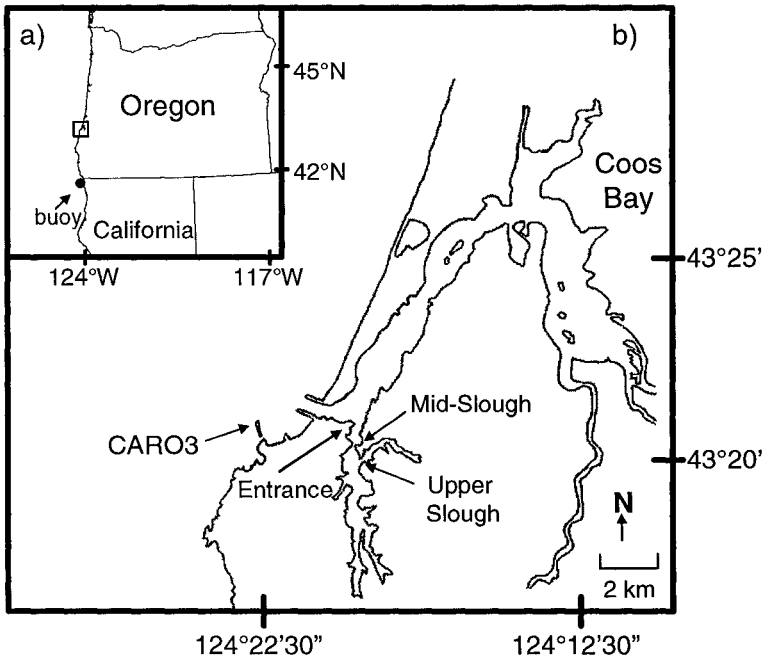

Fig. II.1. Study sites in Coos Bay, OR. (a) the study region and (•) the location of NOAA buoy #46027 (41°51'01"N 124°22'52"W), which provided surface water temperature data (0.6 m water depth) for coastal waters. (b) map of Coos Bay indicating the location of the Entrance, Mid-Slough, and Upper Slough light traps. NOAA's C-MAN station CAR03 (43°20'30"N 124°22'30"W), which provided daily wind speed and direction, is labeled.

referred to as the Entrance site. A set of three light traps was deployed at the Distant Fleet Facility (43°20'12"N, 124°19'14"W), which is located approximately 1 km inside of Coos Bay, from 12 January 2000 to 31 December 2001 (Fig. II.1). Hereafter, this site is referred to as the Mid-Slough site. Both of these sites were associated with a dock and shore power was used. An additional set of three light traps was deployed farther up South Slough (43°19'15"N, 124°19'10"W), approximately 1.5 km from the Outer Boat Basin, from 9 June to 20 September 2001 (Fig. II.1). Hereafter, this site is referred to as the Upper Slough site. These traps were tethered to anchored buoys and powered with 12.0 volt batteries. Traps within each site were deployed 15 to 30 m apart. Dock traps were typically emptied once per day while the tethered, battery-powered traps were emptied every other day. All traps were cleaned regularly to remove encrusting organisms. Larval and juvenile fish were identified to the lowest possible taxa and counted. Individuals were measured to the nearest millimeter. Total length, from dorsal tip to notochord, was used for pre-flexion fish and standard lengths, from tip of the snout to base of the caudal peduncle, for post-flexion fish. The post-flexion stage commences when the notochord tip attains its final position approximately 45° from the notochord axis and the caudal fin rays begin to develop (Moser 1996).

Light traps are passive collectors of positively phototactic organisms. Although collection is biased to organisms with positive phototaxis, light traps offer a number of advantages to more traditional net collections which made them appropriate for this study. The use of light traps allows for simultaneous and integrated sampling over a

relatively long period, i.e. the entire night. This increases the probability of capture of organisms found at low densities. Traps can be placed in nearshore coastal areas that are difficult to sample with more traditional, ship-borne methods. Light traps often capture late-stage larvae and early juveniles, stages that are poorly sampled with nets (Milicich and Doherty 1994). Therefore, this technique may be better suited to determine estuarine use by later stage larvae and early juveniles. Additionally, these later stages may be more indicative of recruitment success, i.e. survival to reproduction, than early larvae (Peterman 1988).

Physical sampling

Average daily wind speed and direction were calculated from hourly data obtained from the National Oceanic and Atmospheric Administration's (NOAA) National Data Buoy Center's C-MAN station CAR03 (43°20'30"N, 124°22'30"W), which is located on the outer coast approximately 2 km south of Coos Bay (Fig. II.1). In the vicinity of Coos Bay, the coastline of Oregon is oriented 20° northeast of true north. Therefore, wind direction was corrected for the angle of coast by subtracting 20° from the average daily wind direction. Daily average alongshore and cross-shore wind stress were calculated using the daily average wind speed and direction, a constant drag coefficient ($C_D = 0.00122$) and air density ($\rho_a = 0.0013$) (Pedolsky 1987). Because we used a constant drag coefficient, the reported wind stress should be considered pseudo-stress values.

Upwelling indices (at 45°N, 125°W) were obtained from the NOAA Pacific Fisheries Environmental Laboratory (PFEL), Pacific Grove, California. PFEL coastal upwelling indices are calculated based upon Ekman's theory of mass transport due to wind stress. Ekman transports are resolved into components parallel and normal to the local coastline orientation. The magnitude of the offshore component is considered to be an index of the amount of water upwelled from the base of the Ekman layer. Positive values are, in general, the result of equatorward wind stress. Negative values imply downwelling, or the onshore advection of surface waters accompanied by a downward displacement of water. The index is produced from six-hourly fields of surface pressure on a global spherical 1° mesh (a 180 x 360 grid). The standard west coast six-hourly upwelling indices are a product of the 3° pressure field interpolated from the 1° grid (PFEL). Units for upwelling indices are in m^3 sec^{-1} per 100 meters of coastline. Daily averages were calculated for the upwelling index.

Data on coastal ocean water temperatures (°C) (0.6 m depth) were obtained from offshore NOAA buoy #46027 (41°51'01"N, 124°22'52"W), which during this study was the closest working coastal buoy. Data on estuarine water temperatures came from two sources. Hourly surface water temperatures (°C) were obtained from NOAA Station #9432780 (43°20'42"N, 124°19'21"W) located in the Outer Boat Basin near the Entrance site (Fig. II.1). Additionally, water temperature and salinity data for the Mid-Slough and the Upper Slough sites were obtained from the South Slough National Estuarine Research Reserve's System Wide Monitoring Program. Maximum daily tidal

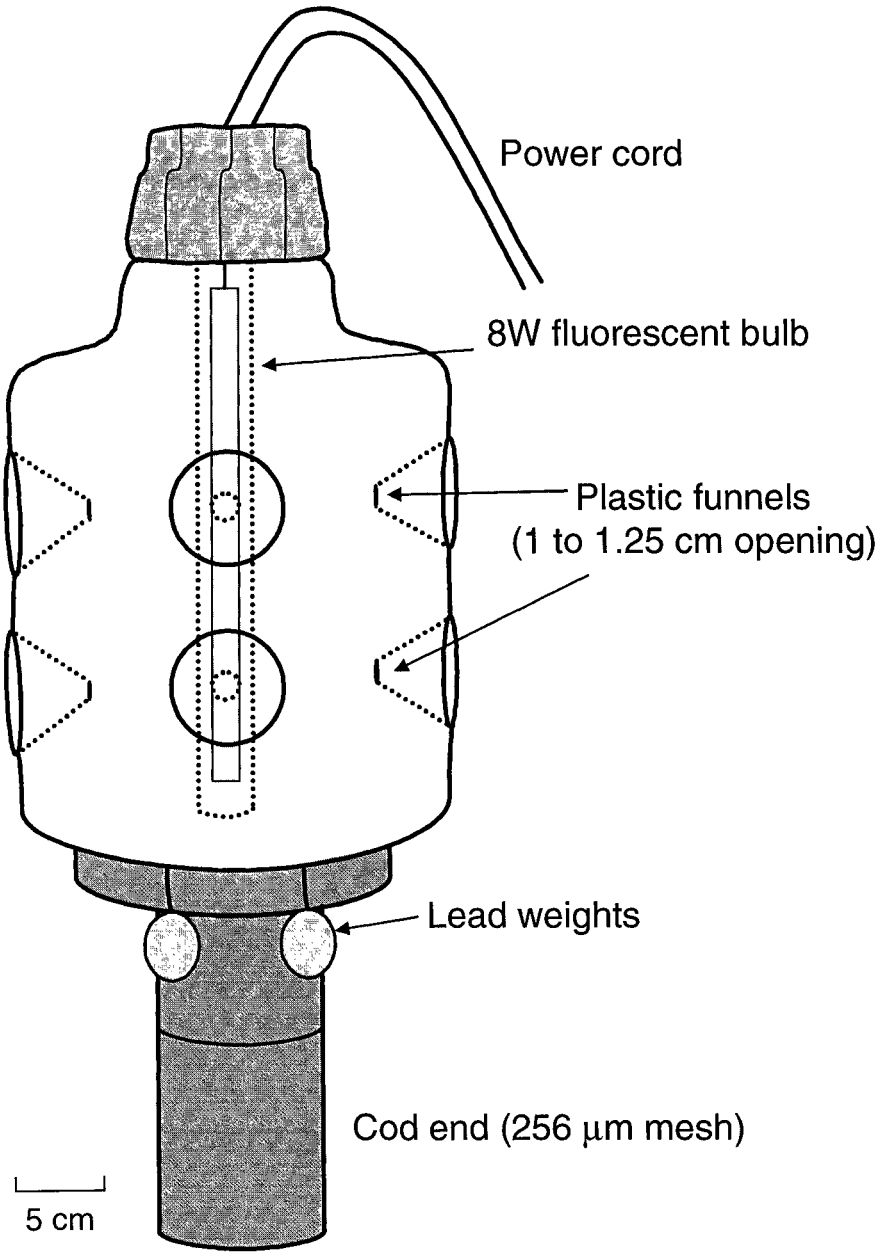

Fig. II.2. Light traps used to collect larval and juvenile fish in Coos Bay, OR. Each trap had ten funnel openings (1 to 1.25 cm in diameter) and an 8W fluorescent light in a sealed tube powered either by shore power or with a 12.0-volt, 12.0 AH rechargeable Pb-Acid battery controlled with a photocell.

ranges (cm) came from Harbor Master™ software program.

Statistical analysis

Time-series analysis was used to determine potential transport mechanisms and compare catch between trap locations. A constant time step, or sample frequency, is necessary for time-series analysis. A daily time step was used for all analyses that did not include samples from the Upper Slough site, which were usually collected every other day. Biological and physical data were averaged over 2 d for analyses that did include Upper Slough samples. Species abundance data were log transformed to reduce the influence of large peaks in the series and examined for trends and/or auto-correlations (Emery and Thomson 1997). If biological data displayed a seasonal trend and/or significant auto-correlation, data were smoothed with an unweighted moving average (19 d average for all time series > 200 d in length and 9 d average for all time series < 200 d in length). The difference, or residual, between the data series and the smoothed data was then computed with Equation 1,

$$X_t = Y_t - Z_t \qquad \text{(Eq 1)}$$

where X_t is the residual at time t, Y_t is the raw data at time t, and Z_t is the smoothed data at time t (Quinn & Keough 2002). Residuals were then smoothed with a 3 d moving average. If a physical data series had a seasonal trend, the trend was removed with Equation 2,

$$X_d = X_i - (a + b * t) \qquad \text{(Eq 2)}$$

where X_d = detrended value at time *t*, X_i = original value at time *t*, *a* (intercept) and *b* (slope) are computed from the original data series via least squares regression, and *t* = time.

The time series' of larval and juvenile fish were statistically compared with physical variables indicative of wind and tidal conditions (e.g. sea surface temperature, alongshore and cross-shore wind stress, upwelling index, and daily tidal range). This allowed identification of potential transport mechanisms. Positive alongshore wind stress cross-correlatations indicate a relationship with northward winds, negative indicate southward winds. Positive cross-shore wind stress cross-correlations indicate a relationship with eastward and negative indicate westward winds. Positive maximum tidal range cross-correlations indicate a relationship with spring tides, negative indicate neap tides. Time-series analyses of fish abundance and physical variables were only completed when adequate numbers of fish were collected (i.e. > 50 individuals year^{-1}). Given the difficulty involved with tracking marine larvae, inferences regarding larval transport are often made through correlations between species abundance and physical variables (Findlay and Allen 2002; Johnson et al. 1986; Shanks 1998). Time-series analysis measures the strength of a relationship between two variables. In this study, lags between variables represent days; the sign indicates whether peaks in the lagged series occurred after (negative values) or before (positive values) changes in the other variable. As in all correlative studies, a significant statistical correlation does not necessarily imply a cause-and-effect relationship. Statistica™ time-series analysis was used to calculate cross-correlations between biological and physical variables.

Annual patterns

Annual patterns in fish abundance were examined in two ways. First, as previously mentioned, the primary alongshore surface current over the continental shelf in the California Current system undergoes a seasonal reversal with predominantly poleward flow during fall and winter and equatorward flow during spring and summer (Huyer et al. 1979; Strub et al. 1987). This transition, which typically occurs between mid-February and mid-May, is accompanied by an increase in the frequency and intensity of upwelling (Strub et al. 1987). Therefore, in order to determine if fish catch varied during these periods, each year was divided into periods dominated by either upwelling or downwelling conditions and the proportion of the fish collected during each period was determined. Years were divided into three periods; 1) winter downwelling–spring transition, 2) upwelling, and 3) fall transition–downwelling. Due to the variation in the timing of the spring transition, two dates were used for the beginning of the upwelling season, 1 April and 1 June. Therefore, the periods examined were 1) 1 Jan to 31 Mar; 2) 1 Apr to 30 Sep; 3) 1 Jan to 31 May; 4) 1 June to 30 Sep; and 5) 1 Oct to 31 Dec. Second, single spectrum (Fourier) analyses were used to identify significant cyclic patterns in abundance of the most common species collected. In 1998, light-trap collections did not begin until 1 April. Therefore, in order to examine only complete annual cycles, this particular analysis was limited to three years of data from the Entrance site, 1999 to 2001. Statistica™ was used to complete the Fourier analyses.

Fish size

Average fish size (mm, standard length) was calculated for species collected at the Entrance from 1998 to 2001, Mid-Slough in 2000 and 2001, and Upper Slough in 2001. Site comparisons of fish size were made between the Entrance and Mid-Slough sites in 2000 and among the Entrance, Mid-Slough, and Upper Slough sites in 2001.

Fish size displayed a discontinuous and non-normal distribution. Therefore, non-parametric statistics were used to examine differences between and among sites. A Mann-Whitney U test was used to test for differences in paired comparisons. A Kruskal-Wallis rank sum test was used for multiple site comparisons.

Results

Overall, 28 species of larval, primarily post-flexion, and juvenile fish were identified in all light traps samples combined. Ten additional and unique species of larvae or juveniles were identified to family. Adult sand lance (*Ammodytes hexapterus*), stickleback (*Gasterosteus acculeatus*), and bay pipefish (*Syngnathus leptorhynchus*) were also frequently collected but will not be discussed here. Larval *S. leptorhynchus* were sometimes collected during late spring and summer. However, these larvae were usually released while the parent was inside the trap and, therefore, were not included in further analyses. Overall, a total of 41 fish taxa were collected in the light traps. Twenty-six of the species were collected at the Entrance (Table II.1), 22 at the Mid-Slough (Table II.2), and just three at the Upper Slough site (Table II.3).

Five species combined comprised the majority (> 70%) of the catch for all years at all sites. These included, in descending order of abundance; northern anchovy

(*Engraulis mordax*), penpoint gunnel (*Apodichthys flavidus*), Pacific sardine (*Sardinops sagax*), rosylip sculpin (*Ascelichthys rhodorus*), and surf smelt (*Hypomesus pretiosus*). Furthermore, these five species were the only species to comprise 10% or more of the catch within a site. Correlations in catch between traps at a site were determined for species collected in adequate numbers for comparison (i.e. > 100) at sites where there were multiple traps. This included northern anchovy, Pacific sardine, and surf smelt. Correlation coefficients ranged from +0.40 to +0.62, with an average of +0.55 (± 0.10 standard deviation).

The majority of the species collected are demersal spawners with attached, adhesive, or guarded eggs. The exceptions include the pelagic spawners, e.g. northern anchovy (*Engraulis mordax*), Pacific sardine (*Sardinops sagax*), and English sole (*Parophyrs vetulus*), and live bearers, e.g. the rockfishes (*Sebastes* spp.). The *Sebastes* spp. group identified in this study (Table II.1 and II.2) comprised at least four species, including black (*S. melanops*), brown (*S. auriculatus*), and yellowtail (*S. flavidus*) rockfish.

Entrance

In 1998, 14 unique taxa were collected at the Entrance and 12 were identified to species (Table II.1). In 1999, 21 unique taxa were collected and 15 were identified to species. In 2000, 21 unique taxa were collected and 14 were identified to species. In 2001, 23 unique taxa were collected and 15 were identified to species.

Mid-Slough

In 2000, 29 unique taxa were collected at Mid-Slough and 21 were identified to species (Table II.2). In 2001, 25 unique taxa were collected and 18 were identified to species.

Upper Slough

Three species were collected at Upper Slough site in 2001, the only year light traps were maintained at this location (Table II.3). Northern anchovy and surf smelt comprised 99.5% of the total catch.

Annual patterns

The majority of the catch, i.e. 60%, at the Entrance occurred during downwelling periods, defined as 1 Oct to 31 Mar (Figure 3). The size of that majority, however, varied considerably when 31 May was used to mark the end of the downwelling period instead of 31 Mar. In that case, the percentage rose to 94% (Table II.4). Furthermore, a significant portion of that majority, from 15% to 62%, occurred during the relatively brief transitional period from April to May. At Mid-Slough, an average of 56% of the catch occurred during the downwelling period defined as 1 Oct to 31 Mar. However, only 8% of the catch occurred during the spring transition period. Additionally, an average of 40% of the catch at Mid-Slough occurred during the fall downwelling period compared with only 14% at the Entrance. Overall, more fish were collected at the Entrance during spring transitions while more were collected at Mid-Slough during fall transitions and subsequent downwelling periods. Rather different patterns of fish abundance were observed at these two locations that are in relatively close proximity.

Table II.1. Taxa collected in light traps at the Entrance site, Coos Bay, OR in 1998, 1999, 2000, and 2001. The lowest taxonomic level identified, common name, total number of individuals collected, and percent of the total are presented.

Species	Common name	1998		1999		2000		2001	
		Total caught	Total percent	Total caught	Total percent	Total caught	Total percent	Total caught	Total percent
Engraulis mordax	northern anchovy	122	21.3	23	2.2	117	29.4	43	6.6
Apodichthys flavidus	penpoint gunnel	140	24.4	578	55	83	20.9	150	23.2
Sardinops sagax	Pacific sardine	163	28.4	15	1.4	9	2.3	43	6.6
Ascelichthys rhodorus	rosylip sculpin	76	13.2	241	22.9	52	13.1	145	22.4
Hypomesus pretiosus	surf smelt	11	1.9	26	2.5	58	14.6	110	17
Sebastes spp.	rockfish	17	3.0	94	8.9	5	1.3	5	<1.0
Clinocottus globiceps	mosshead sculpin	14	2.4	0	0	6	1.5	0	0
Leptocottus armatus	staghorn sculpin	13	2.3	9	<1.0	14	3.5	1	<1.0
Clupea pallasi	Pacific herring	11	1.9	1	<1.0	0	0	0	0
Clinocottus acuticeps	sharpnose sculpin	4	<1.0	18	1.7	8	2.0	10	1.5
Pholis laeta/ornata	gunnel	1	<1.0	17	1.6	11	2.8	39	6.0
Artedius lateralis	smoothhead sculpin	1	<1.0	0	0	0	0	0	0
Artedius sp.	sculpin	0	0	0	0	5	1.3	1	<1.0
Atherinops affinis	top smelt	0	0	0	0	1	<1.0	0	0
Aulorhynchus flavidus	tubesnout	0	0	1	<1.0	0	0	0	0
Clinocottus embryum	mosshead sculpin	0	0	6	0.6	0	0	1	<1.0
Cottus sp.	sculpin	0	0	0	0	11	2.8	0	0
Enophyrs bison	buffalo scuplin	0	0	1	<1.0	0	0	0	0
Hemilepidotus sp.	Irish lord	0	0	0	0	0	0	1	<1.0
Lepidopsetta bilineata	rock sole	0	0	0	0	0	0	9	1.4
Liparis sp.	snailfish	0	0	14	1.3	5	1.3	4	<1.0
Oligocottus sp.	sculpin	0	0	0	0	1	<1.0	0	0
Ophiodon elongatus	lingcod	0	0	0	0	5	1.3	0	0
Parophrys vetulus	English sole	0	0	0	0	0	0	7	1.1
Pholis schultzi	red gunnel	0	0	0	0	1	<1.0	0	0
Ronquilus jordani	ronquil	0	0	1	<1.0	0	0	0	0
Scorpaenichthys marmoratus	cabezon	0	0	0	0	1	<1.0	40	6.2
Total		573		1045		393		609	

Table II.2. Taxa collected in light traps at the Mid-Slough site in Coos Bay, OR in 2000 and 2001. The lowest taxonomic level identified, common name, total number of individuals collected, percent of the total, and the average number of individuals collected are presented.

Species	Common name	2000			2001		
		Total caught	Total percent	Average catch	Total caught	Total percent	Average catch
Engraulis mordax	northern anchovy	1128	61.7	376	845	42.1	281.7
Apodichthys flavidus	penpoint gunnel	52	2.8	17.3	70	3.5	23.3
Sardinops sagax	Pacific sardine	108	5.9	36.0	519	25.9	173.0
Ascelichthys rhodorus	rosylip sculpin	26	1.4	8.7	12	<1.0	4.0
Hypomesus pretiosus	surf smelt	80	4.4	26.7	216	10.8	72.0
Sebastes spp.	rockfish	32	1.7	10.7	51	2.5	17.0
Clinocottus globiceps	mosshead sculpin	1	<1.0	0.3	2	<1.0	0.7
Leptocottus armatus	staghorn sculpin	6	<1.0	2.0	0	0	0
Clupea pallasi	Pacific herring	2	<1.0	0.7	7	<1.0	2.3
Clinocottus acuticeps	sharpnose sculpin	64	3.5	21.3	113	5.6	37.7
Pholis laeta/ornata	gunnel	24	1.3	8.0	1	<1.0	0.3
Anoplarchus purpurescens	high cockscomb	1	<1	0.3	0	0	0
Artedius sp.	sculpin	7	<1	2.3	0	0	0
Atherinops affinis	top smelt	4	<1	1.3	3	<1	1.0
Aulorhynchus flavidus	tubesnout	0	0	0	2	<1	0.7
Clinocottus embryum	mosshead sculpin	13	<1	4.3	2	<1	0.7
Clinocottus recalvus	bald sculpin	1	<1	0.3	0	0	0
Hemilepidotus sp.	Irish lord	0	0	0	2	<1	0.7
Lepidopsetta bilineata	rock sole	0	0	0	8	<1	2.7
Liparis sp.	snailfish	3	<1	1.0	5	<1	1.7
Oligocottus maculosus	tidepool sculpin	2	<1	0.7	0	0	0
Oligocottus snyderi	fluffy scuplin	6	<1	2.0	0	0	0
Oligocottus sp.	sculpin	5	<1	1.7	0	0	0
Ophiodon elongatus	lingcod	0	0	0	13	<1.0	4.3
Ronquilus jordani	ronquil	1	<1	0.3	0	0	0
Total		1566			1871		

Table II.3. Taxa collected in light traps at the Upper Slough site, Coos Bay, OR in 2001. The lowest taxonomic level identified is included with the common name, the total number of individuals collected, the average number, and the percent of the total.

Species	Common Name	Total Caught	Ave.	Total Percent
Engraulis mordax	northern anchovy	158	52.7	72.8
Hypomesus pretiosus	surf smelt	58	19.3	26.7
Pholis ornata	saddleback gunnel	1	0.3	< 1
Total		217		100

Table II.4. Percent of the total catch of larval and juvenile fish collected in light traps in Coos Bay, OR in 1999, 2000, and 2001. Data from the Entrance and Mid-Slough are presented. The year is divided into periods dominated by either upwelling or downwelling conditions.

Period	Entrance			Mid-Slough	
Downwelling dominated	**1999**	**2000**	**2001**	**2000**	**2001**
1 Jan – 31 March	22%	56%	58%	18%	14%
1 Jan – 31 May	84%	81%	73%	26%	22%
Upwelling dominated					
1 April – 30 September	75%	27%	19%	35%	53%
1 June – 30 September	13%	2%	4%	27%	45%
Downwelling dominated					
1 Oct - 31 December	3%	17%	23%	47%	33%

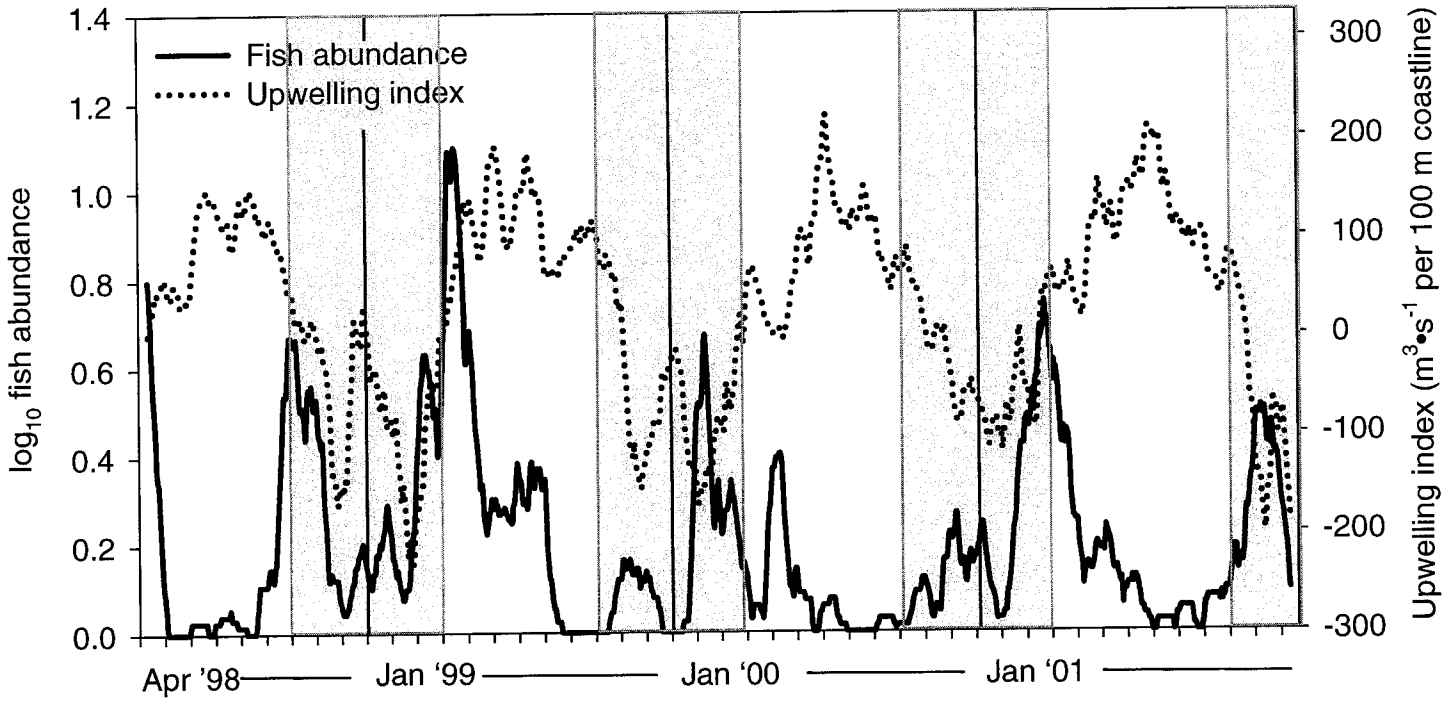

Fig. II.3. The daily abundance (log_{10}) of all larval and juvenile fish collected in light traps at the Entrance site, Coos Bay, OR between 1 Apr 1998 and 31 Dec 2001. Fish abundance data (solid black line) and upwelling indices ($m^3 \bullet s^{-1}$ per 100 m of coastline) (dotted black line) were smoothed with a 19 d moving average. Values above 100 $m^3 \bullet s^{-1}$ typically indicate upwelling. Downwelling periods, 1 Oct through 31 Mar, are indicated by shaded areas.

Further discussion on annual patterns of abundance will be limited to the five species that comprised > 70% of the total catch in all years at all locations, which includes northern anchovy (*Engraulis mordax*), penpoint gunnel (*Apodichthys flavidus*), Pacific sardine (*Sardinops sagax*), rosylip sculpin (*Ascelichthys rhodorus*), and surf smelt (*Hypomesus pretiosus*).

The abundance of the penpoint gunnel and rosylip sculpin displayed a consistent annual cycle (Fig. II.4) that was not observed in northern anchovy, Pacific sardine, or surf smelt (Fig. II.5). This is supported by the lack of any dominant periods (all period values < 1) in the spectral analysis of northern anchovy, Pacific sardine, or surf smelt daily abundance at the Entrance from 1999 to 2001, However, for penpoint gunnel and rosylip sculpin, relatively large period values (> 2.5) occurred on an annual cycle. For penpoint gunnel, a period value of 6.7 occurred at 365 d. For rosylip sculpin, a period value of 2.7 occurred at 365 d. There was a significant annual cycle in the catch of larval and juvenile penpoint gunnel and rosylip sculpin in Coos Bay.

The initial arrival date and the subsequent duration a species was present in light-trap collections were determined for the penpoint gunnel, rosylip sculpin, northern anchovy, Pacific sardine, and surf smelt. Average values were generated for the Entrance based on the three complete years of data collection, 1999 to 2001, and for Mid-Slough based on the two complete years of data collection, 2000 and 2001. Two patterns were evident; 1) discrete peaks in abundance in late winter or 2) relatively consistent abundance throughout much of the year.

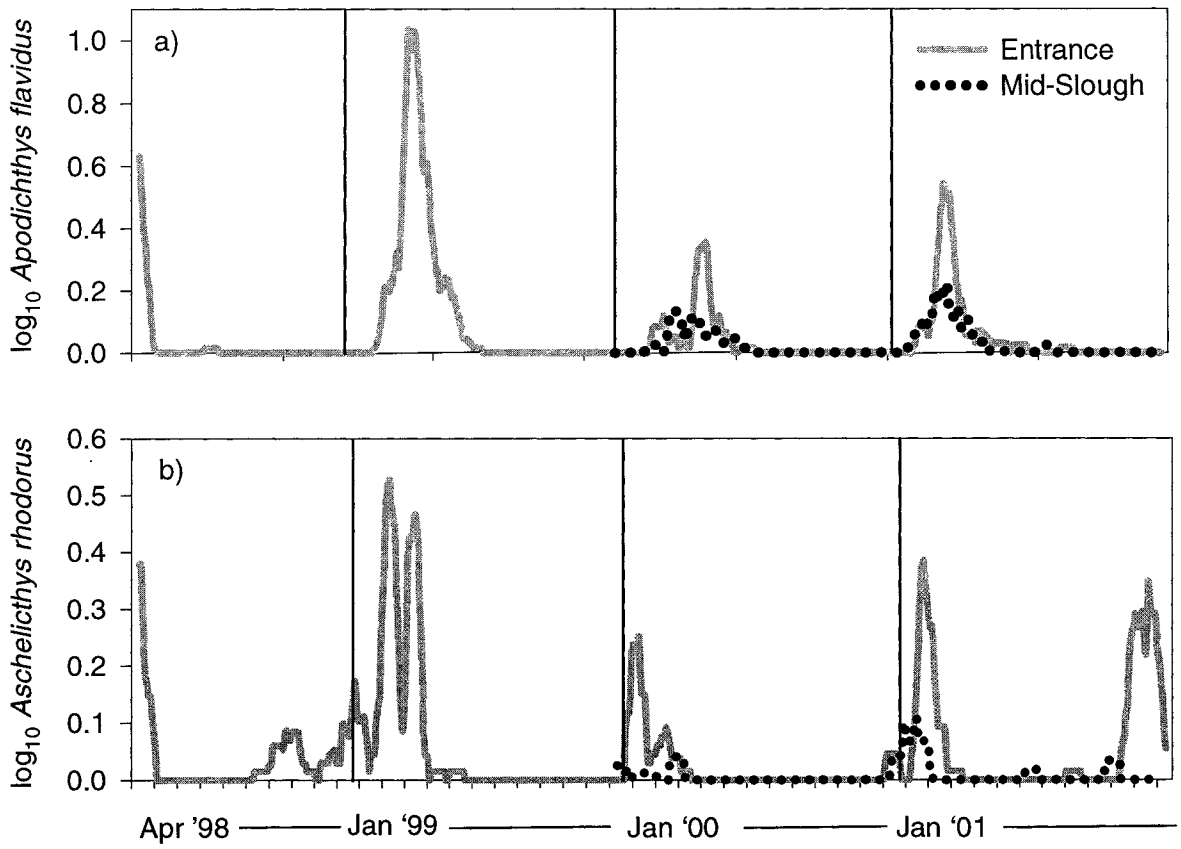

Fig. II.4. The daily catch ($\log_{10}$) of a) the penpoint gunnel (*Apodichthys flavidus*) and b) the rosylip sculpin (*Ascelichthys rhodorus*) collected between 1 Apr 1998 and 31 Dec 2001. Samples were collected at the Entrance (solid gray line) and the Mid-Slough (dotted black line). Fish catch data were smoothed with a 19 d moving average.

On average, the penpoint gunnel (*Apodichthys flavidus*) first appeared in the Entrance light trap on the 17 Feb (± 11 d standard deviation) and remained a component of the catch for 100 d ± 24 d (Figure 4a). On average, the penpoint gunnel first appeared in the Mid-Slough light traps on the 9 Mar (± 11 d SD) and were caught for 114 d ± 11 d.

On average, the rosylip sculpin (*Ascelichthys rhodorus*) first appeared in the Entrance light trap on 16 Jan (± 14 d SD) and were caught for 83 d ± 41 d (Figure 4b). At the Mid-Slough light traps, rosylip sculpin first appeared on 13 Jan in both 2000 and 2001 and remained an average of 73 d ± 7 d.

Northern anchovy (*Engraulis mordax),* Pacific sardine (*Sardinops sagax*), and surf smelt (*Hypomesus pretiosus*) were often present in light traps throughout much of the year (Fig. II.5). These species were usually present in both Entrance and Mid-Slough light traps in January and were frequently collected throughout the year.

Interannual abundance

Interannual patterns in species abundance were examined at the Entrance site from 1998 to 2001 and at the Mid-Slough site in 2000 and 2001. The total number of fish collected each year varied from 393 to 1045 at the Entrance site and from 1566 to 1871 at the Mid-Slough site (Table II.1 and II.2). The interannual differences at the Entrance site are particularly notable. Although the species composition was similar in all years, the total catch in 1999, 1045 individuals, was substantially larger than the next largest catch of 609 individuals in 2001 (Table II.1). Furthermore, relatively large numbers of penpoint gunnel (578), rosylip sculpin (241), and rockfish (94) and relatively small numbers of

northern anchovy (23), Pacific sardine (15), and surf smelt (26) were collected in 1999 compared to the other three years (Table II.1). A similar, although not as pronounced, pattern in species abundance was observed in 2001. At the Mid-Slough site, species composition and abundance were similar in 2000 and 2001 (Table II.2).

Relative abundance

In general, more northern anchovy, Pacific sardine, and surf smelt and fewer penpoint gunnel and rosylip sculpin were collected at Mid-Slough compared with the Entrance (Table II.1 and II.2). In 2000 and 2001, northern anchovy, Pacific sardine, surf smelt, and penpoint gunnel were collected in adequate numbers to compare the relative timing of abundance at the Entrance and Mid-Slough. In 2001, additional comparisons could be made between northern anchovy and surf smelt collected at Mid-Slough and Upper Slough. No comparisons could be made between the Entrance and Upper Slough because very few northern anchovy or surf smelt were collected at the Entrance during the period when the Upper Slough traps were deployed, i.e. between 8 June and 30 Sep 2001.

In 2000 for northern anchovy, surf smelt, and Pacific sardine, peaks in abundances at Mid-Slough were positively correlated with abundances at the Entrance, at -1 to +0 d lags (Fig. II.6). Therefore, peaks in abundance at the Mid-Slough occurred on the same day or one day after peaks in abundance at the Entrance. For penpoint gunnel,

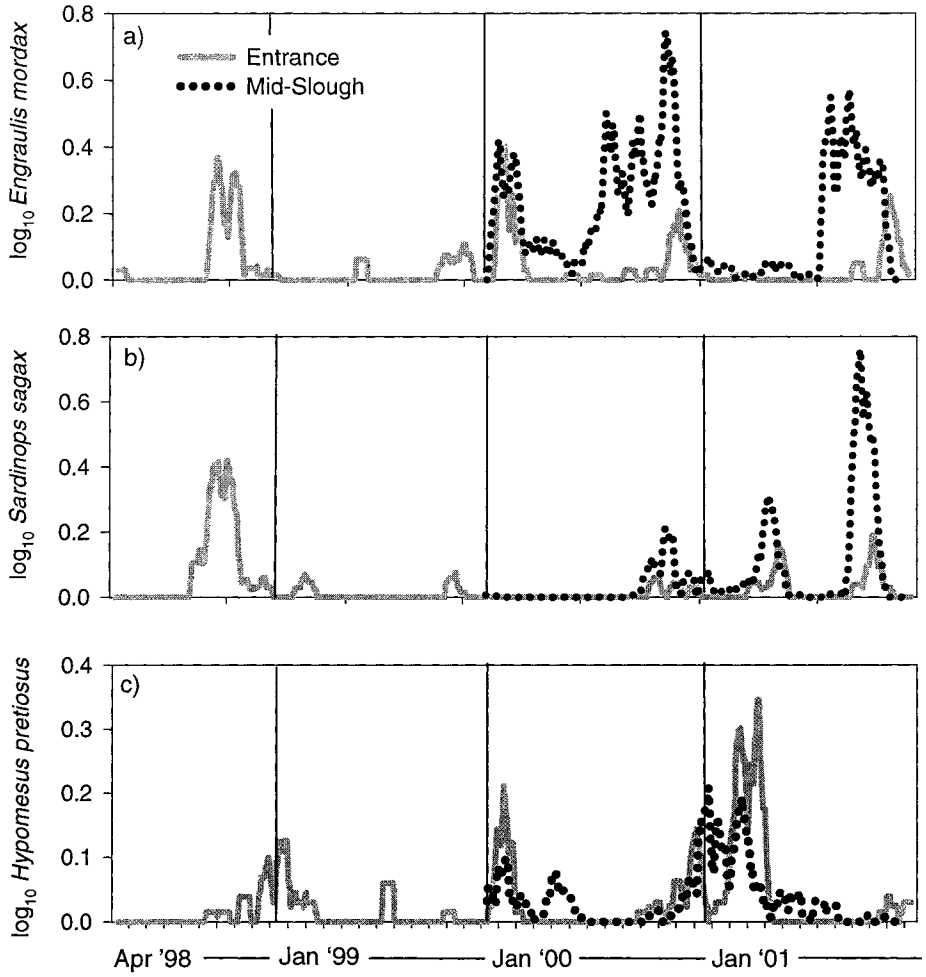

Fig. II.5. The daily catch ($\log_{10}$) of a) northern anchovy (*Engraulis mordax*), b) Pacific sardine (*Sardinops sagax*), and c) surf smelt (*Hypomesus pretiosus*) collected between 1 Apr 1998 and 31 Dec 2001. Samples were collected at the Entrance (solid gray line) and the Mid-Slough (dotted black line). Fish catch data were smoothed with a 19 d moving average.

peaks in abundance at Mid-Slough occurred 2 d and 3 d after peaks in abundance at the Entrance site.

In 2001, the species abundances at Mid-Slough were positively correlated with abundances at the Entrance, at -3 to +1 d lags (Fig. II.7). For northern anchovy, peaks in abundance at Mid-Slough occurred on the same day (r = +0.212) or one day after (r = +0.256) peaks in abundance at the Entrance (Fig. II.7a). Peaks in northern anchovy abundance at the Upper Slough site occurred on the same day (r = +0.321) as the Mid-Slough. There were no significant cross-correlations between the abundance of surf smelt at Mid-Slough and the Entrance (Fig. II.7b). However, peaks in surf smelt abundance at Upper Slough occurred on the same day (r = +0.263) and one day before (r = +0.363) Mid-Slough. Peaks in the abundance of Pacific sardine at Mid-Slough occurred on the same day (r = +0.229) or one day before (r = +0.322) peaks in abundance at the Entrance (Fig. II.7c). For penpoint gunnel, peaks in Mid-Slough abundance occurred 2 d (r = +0.200) and 3 d (r = +0.200) after peaks in abundance at the Entrance.

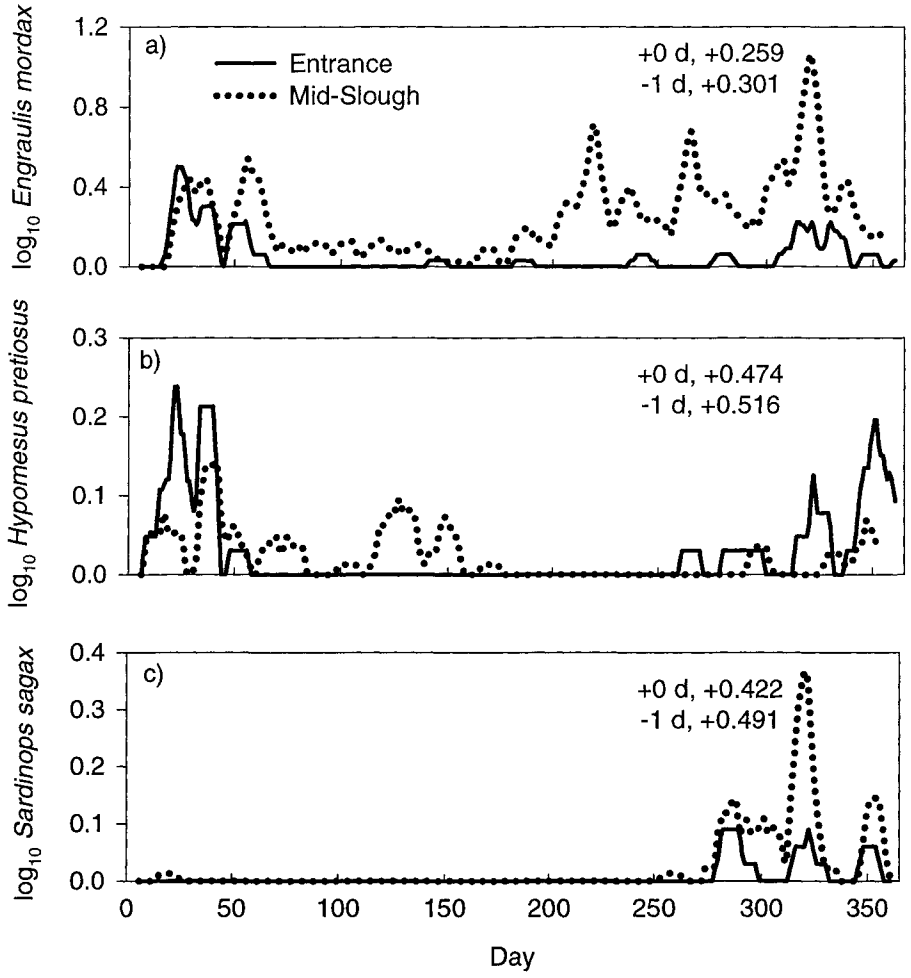

Fig. II.6. The 2000 daily catch ($\log_{10}$) of a) northern anchovy (*Engraulis mordax*), b) surf smelt (*Hypomesus pretiosus*), and c) Pacific sardine (*Sardinops sagax*) collected at the Entrance (solid black line) and the Mid-Slough (dotted black line), Coos Bay, OR. Fish catch data were smoothed with a 19 d moving average. Cross-correlations and the d lag between abundance at the sites are included (d lag, r).

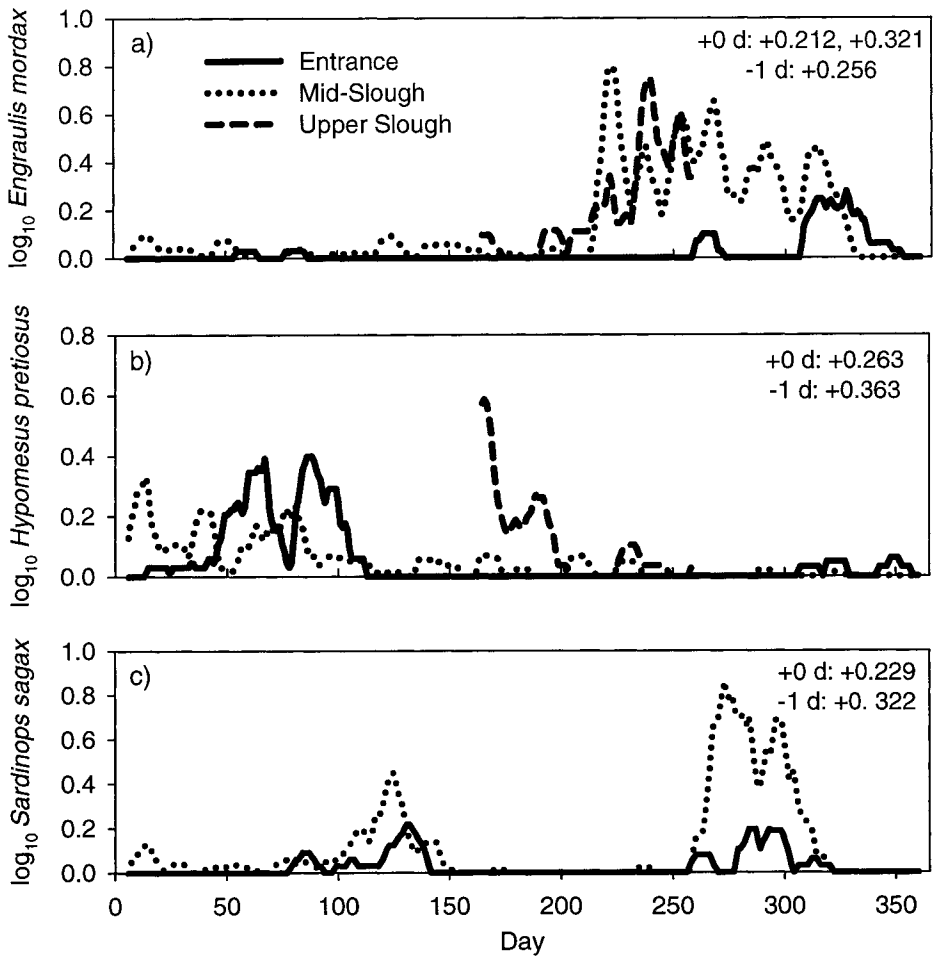

Fig. II.7. The 2001 daily catch (log_{10}) of a) northern anchovy (*Engraulis mordax*), b) surf smelt (*Hypomesus pretiosus*), and c) Pacific sardine (*Sardinops sagax*) collected at the Entrance (solid black line), the Mid-Slough (dotted black line), and the Upper Slough (dashed black line), Coos Bay, OR. Fish catch data were smoothed with a 19 d moving average. Cross-correlations and the d lag between abundance at the sites are included (d lag, r).

Fish size

The average sizes of the most abundant species collected at the Outer Boast Basin were determined on an annual basis (Table II.5). In general, average sizes within species were similar among years. Pacific sardine, however, were progressively larger each year of collection (Table II.5).

In 2000 and 2001, intra-annual size comparisons were made between the Entrance and Mid-Slough sites. Northern anchovy, Pacific sardine, surf smelt, penpoint gunnel, and rosylip sculpin were collected in adequate numbers at the Entrance and Mid-Slough sites for statistical comparisons in 2000 and 2001. However, only two species, northern anchovy and surf smelt, were collected in adequate numbers at all three locations (i.e. Entrance, Mid-Slough, and Upper Slough sites) for statistical comparisons in 2001. In 2000, there were no differences in size (SL) between collection locations (Entrance vs. Mid-Slough) for any of the species examined except penpoint gunnel, which were significantly larger at the Mid-Slough site in both 2000 and 2001 (Table II.6). Additionally, in 2001, the size of surf smelt differed significantly among the three locations (i.e. Entrance, Mid-Slough, and Upper Slough), with progressively large fish collected farther up the estuary (Table II.7). Conversely, significantly smaller Pacific sardine were collected at Mid-Slough, which was located farther up estuary. There were no differences in the size of northern anchovy among any of the sample locations.

Table II.5. The average size (mm, standard length ± standard deviation) of the five most common species collected in Coos Bay Entrance light traps from 1998 to 2001. The sample size (*N*) is included.

	Entrance			
Species	**1998**	**1999**	**2000**	**2001**
northern anchovy (***Engraulis mordax***)	36.0 ± 6.9 *N* = 45	34.7 ± 5.0 *N* = 22	37.4 ± 16.6 *N* = 95	33.6 ± 9.3 *N* = 20
Pacific sardine (***Sardinops sagax***)	37.2 ± 7.3 *N* = 62	47.2 ± 7.9 *N* = 9	56.4 ± 6.3 *N* = 9	60.0 ± 16.0 *N* = 34
surf smelt (***Hypomesus pretiosus***)	34.0 ± 5.3 *N* = 6	40.6 ± 6.6 *N* = 20	34.9 ± 7.1 *N* = 53	27.5 ± 6.3 *N* = 83
penpoint gunnel (***Apodicthys flavidus***)	23.9 ± 0.5 *N* = 106	24.4 ± 2.1 *N* = 140	22.9 ± 5.7 *N* = 93	21.9 ± 10.5 *N* = 84
rosylip sculpin (***Ascelichthys rhodorus***)	9.2 ± 1.7 *N* = 57	11.9 ± 1.7 *N* = 35	10.6 ± 1.6 *N* = 49	10.5 ± 2.0 *N* = 65

Table II.6. The 2000 average size (mm, standard length ± standard deviation) of the five most common species collected in Coos Bay light traps. The two light trap locations, the sample size (*N*), the Mann Whitney U test *z*-statistic, and the significance value (*p*) are included.

2000	**Entrance**	**Mid-Slough**	***z*-statistic**	***p*-value**
northern anchovy (***Engraulis mordax***)	37.4 ± 16.6 *N* = 95	38.1 ± 11.9 *N* = 340	-1.1	0.23
Pacific sardine (***Sardinops sagax***)	56.4 ± 6.3 *N* = 9	52.7 ± 9.8 *N* = 105	-1.5	0.14
surf smelt (***Hypomesus pretiosus***)	34.9 ± 7.1 *N* = 53	38.4 ± 11.8 *N* = 60	-1.1	0.29
penpoint gunnel (***Apodicthys flavidus***)	22.9 ± 5.7 N = 93	33.1 ± 18.3 *N* = 35	-3.8	< 0.01
rosylip sculpin (***Ascelichthys rhodorus***)	10.6 ± 1.6 *N* = 49	10.4 ± 1.2 *N* = 25	1.5	0.15

Table II.7. The 2001 average size (mm, standard length ± standard deviation) of the five most common species collected in Coos Bay light traps. The light trap locations, the sample size (*N*), the test statistic used (Mann Whitney U test *z*-statistic for two site comparisons and the Kolmogorov-Smirnov χ^2 statistic for three site comparisons), and the significance value (*p*) are included. «na» indicates that no fish were collected at a location so no statistical comparisons were made.

2001	Entrance	Mid-Slough	Upper Slough	test statistic	*p*-value
northern anchovy (***Engraulis mordax***)	33.6 ± 9.3 *N* = 20	32.9 ± 9.2 *N* = 766	34.8 ± 6.7 *N* = 112	$\chi^2 = 14.9$	0.006
Pacific sardine (***Sardinops sagax***)	60.0 ± 16.0 *N* = 34	48.8 ± 10.5 *N* = 404	na	*Z* = 5.3	< 0.01
surf smelt (***Hypomesus pretiosus***)	27.5 ± 6.3 *N* = 83	47.2 ± 10.9 *N* = 205	61.2 ± 11.4 *N* = 78	$\chi^2 = 135.7$	< 0.01
penpoint gunnel (***Apodicthys flavidus***)	21.9 ± 10.5 *N* = 83	26.9 ± 11.9 *N* = 61	na	*Z* = -3.5	< 0.01
rosylip sculpin (***Ascelichthys rhodorus***)	10.5 ± 2.0 *N* = 65	11.1 ± 0.9 *N* = 10	na	*Z* = -1.3	0.18

For northern anchovy, there were adequate numbers collected at the Mid-Slough site in 2000 and 2001 to examine size distributions over time. (Fig. II.8 and II.9). In 2000, juveniles were collected primarily during two periods, one at the beginning and one at the end of the year. Few individuals were collected from early May to early August (Fig. II.8). The youngest fish, 21 to 33 mm SL, comprised consistent but relatively small proportions of the catch throughout the year (Fig. II.8a). On the contrary, in 2001, there was only one peak in juvenile catch; almost all were collected between

August and September (Fig. II.9). Additionally, in 2001, fewer larger juveniles (41 to 50 mm SL) were collected than in 2000 (Fig. II.9c).

Potential transport mechanisms

Figure II.10 presents the physical variables observed during the study. Water temperature at the coastal station ranged from 6.7 to 14.4°C with an average of 10.6 ± 1.3°C. In the estuary, water temperature ranged from 8.0 to 15.1°C with an average of 11.2 ± 1.2°C. The water temperature near the entrance to Coos Bay was significantly and positively correlated with the temperature offshore at +0 d, -1 d, and -2 d lags (r = +0.253 to +0.421). However, estuarine water temperatures, particularly during spring, were often warmer than at the offshore station (Fig. II.10c). At Mid-Slough, the annual range in water temperature was larger, from 7.0 to 19.5°C with an average of 12.1 ± 2.0°C. Salinity at Mid-Slough ranged from 9.0 to 34.0 and averaged 29.7 ± 4.1. At Upper Slough, from June to September when light traps were deployed, water temperature ranged from 10.0 to 18.0°C with an average of 14.2 ± 2.1 °C while salinity ranged from 4.0 to 34.0 with an average of 28.0 ± 5.1.

Northern anchovy (*Engraulis mordax*)

The abundance of northern anchovy varied significantly with a tidal periodicity in both 2000 and 2001. In 2000, northern anchovy abundance was significantly and positively cross-correlated with spring tides at -2 d to -4 d lags at the Entrance and Mid-Slough (Table II.8). In 2001, significant and positive cross-correlations occurred in between spring and neap tides at the Mid-Slough and around neap tides farther up the

estuary at the Upper Slough (Table II.8). The only other significant correlation occurred in 1998 when northern anchovy abundance was significantly and positively cross-correlated with positive alongshore wind stress (i.e. downwelling favorable). Time-series analyses of northern anchovy were not completed at the Entrance in 1999 and 2001 due to the small number of fish collected (i.e. < 50).

Pacific sardine (*Sardinops sagax*)

The abundance of Pacific sardine varied significantly with a tidal periodicity in 1998, 2000 and 2001 (Table II.9). In 1998, significant and positive cross-correlations occurred in between spring and neap tides, at -4 and -5 d lags, at the Entrance. In 2000 and 2001, significant cross-correlations occurred around spring tides, at -3 d and +1 d lags, at the Mid-Slough. Additionally, in 1998, Pacific sardine abundance was significantly and positively cross-correlated with positive alongshore (downwelling favorable) wind stress and negative upwelling indices at the Entrance. Similarly, at the Mid-Slough in 2000, abundance was significantly cross-correlated with positive alongshore (downwelling favorable) wind stress (Table II.9). Time-series analyses of Pacific sardine were not completed at the Entrance in 1999, 2000, and 2001 due to the small number of fish collected (i.e. < 50).

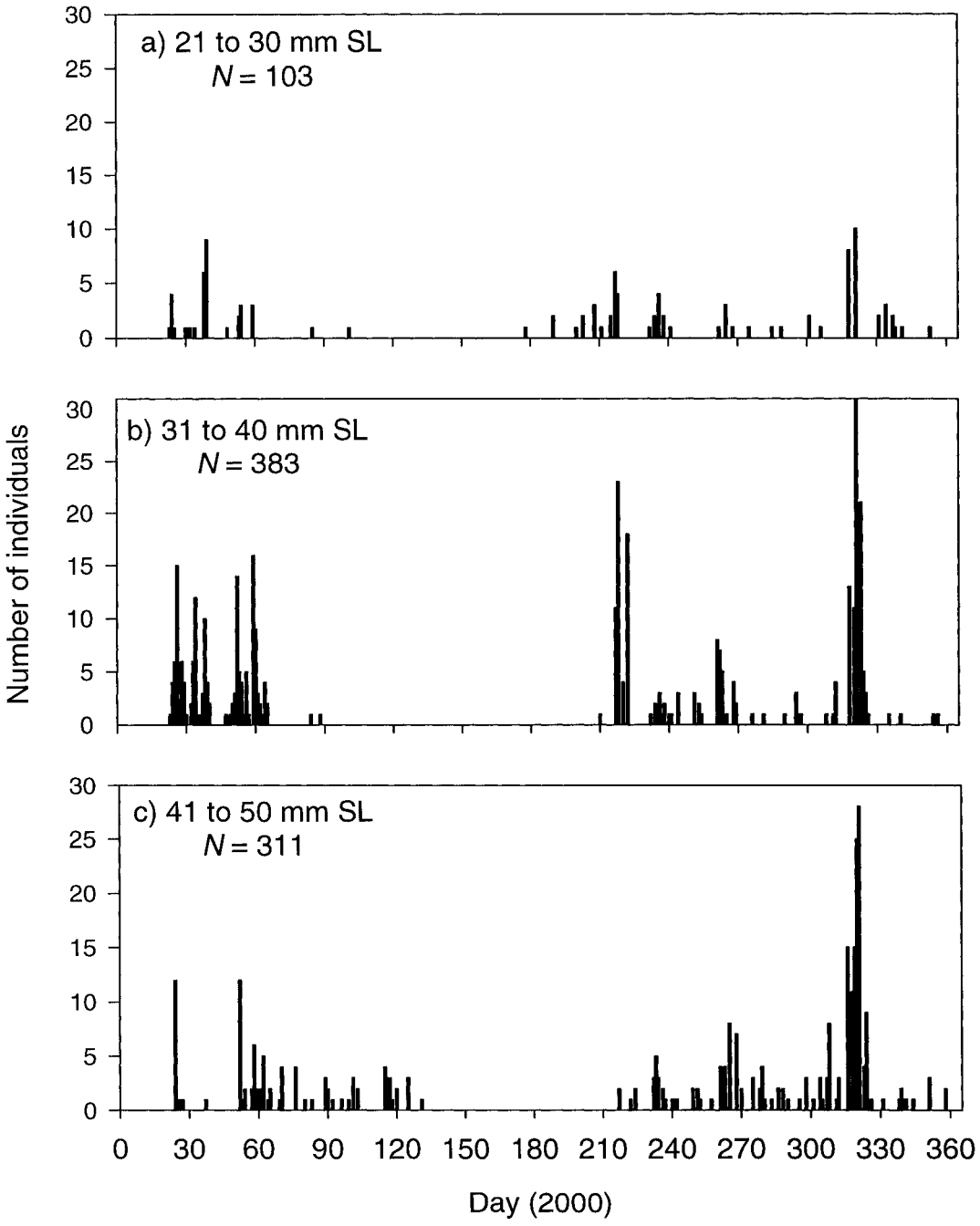

Fig. II.8. The 2000 daily catch of northern anchovy (*Engraulis mordax*) collected at Mid-Slough light traps, Coos Bay, OR. The number of individuals with standard length (SL) between a) 21 to 30 mm, b) 31 to 40 mm, and c) 41 to 50 mm are presented. Total sample sizes (*N*) are included.

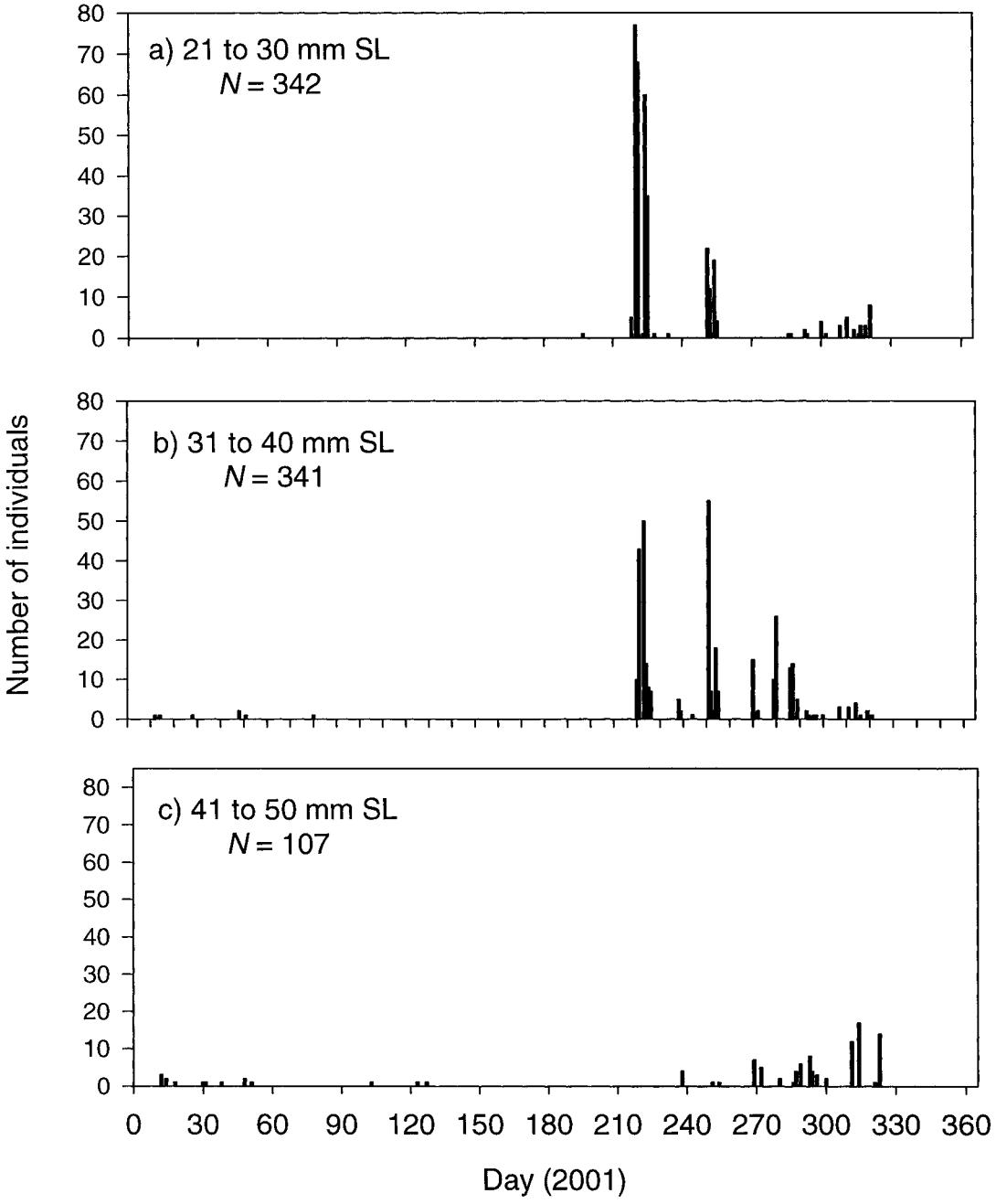

Fig. II.9. 2001 daily catch of northern anchovy (*Engraulis mordax*) collected in Mid-Slough light traps, Coos Bay, OR. The number of individuals with standard length (SL) between a) 21 to 30 mm, b) 31 to 40 mm, and c) 41 to 50 mm are presented. Total sample sizes (*N*) are included.

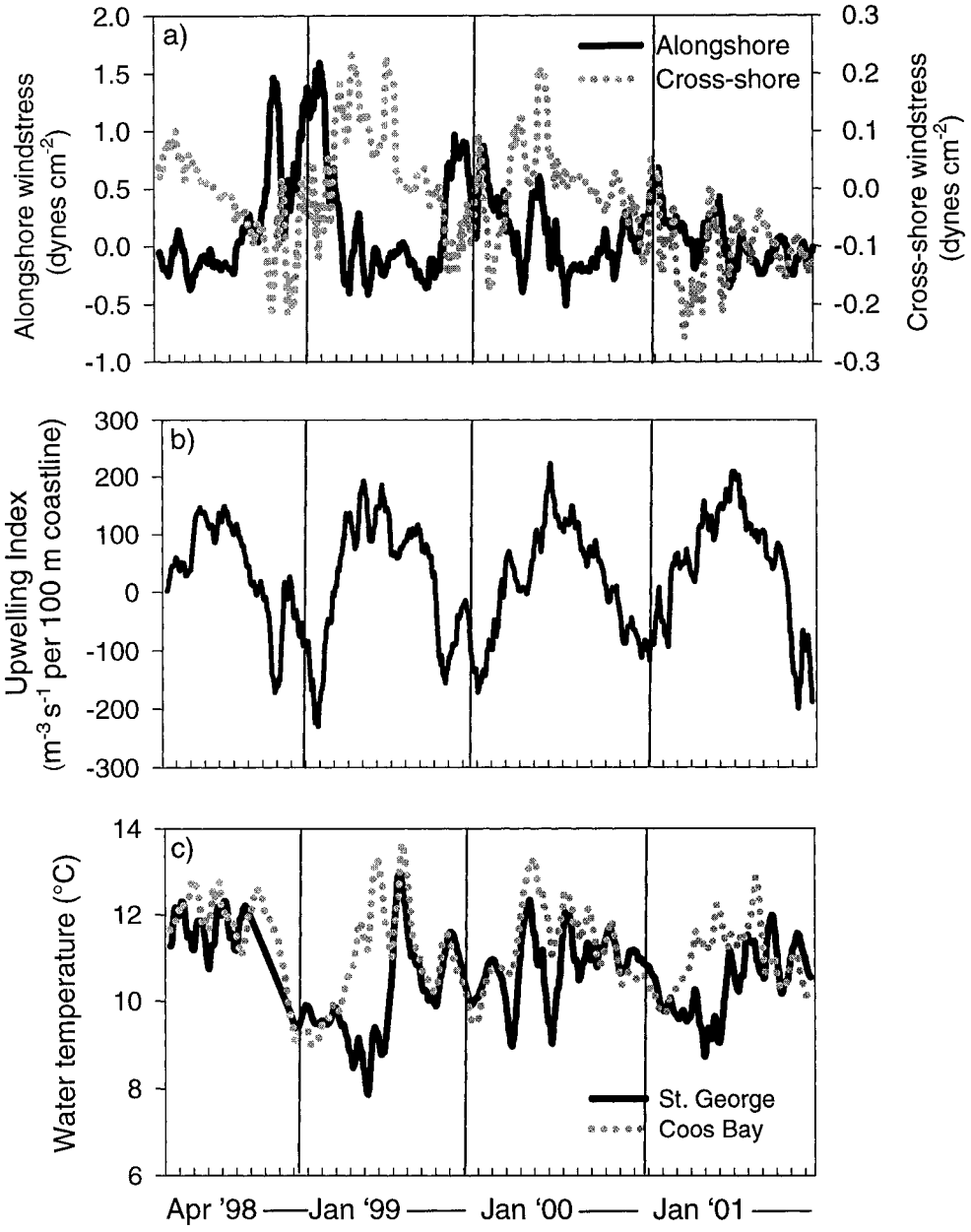

Fig. II.10. Time series of the physical variables during the study. (a) Average daily alongshore (solid line) and cross-shore (dotted line) wind stress (dynes cm^{-2}). Positive values are northward (alongshore) and eastward (cross-shore); negative values are southward (alongshore) and westward (cross-shore). Data are from NOAA's C-MAN station CAR03 (43°20'30"N 124°22'30"W). (b) Average daily upwelling indices at 45°N 125°W. (c) Average daily surface water (0.6 m depth) temperature (°C). Outer coast data (solid line) are from NOAA buoy #46027 (41°51'01"N 124°22'52"W) and estuarine data (dashed line) are from NOAA station #9432780 (43°20'42"N 124°19'21"W).

Table II.8. Cross-correlations (lags: r value at that lag) between northern anchovy (*Engraulis mordax*) abundance at the Coos Bay light trap locations and physical variables. Lags represent days; the sign indicates whether peaks in northern anchovy occur after (negative values) or before (positive values) changes in the physical variable. Only statistically significant ($p \leq 0.05$) cross-correlations are presented. « ns » indicates no statistical significance. « na » indicates insufficient data for analysis. The collection location and year are included.

	Temperature	**Alongshore wind stress**	**Cross-shore wind stress**	**Upwelling index**	**Maximum tidal range**
Northern anchovy (*Engraulis mordax*)					
Entrance					
1998	ns	-2 d: +0.170	ns	ns	ns
1999	na	na	na	na	na
2000	ns	ns	ns	ns	+4 d: -0.210 +5 d: -0.234 -2 d: +0.234 -3 d: +0.236
2001	na	na	na	na	na
Mid-Slough					
2000	ns	ns	ns	ns	+3 d: -0.376 +4 d: -0.345 -3 d: +0.294 -4 d: +0.365
2001	ns	ns	ns	ns	+1 d: -0.323 +2 d: -0.394 -3 d: +0.235 -4 d: +0.332
Upper Slough					
2001	ns	ns	ns	ns	+0 d: -0.389 +2 d: -0.411 -4 d: +0.355 -6 d: +0.450

Surf smelt (*Hypomesus pretiosus*)

The abundance of surf smelt varied significantly with a tidal periodicity in 2000 at both the Entrance and Mid-Slough (Table II.10). Significant, positive cross-correlations between surf smelt abundance and the tides were observed between spring and neap tides at the Entrance and around spring tides at Mid-Slough. Additionally, in 2000, surf smelt abundance was significantly and positively cross-correlated with positive alongshore (downwelling favorable) wind stress and negative upwelling indices. At Mid-Slough, 2000 abundance was positively cross-correlated with positive cross-shore (shoreward) wind stress. Time-series analyses of surf smelt were not completed the Entrance in 1998 and 1999 due to the small number of fish collected (i.e. < 50).

Penpoint gunnel (*Apodichthys flavidus*) and rosylip sculpin (*Ascelichthys rhodorus*)

There were no significant cross-correlations between the abundance of penpoint gunnel or rosylip sculpin and any of the physical variables examined.

Table II.9. Cross-correlations (lags: r value at that lag) between Pacific sardine (*Sardinops sagax*) abundance at the Coos Bay light trap locations and physical variables. Lags represent days; the sign indicates whether peaks in Pacific sardine occur after (negative values) or before (positive values) changes in the physical variable. Only statistically significant ($p \leq 0.05$) cross-correlations are presented. « ns » indicates no statistical significance. « na » indicates insufficient data for analysis. The collection location and year are included.

	Temperature	**Alongshore wind stress**	**Cross-shore wind stress**	**Upwelling index**	**Maximum tidal range**
Pacific sardine (*Sardinops sagax*)					
Entrance					
1998	ns	-1 d: +0.155	ns	-2 d: -0.136	+2 d: -0.243 +3 d: -0.293 -4 d: +0.170 -5 d: +0.199
1999	na	na	na	na	na
2000	na	na	na	na	na
2001	na	na	na	na	na
Mid-Slough					
2000	ns	-3 d: +0.153 -4 d: +0.153	ns	ns	-2 d: +0.145 -3 d: +0.151 -9 d: -0.114 -10 d: -0.136
2001	ns	ns	ns	ns	+0 d: +0.142 +1 d: +0.155 -7 d: -0.150 -8 d: -0.151

Table II.10. Cross-correlations (lags: r value at that lag) between surf smelt (*Hypomesus pretiosus*) abundance at the Coos Bay light trap locations and physical variables. Lags represent days; the sign indicates whether peaks in surf smelt occur after (negative values) or before (positive values) changes in the physical variable. Only statistically significant ($p \leq 0.05$) cross-correlations are presented. « ns » indicates no statistical significance. « na » indicates insufficient data for analysis.The collection location and year are included.

	Temperature	Alongshore wind stress	Cross-shore wind stress	Upwelling index	Maximum tidal range
Surf smelt (*Hypomesus pretiosus*)					
Entrance					
1998	na	na	na	na	na
1999	na	na	na	na	na
2000	ns	-5 d: +0.149	ns	-6 d: -0.145	-3 d: +0.170 -4 d: +0.160
2001	ns	ns	ns	ns	ns
Mid-Slough					
2000	ns	ns	+0 d: +0.236	ns	+0 d: +0.190 -1 d: +0.180
2001	ns	ns	ns	ns	ns
Upper Slough					
2001	ns	ns	ns	ns	ns

Discussion

Thirty-eight taxa of larval and juvenile fish were collected in light traps in Coos Bay, Oregon over the 3¾ year study. Twenty-eight of these taxa were identified to species. Five species, represented primarily by post-flexion larvae and juveniles, consistently comprised > 70% of the total catch. These were northern anchovy (*Engraulis mordax*), penpoint gunnel (*Apodichthys flavidus*), Pacific sardine (*Sardinops sagax*), rosylip sculpin (*Ascelichthys rhodorus*), and surf smelt (*Hypomesus pretiosus*).

Other research in the Pacific Northwest on the use of estuaries by fish includes surveys that targeted larval and post-larval planktonic (Mistano 1977; Pearcy and Myers 1973) and benthic fishes (Bottom et al. 1987; Haertel and Osterberg 1967). Over 11 years of weekly sample collection, Pearcy and Myers (1973) collected 45 unique types of larval fish and identified 22 to species; their catch was dominated by Pacific herring (*Clupea harengus pallasi*) and the bay goby (*Lepidogobius lepidus*). In a one year survey of the Columbia River estuary, Mistano (1977) collected 22 species of larval, post-larval, and juvenile fish representing 13 families; the catch was dominated by anadromous osmerids (smelts). Haertel and Osterberg (1967) documented 25 species of fish in the Columbia River estuary; starry flounder (*Platichthys stellatus*) and two sculpin (*Cottus asper* and *Leptocottus armatus*) comprised the majority of their larval and juvenile catch. Bottom et al. (1987) collected 33 species, including adults and numerous anadromous species, in the South Slough, Coos Bay between April and October 1987. In their study, the peak in species richness, density, and biomass occurred in the summer and declined in October. Surfperches (Embiotocidae) and staghorn sculpin (*Leptocottus armatus*), including both juveniles and adults, comprised the majority of their catch. Finally, a regional characterization of U. S. west coast estuaries (Monaco et al. 1992), based on published and unpublished information, listed 71 species of fish in Coos Bay. Comparatively, the species richness (i.e. 41 taxa) collected with light traps in Coos Bay was in the range of previous regional studies. However, the relative species abundances were quite different. This was due, in part, to relatively large numbers of northern anchovy and Pacific sardine

that were consistently collected in light traps. Juvenile fish are often poorly sampled with nets due to their relatively good sensory and swimming abilities. The results of my study, in conjunction with previous work, indicate that a diversity of collection methods is necessary to adequately sample larval and juvenile fish in Pacific Northwest estuaries.

Annual patterns

The majority of fish at the Entrance were collected during downwelling, which is similar to other studies in the region (Mistano 1977; Pearcy and Myers 1973) and supports Parrish et al.'s (1981) hypothesis. However, a significant portion (i.e. 15% to 62%) of the total catch occurred during the spring transition (i.e. April to May). The abundance of larvae and juveniles during the spring transition may be due, in part, to a correspondence between reproductive and development timing and the end of the downwelling season. However, at Mid-Slough, which was < 1 km farther up estuary, only 8% of the total catch occurred during the spring transition. Furthermore, more fish were collected at Mid-Slough during the fall transition and subsequent downwelling period than at the Entrance. There were quite different patterns in fish abundance at these two sites, which are in relatively close proximity.

The annual abundance data suggest that larvae and juveniles enter the estuary during downwelling. However, there were no significant cross-correlations between indicators of downwelling conditions in two of the most abundant species (penpoint gunnel and rosylip sculpin) and infrequent, relatively weak cross-correlations for the other three most abundant species (northern anchovy, Pacific sardine, and surf smelt) in

only two of the four years examined. Significant cross-correlations between abundance and the spring-neap tidal cycle were more common. These data indicate that the presence of larval and juvenile fish within the Coos Bay estuary may have been more controlled by a combination of reproductive timing and tidal transport than by wind-driven delivery. This is further supported, at least for penpoint gunnel and rosylip sculpin, by the presence of significant annual cycles in their abundance.

Interannual abundance

In 1999, the abundances of penpoint gunnel and rosylip sculpin, which are benthic as adults, were high compared to other years, i.e. 1998, 2000, and 2001. At the same time, the 1999 annual abundances of the northern anchovy, Pacific sardine, and surf smelt, which are pelagic as adults, were the lowest observed in this study. Given the lack of any significant cross-correlations between fish abundance and the physical variables examined in 1999, it is difficult to determine if these differences are due to actual differences in the number of juveniles present in the bay or, possibly, different transport patterns.

One notable difference in the annual wind patterns during this study was observed in the alongshore wind stress. Larval and juvenile penpoint gunnel and rosylip sculpin were present in Coos Bay from January to May, with peaks typically from February to April. The mean and variance in alongshore wind stress for the 1st 100 d of each year was: 1998, 0.46 ± 0.6 dynes cm^{-2}; 1999, 0.84 ± 1.5 dynes cm^{-2}; 2000, 0.27 ± 0.7 dynes cm^{-2}; and 2001, 0.11 ± 0.3 dynes cm^{-2}. The mean and variance in 1999 were the greatest

of the four years. Potentially, the greater northward alongshore wind stress in the first part of the year resulted in strong downwelling that contributed to enhanced estuarine ingress of the winter spawned larvae of penpoint gunnel and rosylip sculpin. Alternatively, it is possible that penpoint gunnel and rosylip sculpin are spawned within the estuary and the enhanced northward alongshore wind stress in the first part of the year helped retain larvae in the estuary. However, alongshore wind stress and upwelling intensity later in the year were not unusual. Therefore, it is not clear why juveniles of species with more protracted spawning periods that typically begin somewhat later in the year, i.e. northern anchovy, Pacific sardine, and surf smelt, would have experienced reduced survival and/or enhanced offshore transport in 1999.

Relatively small juvenile northern anchovy, < 30 mm SL, were present in Coos Bay during late summer through fall in both 2000 and 2001. The presence of juveniles of this size in the estuary at the beginning of August supports previous observations that the northern sub-population spawns in July and August. Juveniles were caught until the end of the year in 2000 and into November in 2001. However, in 2001, younger fish (21 to 30 mm SL) were also collected in mid-January and were present throughout most of the remainder of the year. Given the reported spawning times for the northern sub-population, it is unlikely that these early juveniles came from that population. They may have come from more southerly locations, i.e. the central sub-population, where more protracted spawning occurs (Richardson 1981). During winter months, the predominant alongshore flow off Oregon is northward, i.e. the Davidson or Inshore Counter Current.

Therefore, transport northward toward Coos Bay from more southerly locations is possible. If this is the case, these two sub-populations overlap geographically in their use of Coos Bay during their early life history. However, their residence in Coos Bay appears to be distinctly separated in time.

Relative abundance and size

In 2000 and 2001, species abundances at sample locations farther up estuary were significantly and positively cross-correlated, at +0 to -3 d lags, with abundances at sample locations closer to the estuary mouth; this occurred for northern anchovy, Pacific sardine, surf smelt, and penpoint gunnel. These correlations indicate that individuals moved up estuary after arrival at the Entrance site. However, in 2001, peaks in the abundance of Pacific sardine and surf smelt at sample locations farther up the estuary occurred a day prior to peaks at sample locations closer to the estuary mouth. This may indicate that, at times, juvenile Pacific sardine and surf smelt remained in the South Slough arm of Coos Bay for extended periods. This is further supported by the relatively large numbers of northern anchovy, Pacific sardine, and surf smelt collected at Mid-Slough and Upper Slough sites during extended periods when few were collected at the Entrance.

Generally, when fish size varied between sites, larger fish were collected farther up the estuary. This was the case for penpoint gunnel in 2000 and 2001. Similarly, for surf smelt in 2001, progressively larger fish were collected farther up estuary. Conversely, smaller Pacific sardine were collected farther up estuary in 2001. These data

suggest that, at least for some species, larvae and juveniles moved progressively farther up estuary after their initial entrance. Such movements may be facilitated by selective tidal-stream transport, which is known to occur in numerous marine organisms (Forward and Tankersley 2001; Kimura et al. 2000; Laprise 1989). The occurrence of larger individuals farther up estuary may be due to high growth rates, enhanced tidal-stream transport by older juveniles which have increased swimming ability, the ingress of smaller individuals into the estuary from marine waters, or a combination of such factors.

Transport and estuarine ingress

Significant cross-correlations between species abundance and the spring-neap tidal cycle suggest that tidal transport may have contributed to estuarine ingress and transport in northern anchovy, Pacific sardine, and surf smelt. Peaks in abundance occurred most frequently during spring tides, then in between spring and neap, and, in one instance, during neap tides. This one exception was for 2001 northern anchovy at the Upper Slough site, which was located farthest up the estuary. At times, the fortnightly variation in abundance was consistent among all three species. For example, at Mid-Slough in 2000, peaks in abundance of all three species were associated with spring tides. Similarly, at the Entrance in 2000, the abundances of northern anchovy and surf smelt were significantly cross-correlated with spring tides.

The significant cross-correlations between species abundance and the spring-neap tidal cycle observed in this study suggest that tidally driven processes contributed to the estuarine ingress, and potentially shoreward transport, of northern anchovy, Pacific

sardine, and surf smelt. This may occur, in part, via selective tidal-stream transport (STST). Numerous studies have documented STST of organisms in estuaries (Forward and Tankersley 2001; Kimura et al. 2000; Laprise 1989). Furthermore, modeling efforts have shown that net horizontal displacement of zooplankton may occur in the presence of oscillatory tidal currents and daily vertical migrations (Hill 1998). Another potential mechanism of shoreward transport is non-linear internal tides and bores. Increased concentrations of larval fish and invertebrates (Pineda 1991; Pineda 1994; Shanks 1983; Shanks 1988; Shanks 1995; Shanks 1998), juvenile fish (Kingsford and Choat 1986), and small adult fish (Rogachev et al. 1996) have been observed in slicks associated with internal waves and bores. Tidal frequencies have also been identified in the nearshore abundance of larval invertebrates and fish observed in surface slicks associated with internal waves (Shanks 1983; Shanks 1998). Therefore, it is likely that a combination of selective tidal-stream transport and non-linear internal tides and bores contributed to the abundance patterns observed in this study.

The only other significant cross-correlations between species abundances and the physical variables examined in this study were with indicators of downwelling, or the onshore transport of surface waters. In 1998, the abundances of northern anchovy and Pacific sardine were significantly and positively cross-correlated with positive alongshore (downwelling favorable) wind stress. In 2000, the abundances of Pacific sardine and surf smelt were significantly cross-correlated with indicators of downwelling (positive alongshore wind stress and negative upwelling indices) or onshore transport of surface

waters (positive cross-shore wind stress). Previous research on both invertebrates (Goodrich et al. 1989; Johnson et al. 1986; Wing et al. 1995) and fish (Munch and Conover 2000) have documented correlations between abundance and indicators of downwelling. Although, in this study, significant cross-correlations between juvenile fish abundance and wind-related physical variables were not as common as tidal signals, it is likely that wind-driven transport is an important component of shoreward transport and estuarine ingress.

Related research on the abundance of juvenile fish and crab megalopae (Chapter III) at both nearshore and estuarine sample locations observed significant cross-correlations between the abundance of juvenile northern anchovy in the estuary and indicators of upwelling (i.e. negative alongshore windstress and positive upwelling indices). For that study, samples were collected and analyzed only from June 9 to October 12, the period when upwelling occurs most frequently. It is possible that the primary transport mechanisms responsible for the shoreward transport and estuarine ingress of northern anchovy vary throughout the year. Alternatively, northern anchovy that reproduce during summer months may have distinct behaviors that help maintain populations under the different oceanographic conditions that occur during upwelling.

The potential nursery function of Coos Bay is difficult to determine without additional information from areas outside of the estuary. In a related study, simultaneous collections of northern anchovy were made at an outer coastal and estuarine site (Chapter III). In that case, significantly more northern anchovy were collected at the outer coast

compared to the estuary. However, relatively large numbers of some species, i.e. penpoint gunnel and rosylip sculpin, were present as larvae in Coos Bay and some species, i.e. northern anchovy and surf smelt, were present throughout much of the year. It would be premature to conclude that Coos Bay does not provide nursery areas for some of these species without additional information on growth and survival,

I conclude, as did Doherty (1987), that light traps are selective but useful devices for determining the distribution and relative abundance of larval and juvenile fishes. My results further support the utility of light traps in temperate estuaries (Hickford and Schiel 1999). The relative abundance patterns observed in this study indicate that there is seasonal variation in which portions of the estuary are used by larvae and juveniles, i.e. more fish were collected Mid-Slough in summer and fall. The interannual variation in the relative abundance of benthic vs. pelagic species was, at times, very large. And the juveniles of some species, such as northern anchovy and surf smelt, resided within portions of the estuary for extended periods of time. Additionally, there were indications that shoreward transport and estuarine ingress may have occurred via selective stream tidal transport and/or internal tides and bores. The lack of much evidence for wind-driven transport suggests that the presence of the larvae and juveniles within the Coos Bay estuary may have been more controlled by a combination of reproductive timing and tidal transport than wind-driven delivery.

Bridge

The following chapter, Chapter III, "Ocean-estuary coupling in the Oregon upwelling region: abundance and transport of juvenile fish and of crab megalopae," compares a portion (4 months in 2000) of the estuarine light trap data presented in the preceding chapter with light trap data collected during the same 4 month period at an adjacent outer coastal location. The comparison, which also involves time-series analysis, allowed me to examine nearshore and estuarine delivery of the same species separately to determine if, and when, similar mechanisms regulated nearshore and estuarine transport. Furthermore, it builds upon the previous chapter by providing information on the exchange of materials between the coastal ocean and an adjacent estuary. The study presented in Chapter III is published in *Marine Ecology Progress Series*, authored by myself and A. L. Shanks. I completed all of the field work, data analysis, and writing for that manuscript.

Chapter III

Ocean-estuary coupling in the Oregon upwelling region: abundance and transport of juvenile fish and of crab megalopae

Introduction

The exchange of materials, such as nutrients, plankton, and nekton, between estuaries and the ocean is of key interest to coastal scientists. Many species of fish and invertebrates move between the continental shelf and estuaries during their early life-history (Gunderson et al. 1990, Thorpe 1994, DiBacco et al. 2001, Epifanio & Garvine 2001). A common assumption in marine population ecology is that population size is altered by larval transport toward or away from adequate rearing or settlement areas which, for many species, are in coastal areas (Hjort 1914, Cushing 1975, Sinclair 1988). The regulation of population cycles may, in some cases, depend on how and when transport to and exchange between the coastal ocean and estuaries occurs.

The dominant mechanisms of cross-shelf transport and estuarine ingress include wind-driven Ekman transport, tidal-stream transport through vertical migrations, non-linear internal waves and bores, moving frontal systems, and density-driven currents (Shanks 1983, 1988, Pineda 1991, Shanks et al. 2000, Epifanio & Garvine 2001, Forward

& Tankersley 2001). Which of these mechanisms, if any, dominate transport to near-shore areas and ingress into estuaries is not well understood. It is also unclear how, or whether, similar physical mechanisms regulate transport to and between outer coast and estuarine areas. If estuarine ingress of coastal organisms is a two stage process, with the initial arrival in the near-shore as the first stage and subsequent entrance into nearby estuaries as the second stage (Boehlert & Mundy 1988), each stage may be regulated by different transport mechanisms.

Estuaries worldwide are known to be nursery and/or settlement areas for numerous species of coastal fish and invertebrates (Elliott & Hemingway 2002). Some NE Pacific species, such as the northern anchovy (*Engraulis mordax*) and Dungeness crab (*Cancer magister*), enter estuaries as larvae and juveniles. The potential advantages to estuarine residence include increased prey and refugia, which may increase growth and enhance survival (Miller & Dunn 1981, Gunderson et al. 1990, Jackson et al. 2001). The proportion of individuals within a cohort, however, that enter estuaries and the timing of and mechanisms regulating that entrance are not well known.

In this study, simultaneous measurements of the abundance of juvenile fish and crab megalopae at an outer coastal and estuarine site provide information on transport mechanisms and the exchange of organisms between the coastal ocean and an adjacent estuary. We collected organisms from late spring through early fall to compare the timing of arrival and relative abundance at each site. We also used these data to identify potential wind-driven and tidal-transport mechanisms. We chose an estuarine site within

Coos Bay, Oregon and a nearby outer coastal site to address these topics. Coos Bay is at the southern end of the Pacific Northwest region, defined as Vancouver Island, British Columbia to Cape Blanco, Oregon (Parrish et al. 1981). The area is characterized by seasonal, wind-driven upwelling (during late spring/summer) and downwelling (during late fall/winter) due to Ekman transport of surface waters (Huyer 1976).

During spring and summer in Oregon, northwesterly winds result in persistent upwelling and the establishment of an upwelling front where low density off-shore waters meet high density, recently upwelled waters (Mooers 1976). The upwelling front is a convergence zone that can lead to increased concentrations of organisms (Peterson et al. 1979). Research efforts have focused on the role of upwelling relaxation and the shoreward movement of this front in promoting shoreward transport of larvae within the front (Roughgarden et al. 1988, Wing et al. 1995b, Shanks et al. 2000). We hypothesized that wind-driven transport, specifically associated with upwelling relaxation, would be a factor regulating the abundance of juvenile fish and crab megalopae at the outer coastal site.

Non-linear internal tides and bores and tidal-stream transport through vertical migration may also cause shoreward transport of organisms. Internal tides are generated at the shelf break or over other topographic features on the seafloor and typically occur on diurnal and semi-diurnal frequencies (Kropfli et al. 1999, Inall et al. 2000). Although the mechanisms are not well understood, the generation and strength of internal tidal waves depend on the degree of water column stratification, and their structure and

frequency vary throughout the spring-neap tidal cycle. Strong spring tidal currents can generate more frequent and widespread internal tidal waves (Kropfli et al. 1999). Numerous studies document increased concentrations of larval fish and invertebrates (Shanks 1983, 1988, 1995, 1998, Shanks & Wright 1987, Pineda 1991, 1994), juvenile fish (Kingsford & Choat 1986), and small adult fish (Rogachev et al. 1996) in slicks associated with internal waves and bores. Some of these studies (Shanks 1983, 1988, Shanks & Wright 1987) directly observed the shoreward transport of material concentrated in slicks associated with internal waves and/or identified tidal frequencies in the near-shore abundance of larval invertebrates and fish (Shanks 1983, 1988, 1998, Pineda 1991, 1994, Johnson & Shanks 2002). Furthermore, modeling efforts demonstrate the potential for net horizontal transport to occur in organisms that undergo diel vertical migration in oscillatory tidal currents over the continental shelf (Hill 1998). If an organism was transported shoreward due to tidal-stream transport, a tidal periodicity in near-shore abundance would also be expected but the overall abundance pattern should be proportional to water flux and, therefore, to tidal range. We hypothesized that, at the outer coast, there would be a tidal periodicity in the abundance of species, which could be due to either of these tidally driven mechanisms.

The physical oceanography of Oregon's estuaries is strongly influenced by the coastal ocean (Roegner & Shanks 2001, Roegner et al. 2003). Therefore, we hypothesized that the estuarine abundance of post-larvae and juveniles of species that use estuaries as a nursery would be temporally correlated with their abundance at the outer

coast. Furthermore, tidal-stream transport can promote the ingress and retention of larvae and juveniles in estuaries (Forward & Tankersley 2001). Estuarine ingress may also be associated with onshore or downwelling winds that force coastal waters into the estuary (Goodrich et al. 1989). Therefore, we predicted that both tidal and wind-driven transport would promote the estuarine ingress of juvenile fish and crab megalopae.

To examine these hypotheses, the time series of juvenile fish and crab megalopae abundance from the outer coast and estuarine sites were statistically compared with each other and with physical variables indicative of wind and tidal conditions (e.g. sea surface temperature, alongshore and cross-shore wind stress, upwelling index, and daily tidal range). This allowed us to compare the timing and magnitude of the relative abundance of organisms at the two locations and identify potential transport mechanisms. Given the difficulty involved with tracking marine larvae, inferences regarding larval transport are often made through correlations between species abundance and physical variables (Shanks 1983, Johnson et al. 1986, Shanks & Wright 1987, Pineda 1991, Jones & Epifanio 1995, Wing et al. 1995b, Shanks 1998, Findlay & Allen 2002).

Methods

Study area

Samples were collected at two sites, Coos Bay and Sunset Bay. The Coos Bay estuary is located on Oregon's south coast (Fig. III.1). The drowned river valley, Coos Bay is, at approximately 54 km^2, the second largest estuary in Oregon. Tides are mixed, semi-diurnal with a mean amplitude of 2.0 m. Sunset Bay is an outer coast embayment,

approximately 2 km south of the entrance to Coos Bay. A small tributary, Big Creek, empties into Sunset Bay. During summer months, when the majority of the data were collected, Big Creek monthly flow is minimal, < 0.02 to 0.08 $m^3 sec^{-1} mos^{-1}$ (Coos County Water Resources Department data).

Biological data

Light traps were used to collect organisms. Traps consisted of a 10 L polycarbonate (clear) carboy with ten circular funnel openings (1 to 1.25 cm in diameter) and an 8 W fluorescent light in a sealed tube powered either by shore power or with a 12.0 volt, 12.0 AH rechargeable Pb-Acid battery controlled with a photocell (Fig. III.2). Three light traps were deployed at each of two sites: (1) within the South Slough, approximately 1 km inside of Coos Bay (43°20'12"N, 124°19'14"W) and (2) at Sunset Bay, approximately 2 km south of Coos Bay (43°20'7" N, 124°22'23"W) (Fig. III.1). Traps within each site were deployed, 15 to 30 m apart, from June 9 to October 12, 2000. Samples from Coos Bay were collected daily throughout the study whereas Sunset Bay samples were collected daily for the initial 31 d of the study and then collected every other day for the remaining 96 d. Sunset Bay will be referred to hereafter as the "outer coast site" and Coos Bay as "the estuarine site." Juvenile fish and crab megalopae were identified to species or, in some cases, genus, and counted. Standard lengths (SL) of fish were measured to the nearest millimeter.

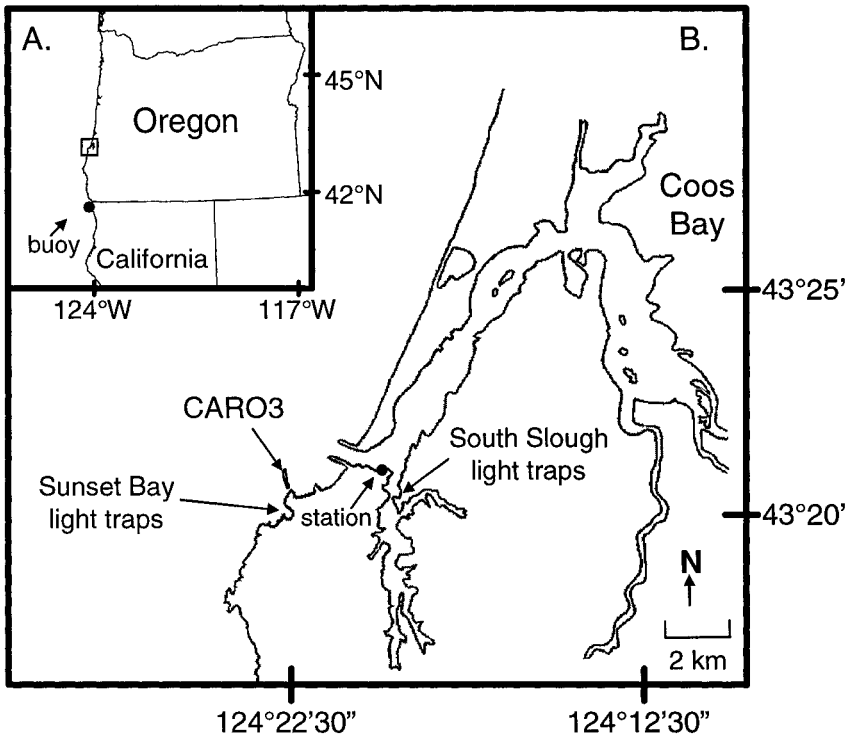

Fig. III.1. Study sites in Oregon. (A) identifies region of study and (•) indicates the location of NOAA buoy #46027 (41°51'01"N 124°22'52"W), which provided surface water temperature data (0.6 m water depth) for outer coast analysis. (B) shows the location of Sunset Bay (outer coast site) and South Slough (estuarine site) light traps. (•) indicates the location of NOAA station #9432780 (43°20'42"N 124°19'21"W), which provided surface water temperature data for estuarine analysis. NOAA's C-MAN station CAR03 (43°20'30"N 124°22'30"W), which provided daily wind speed and direction, is labeled.

Light traps are passive collectors of positively phototactic organisms. Although collection is biased to organisms with positive phototaxis, light traps offer a number of advantages to more traditional net collections which made them appropriate for this study. The use of light traps allows for simultaneous and integrated sampling over a relatively long period, i.e. the entire night. This increases the probability of capture of organisms found at low densities. Traps can be placed in near-shore coastal areas that are difficult to sample with more traditional, ship-borne methods. Light traps often capture late-stage larvae and early juveniles, stages that are poorly sampled with nets (Milicich & Doherty 1994). Although there is only one published report of light traps being used in the North Pacific (Roegner et al. 2003), they have been used to collect larval and juvenile fish and invertebrates in tropical (Doherty 1987, Thorrold 1992, Kingsford & Battershill 1998) and temperate (Hickford & Schiel 1999) regions. Over 30 fish taxa (larvae and juveniles) and over 40 invertebrate taxa (larvae, juveniles, and adults) have been collected in light traps in Coos Bay (Miller & Shanks, unpublished data). In this study, we examined juvenile *Engraulis mordax* (northern anchovy), *Sardinops sagax* (Pacific sardine), *Sebastes melanops* and *S. caurinus* combined (black and copper rockfish), and megalopae of *Cancer magister* (Dungeness crab), *C. oregonensis* and *C. productus* combined (pygmy and red rock crabs), and *Pagurus* spp. (hermit crabs).

Engraulis mordax (northern anchovy) and *Sardinops sagax* (Pacific sardine) belong to the Families Engraulidae and Clupeidae, respectively. Both species produce pelagic eggs and larvae (Matarese et al. 1989). The northern extent of *E. mordax* is

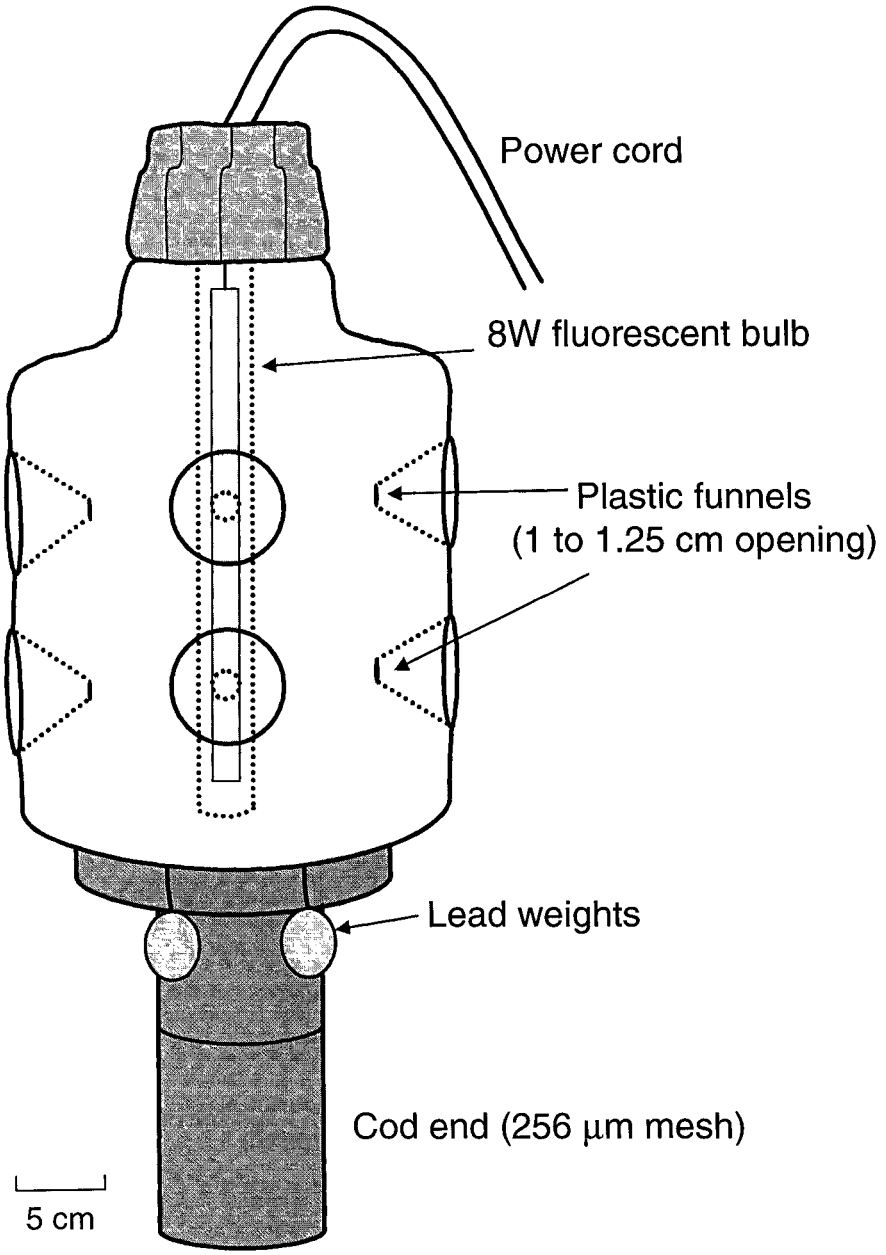

Fig. III.2. Light traps used to collect organisms in outer coast and estuarine waters. Each trap had ten funnel openings (1 to 1.25 cm in diameter) and an 8W fluorescent light in a sealed tube powered either by shore power or with a 12.0-volt, 12.0 AH rechargeable Pb-Acid battery controlled with a photocell. Note 5 cm scale bar.

typically northern British Columbia, Canada. *S. sagax* extend farther north into southeast Alaska, USA. The southern extent of both species is southern Baja California, Mexico. *E. mordax* spawn throughout the year in California, but farther north spawning appears to be concentrated in summer months (Hart 1973). *S. sagax* spawn in central California from January to June with a peak in April to May.

Sebastes melanops and *S. caurinus* (black and copper rockfish, respectively) belong to the Family Scorpaenidae, which are relatively long-lived, viviparous fishes with pelagic larval and juvenile periods typically between 2 and 5 months. *S. melanops* range from central California to the Aleutian Islands. *S. caurinus* range from Baja California to the Gulf of Alaska (Matarese et al. 1989). Juveniles of these two species are often found along the outer coast and in estuaries in late spring through summer.

The *Cancer* crabs, *C. magister*, *C. oregonensis*, and *C. productus*, undergo indirect development. A naupliar stage, typically passed within the egg, is followed by five zoeal and a megalopal (= post-larval) stage prior to metamorphoses to the benthic juvenile stage. In Oregon, females become ovigerous in the fall and release the first zoeal stage after a 3 to 4 month brood period (Reilly 1983, Strathmann 1987). Settlement, which usually occurs along the coast or in estuaries, typically begins in April and peaks in May but can continue through the fall (Lough 1975, Gunderson et al. 1990, Roegner & Shanks, unpublished data). The entire larval period for *C. magister* (Dungeness crab) ranges between 75 and 180 d with the final 25 to 30 d as megalopae (Reilly 1983, Strathmann 1987, Moloney et al. 1994). The larval period of *C. oregonensis* (pygmy rock

crab) is estimated at 155 d, with a range of 123 to 203 d (Lough 1975). Due to similarities in size and appearance, *C. oregonensis* and *C. productus* were indistinguishable as megalopae and were combined for all analyses.

The *Pagurus* spp. crabs also undergo indirect development. They pass through four zoeal and one megalopal stage prior to metamorphoses to a benthic juvenile. Larval durations are estimated to average 49 to 76 d with the final 17 to 19 d as megalopae (Strathmann 1987).

Physical data

Average daily wind speed and direction were calculated from hourly data obtained from the National Oceanic and Atmospheric Administration's (NOAA) National Data Buoy Center's C-MAN station CAR03 (43°20'30"N 124°22'30"W), which is located on the outer coast between Sunset Bay and the mouth of Coos Bay (Fig. III.1). In the vicinity of Coos Bay, the coastline of Oregon is oriented 20° northeast of true north. Therefore, wind direction was corrected for the angle of coast by subtracting 20° from the average daily wind direction. Daily average alongshore and cross-shore wind stress were calculated using the daily average wind speed and direction, a constant drag coefficient ($C_D = 0.00122$) and air density ($\rho_a = 0.0013$) (Pedolsky 1987). Because we used a constant drag coefficient, the reported wind stress should be considered pseudo-stress values. For the outer coast time series, hourly surface water (0.6 m depth) temperatures (°C) were obtained from offshore NOAA buoy #46027 (41°51'01"N 124°22'52"W), which was the closest working coastal buoy during this study (Fig. III.1). For the

estuarine time-series analyses, hourly surface water temperatures (°C) were obtained from NOAA Station #9432780 (43°20'42"N 124°19'21"W), located near Coos Bay's south jetty. Maximum daily tidal range (cm) was obtained from Harbor Master™ software program. Upwelling indices (at 45°N 125°W) were obtained from the NOAA Pacific Fisheries Environmental Laboratory (PFEL), Pacific Grove, California. PFEL coastal upwelling indices are calculated based upon Ekman's theory of mass transport due to wind stress. Ekman transports are resolved into components parallel and normal to the local coastline orientation. The magnitude of the offshore component is considered to be an index of the amount of water upwelled from the base of the Ekman layer. Positive values are, in general, the result of equator-ward wind stress. Negative values imply downwelling, or the onshore advection of surface waters accompanied by a downward displacement of water. The index is produced from six-hourly fields of surface pressure on a global spherical 1° mesh (a 180 x 360 grid). The standard west coast six-hourly upwelling indices are a product of the 3° pressure field interpolated from the 1° grid (PFEL). Units for upwelling indices are in m^3 sec^{-1} per 100 meters of coastline. Daily averages were calculated for offshore and estuarine surface water temperature and the upwelling index.

Statistical analysis

Outer coast samples were initially collected daily and then every other day. Therefore, daily collections were summed over 2 d to ensure valid comparisons with collections made every other day, which resulted in 64 samples. The physical data series

were averaged over 2 d periods for comparison with the outer coast biological data series. For the estuarine site, however, daily measurements of both biological and physical variables were used to determine potential transport mechanisms, which resulted in 127 samples. For all paired comparisons between biological data from the outer coast and the estuary, 2 d sums (64 samples) were used.

Species abundance data were log transformed to reduce the influence of large peaks in the series and examined for trends and/or auto-correlations (Emery & Thomson 1987). If biological data displayed a seasonal trend and/or significant auto-correlation, data were smoothed with an unweighted moving average (10 d average in the estuary and 4 d average at the outer coast) (Fig. III.3A & III.3B). The difference, or residual, between the data series and the smoothed data was then computed with Equation 1,

$$X_t = Y_t - Z_t \qquad \text{(Eq 1)}$$

where X_t is the residual at time t, Y_t is the raw data at time t, and Z_t is the smoothed data at time t (Quinn & Keough 2002) (Fig. III.3C). Residuals were then smoothed with a 2 sample moving average (i.e. 2 d in the estuary and 4 d at the outer coast) (Fig. III.3D). If a physical data series had a seasonal trend, the trend was removed with Equation 2,

$$X_d = X_i - (a + b * t) \qquad \text{(Eq 2)}$$

where X_d = detrended value at time t, X_i = original value at time t, a (intercept) and b time. Statistica™ time-series analysis was used to calculate cross-correlations between biological and physical series. Time-series analysis is used to measure the strength of a relationship between two variables. In this study, lags between variables represent days;

the sign indicates whether peaks in lagged series occurred after (negative values) or before (positive values) changes in the other variable. Positive (negative) cross-correlations indicate a postive (negative) relationship between variables. A significant statistical correlation does not necessarily imply a cause-and-effect relationship. Typically, in time-series analyses, only lags < 10% of the length of the time series are considered valid. Therefore, only lags < 6 d at the outer coast and < 12 d at the estuarine site are presented (Emery & Thomson 1987).

Species abundances at the outer coast and estuarine site were compared in two ways: (1) the average catch of three light traps per location for each sample day (64 samples from each site) and (2) the average total catch of three light traps per location over the entire study (3 samples from each site). Species abundance at both sites was typically pulsed, with numerous days of low or no catch. Few, even log transformed, biological time series met the assumption of normality. Therefore, the average catch per sample for each species at the two sites (n = 64) was compared with the non-parametric Mann-Whitney U test. Similarly, for fish length (SL), only *Sardinops sagax* data were normally distributed. Therefore, for consistency and because statistical results did not differ between parametric and non-parametric approaches, average fish size (SL) per site was compared with the Mann-Whitney U test. For sample sizes < 20, the Mann-Whitney U test U statistic for small samples is presented in lieu of the Z statistic (Sokal & Rohlf 1987).

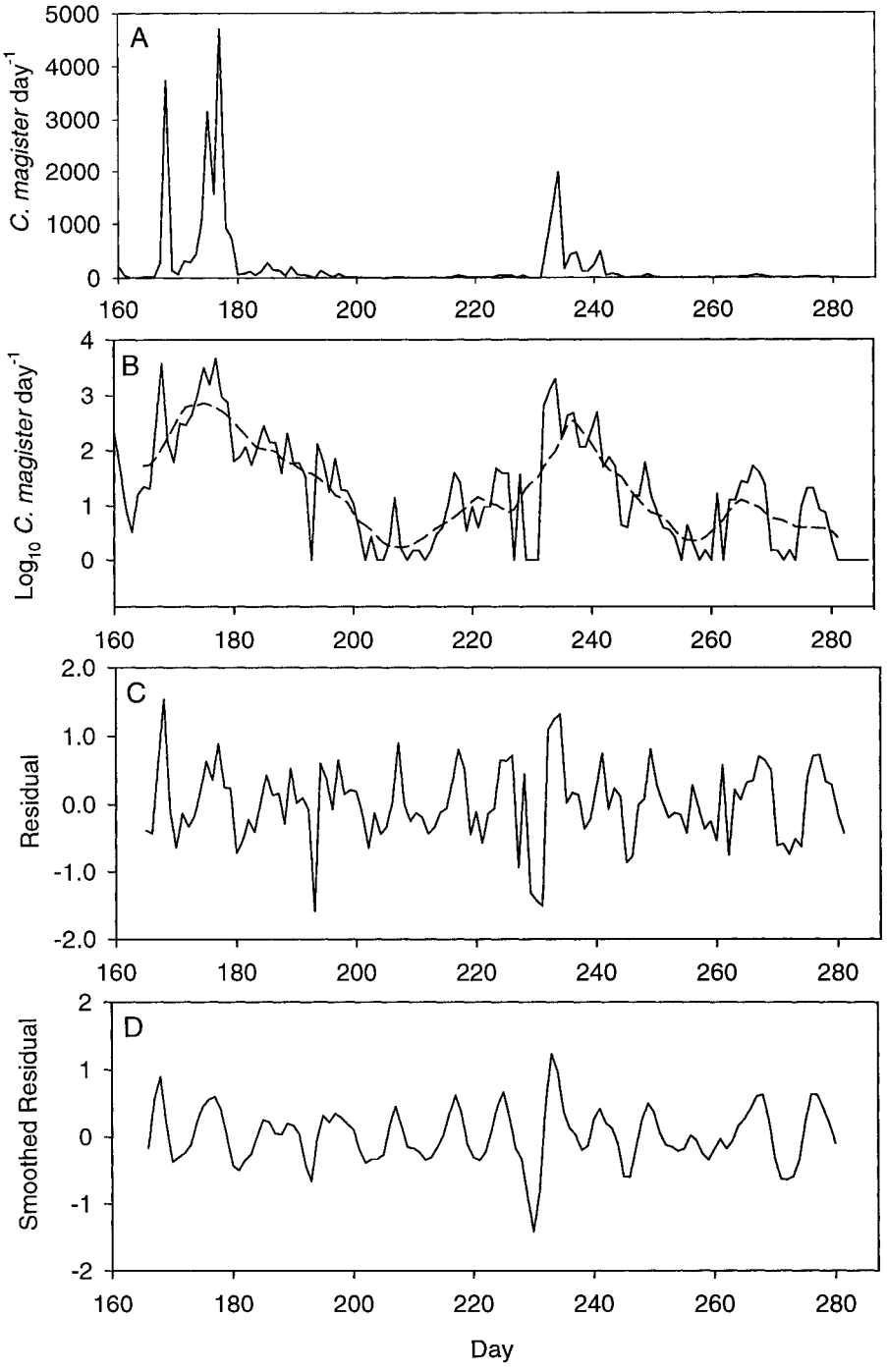

Fig. III.3. (A) The average abundance of Dungeness crab (*Cancer magister*) collected per day at the estuarine site. (B) The $\log_{10}$ *C. magister* average abundance (solid line) and a 10 d moving average (dashed line). (C) The difference, or residual, between $\log_{10}$ *C. magister* daily abundance and the 10 d moving average. (D) The smoothed (2 d) residuals for *C. magister* in (C).

Results

Physical setting

The majority of the study occurred during the summer upwelling period when winds are predominantly northwesterly (Fig. III.4A). Upwelling-favorable winds occurred during 73% of the study while downwelling-favorable winds occurred the remaining 27% (Fig. III.4A & III.4B). Water temperatures averaged 10.8° ± 1.4°C (±SD) with a range of 7.0 to 14.2°C along the outer coast and 11.7° ± 0.9°C (±SD) with a range of 10.4 to 14.8°C inside the estuary (Fig. III.4C). Alongshore and cross-shore wind stress were strongly negatively correlated (0 d lag: $r = -0.79$), i.e. when alongshore wind stress was positive (northward), cross-shore wind stress was typically negative (westward) (Fig. III.4A). Water temperature at the outer coast buoy and estuarine station were significantly correlated with each other (-1 d lag: $r = +0.60$) and with along- and cross-shore wind stresses (0 to -2 d lags: $r \geq \pm 0.40$), i.e. positive alongshore and negative cross-shore wind stresses (downwelling winds) were correlated with warmer sea surface temperatures. Positive values of the upwelling index (at 42°N 125°W) were significantly correlated with negative (southward and upwelling-favorable) alongshore wind stress (0 d lag: $r = -0.66$). Positive cross-shore wind stress (eastward) was significantly positively correlated with the upwelling index (0 d lag: $r = +0.48$). Therefore, surface water temperatures decreased and upwelling indices increased with winds from the northwest. The opposite conditions (i.e. winds from the south-southeast) resulted in warmer water temperatures and lower upwelling indices.

Biological data

Eight species of fish and eight species of invertebrates were collected from both the outer coast and estuarine site (Table III.1). Average correlations of catch between light traps within a site during the study were $r^2 = 0.50$ for *Engraulis mordax* and $r^2 = 0.80$ for *Cancer magister*. The lower correlation for *E. mordax* is due, in part, to their lower total catch (< 500 individuals) compared with the total catch (> 20,000 individuals) of *C. magister.* Abundances at the two sites were compared if a species or genus was present in light traps > 5% of the time, which included juvenile *Engraulis mordax* (northern anchovy), *Sardinops sagax* (Pacific sardine), *Sebastes melanops* and *S. caurinus* combined (black and copper rockfish), and megalopae of *C. magister* (Dungeness crab), *C. oregonensis* and *C. productus* combined (pygmy and red rock crabs), and *Pagurus* spp. (hermit crabs) (Table III.2). Time-series analyses were completed on all taxa present > 25% of the time, which excluded *S. sagax* and the *Sebastes* species (Table III.2). Sampling began after the initial seasonal pulse in *C. magister* settlement that typically occurs during May. However, data from estuarine light traps maintained year-round indicate that approximately 60% of the *C. magister* settlement in 2000 occurred during this study (Miller & Shanks, unpublished data).

Table III.1. Juvenile fish and crab megalopae collected in light traps at both the outer coast and estuarine site. Size range (standard length; SL) for fishes is included. Species in bold letters are discussed in the text.

Taxa	Common name	Size (mm) or Stage
Fishes		
Engraulis mordax	northern anchovy	21 – 80
Sardinops sagax	Pacific sardine	35 – 71
Sebastes melanops	black rockfish	20 – 61
Sebastes caurinus	copper rockfish	20 – 33
Gobiesox maeandricus	clingfish	7 – 11
Scorpaenichthys marmoratus	cabezon	30 – 47
Clinocottus globiceps	mosshead sculpin	12 – 16
Artedius sp.	sculpin	14 – 18
Crabs		
Cancer magister	Dungeness crab	megalopae
Cancer oregonensis/productus	pygmy/red rock crab	megalopae
Hemigrapsus oregonensis	yellow shore crab	megalopae
***Pagurus* spp. (Species A & B)**	hermit crab	megalopae
Pachycheles sp.	porcelain crab	megalopae
Petrolisthes sp.	porcelain crab	megalopae

Table III.2. The abundance of juvenile fish and crab megalopae collected at the outer coast and estuarine sites. The percentage of days (% Time) during the study that taxa were present in light trap samples is also presented. Abundance data are presented as 1) total mean abundance (±SE) over the entire study (average of three traps from each site, n = 3) and 2) mean (±SE) per sample period (average of three light traps from each 2 d sampling period, n = 64). Results from Mann Whitney U test (the Z statistic and the p-value) for the mean per sample (n = 64) are included.

Taxa	**% Time**	**Total mean abundance (n = 3)**		**Mean per sample (n = 64)**		**Mann-Whitney**	
		Outer Coast	Estuary	Outer Coast	Estuary	*Z*	*p*
Engraulis mordax	84.4	424.5 ± 12.7	182.0 ± 9.3	9.5 ± 3.8	2.8 ± 0.5	-1.3	0.18
Sardinops sagax	7.8	7.0 ± 3.3	5.7 ± 3.0	0.13 ± 0.09	0.02 ± 0.01	-0.8	0.43
Sebastes melanops/caurinus	20.3	5.0 ± 0.8	9.5 ± 2.1	0.09 ± 0.03	0.30 ± 0.21	-1.1	0.29
Cancer magister	98.4	513.5 ± 69.9	24,928 ± 733.1	8.5 ± 1.8	404.3 ± 137.7	-5.8	<0.001
Cancer oregonensis/productus	50.0	77.5 ± 3.7	47.3 ± 12.2	2.3 ± 0.8	2.2 ± 1.8	0.91	0.36
***Pagurus* spp. A & B**	29.7	678.0 ± 4.2	1.3 ± 0.30	23.1 ± 11.3	0.03 ± 0.02	-2.7	0.02

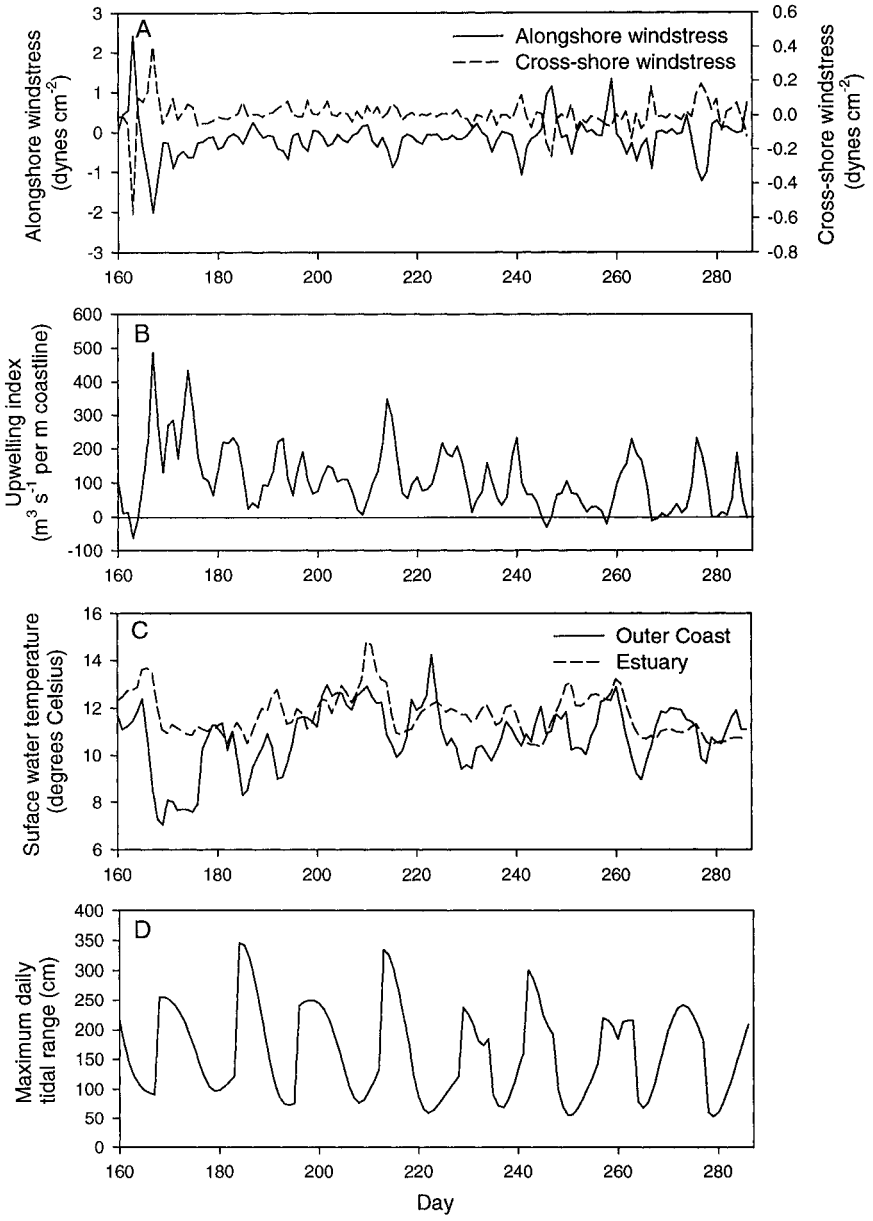

Fig. III.4. Time series of the physical variables during the 127 d study. (A) Average daily alongshore (solid line) and cross-shore (dotted line) wind stress (dynes cm^{-2}). Positive values are northward (alongshore) and eastward (cross-shore); negative values are southward (alongshore) and westward (cross-shore). Data are from NOAA's C-MAN station CAR03. (B) Average daily upwelling indices (m^3 s^{-1} per 100 m of coastline) at 45°N 125°W. Data are from NOAA's Pacific Fisheries Environmental Laboratory. (C) Average daily surface water (0.6 m depth) temperature (°C). Outer coast data (solid line) are from NOAA buoy #46027 and estuarine data (dashed line) are from NOAA station #9432780. (D) Maximum daily tidal range (cm). Data are from HarborMaster™ tidal prediction program.

Northern anchovy (*Engraulis mordax*)

The abundance of juvenile *Engraulis mordax* at the outer coast and estuarine site were significantly cross-correlated. Peaks in estuarine abundance tended to occur 2 to 4 d after peaks in outer coast abundance (r = +0.36, +0.40, respectively, $p \leq 0.05$) (Fig. III.5A). More *E. mordax* were collected at the outer coast compared to the estuarine site although the difference was not statistically significant (Table III.2). The average size (SL) of outer coast individuals was significantly larger than those collected in the estuary (Table III.3).

Table III.3. Mean standard length (±SD) and size range (mm) of juvenile fish collected at the outer coast and estuarine sites. n = number of fish used in analysis. Results of Mann-Whitney U test (the Z statistic and the p-value) are included. For comparisons with < 20 individuals, the U statistic is presented.

	Outer Coast			Estuary			Mann-Whitney	
Taxa	**Mean Size (mm)**	**Range (mm)**	**n**	**Mean Size (mm)**	**Range (mm)**	**n**	***U* (*Z*)**	***p***
Northern anchovy (*Engraulis mordax*)	57.2 ± 16.8	28 - 80	712	38.8 ± 14.3	21 - 71	269	13.1	<0.001
Pacific sardine (*Sardinops sagax*)	50.9 ± 6.9	35 - 61	14	60.1 ± 7.3	41 - 71	16	31.5	<0.001
Rockfish (*Sebastes* spp.)	37.5 ± 19.0	20 - 61	8	24.8 ± 5.2	20 - 60	18	59	0.46

A tidal signal was evident in the abundance of *Engraulis mordax* at both sites. Significant cross-correlations between maximum tidal range and abundance occurred at 0

to 2 d after spring tides at the outer coast (i.e. 0 to 2 d after spring tides and 4 d before neap tides) and between spring and neap tides in the estuary (i.e. 3 to 4 d after spring tides and 2 to 3 d before neap tides) (Table III.4). Abundance at the outer coast was not cross-correlated with any other physical variables. Abundance in the estuary, however, was significantly cross-correlated with negative alongshore wind stress (upwelling-favorable) and positive upwelling indices. These data suggest that there is a tidal periodicity in the transport of juvenile *E. mordax* to both the outer coast and the estuary and that estuarine ingress may have occurred shortly after initiation of upwelling conditions

Pacific sardine (*Sardinops sagax*)

The abundance of juvenile *Sardinops sagax* at the outer coast and estuarine site were significantly cross-correlated, with peaks in estuarine abundance 0 and 2 d after peaks in outer coast abundance ($r = +0.66$ and $+0.90$, respectively, $p \leq 0.05$). More individuals were collected at the outer coast compared to the estuary but the difference was not statistically significant (Table III.2). The average size (SL) of individuals at the outer coast was significantly smaller than those in the estuary (Table III.3). No further time-series analysis was completed because *S. sagax* were present in the light traps < 25% of the study (Table III.2).

Pacific rockfish (*Sebastes melanops* and *S. caurinus*)

The abundance of juvenile *Sebastes* at the estuarine site was not correlated with abundance at the outer coast. More individuals were collected at the estuarine site

compared to the outer coast but the difference was not statistically significant (Table III.2). The average size (SL) of individuals collected at the outer coast was not significantly different from those in the estuary (Table III.3). *Sebastes* juveniles were present in light traps < 25% of the study period, therefore no further time-series analysis was attempted (Table III.2).

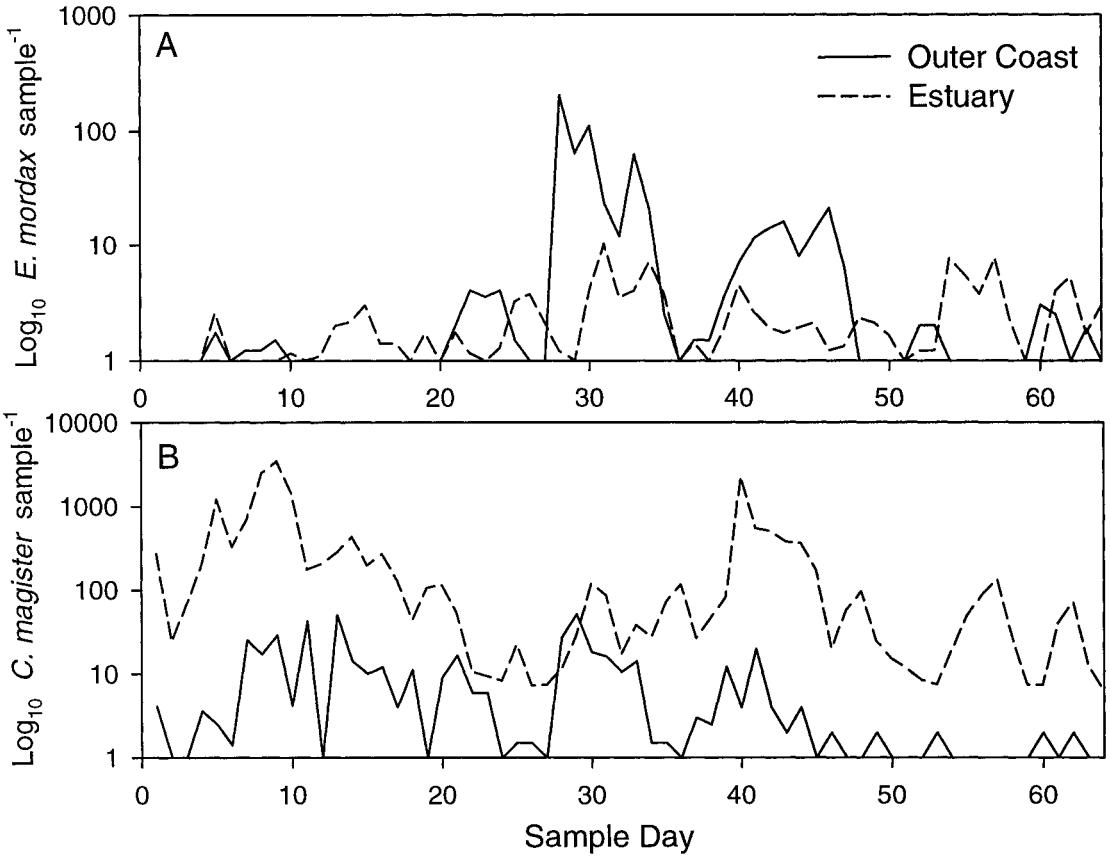

Fig. III.5. The log transformed abundance of (A) northern anchovy (*Engraulis mordax*) and (B) Dungeness crab (*Cancer magister*) collected per sample day (n = 64) during the 127 d study. Daily collections were summed over 2 d periods for comparison with samples collected every other day. Solid line represents the outer coast site. Dashed line represents the estuarine site.

Table III.4. Results of time-series analyses between biological and physical variables at the outer coast and estuarine sites. Lags represent days; the sign indicates whether peaks in the biological series occur after (negative values) or before (positive values) changes in the physical variable. Positive alongshore wind stress cross-correlatations indicate a relationship with northward winds, negative indicate southward winds. Postive cross-shore wind stress cross-correlations indicate eastward and negative indicate westward winds. Only statistically significant ($p \leq 0.05$) cross-correlations are presented. « ns » indicates no statistical significance. « -- » indicates insufficient data for analyses.

	Temperature	**Alongshore wind stress**	**Cross-shore wind stress**	**Upwelling index**	**Maximum tidal range**
Northern anchovy (*Engraulis mordax*)					
Outer Coast	ns	ns	ns	ns	+0 d = +0.272 +4 d = -0.369 -2 d = +0.266
Estuary	ns	+0 d = -0.251 -1 d = -0.235	ns	-2 d = +0.248	+2 d = -0.387 +3 d = -0.426 -3 d = +0.279 -4 d = +0.410
Dungeness crab (*Cancer magister*)					
Outer Coast	+0 d = -0.265	+0 d = -0.261	ns	-2 d = +0.352	+0 d = +0.265 +4 d = -0.309 -2 d = +0.302
Estuary	+0 d = -0.333 -1 d = -0.302	+0 d = -0.235 -1 d = -0.220	ns	-2 d = +0.256 -3 d = +0.263	+1 d = -0.285 +2 d = -0.317 -4 d = +0.246 -5 d = +0.299
Cancer crab (*Cancer oregonensis & productus*)					
Outer Coast	-4 d = -0.318	ns	ns	ns	+4 d = -0.289 -4 d = +0.297
Estuary	+ 0 d = +0.229 -1 d = +0.238	-4 d = +0.204	-4 d = -0.206	ns	ns
Hermit crab (*Pagurus* sp. A and sp. B)					
Outer Coast	ns	+0 d = +0.320	ns	-2 d = -0.257	ns
Estuary	--	--	--	--	--

Dungeness crab (*Cancer magister*)

The abundance of *Cancer magister* megalopae at the outer coast and estuarine site were significantly cross-correlated. Peaks in estuarine abundance occurred 0 and 2 d after peaks in outer coast abundance ($r = +0.39$ and $+0.42$, respectively, $p \leq 0.05$) (Fig. III.5B). However, significantly fewer *C. magister* were collected per sample at the outer coast (8.5 ± 1.8 SE) compared to the estuary (404.3 ± 137.7 SE) (Table III.2).

Cancer magister abundances at the outer coast and in the estuary were significantly cross-correlated with the tides (Table III.4). Significant cross-correlations between maximum tidal range and abundance occurred 0 to 2 d after spring tides at the outer coast and, in the estuary, between spring and neap tides. The abundance of *C. magister* megalopae at both the outer coast and estuarine site were significantly cross-correlated with lower water temperatures, negative alongshore wind stress (southward and upwelling-favorable), and positive upwelling indices (Table III.4). These data suggest that *C. magister* megalopae may be transported shoreward during active upwelling, spring tides, or both, and estuarine ingress can occur during upwelling events and/or between spring and neap tides.

Pygmy rock and red rock crab (*Cancer oregonensis* and *productus*)

The abundance of *Cancer oregonensis* and *productus* megalopae at the outer coast was not cross-correlated with abundance at the estuarine site. More individuals were collected at the outer coast site compared to the estuary but the difference was not statistically significant (Table III.2).

The abundance of *Cancer oregonensis* and *productus* megalopae at the outer coast site displayed a tidal periodicity; significant cross-correlations occurred between spring and neap tides (Table III.4). Abundance at the outer coast site was also significantly cross-correlated with cooler water temperatures. No tidal signal was evident at the estuarine site. Abundance in the estuary, however, was significantly cross-correlated with warmer water temperatures and, although weakly, southeasterly wind stress (downwelling favorable) (Table III.4). These data suggest that shoreward transport of post-larval *C. oregonensis* and *productus* may occur during upwelling and that downwelling conditions may promote estuarine ingress.

Hermit crabs (*Pagurus* spp.)

The total catch of *Pagurus* megalopae at the outer coast was 1489 individuals with an average sample abundance of 23.1 ± 11.3 SE individuals (Table III.2). Few *Pagurus* megalopae (< 5 total) were collected in the estuary. Therefore, no further statistical analyses were completed on the estuarine time series. *Pagurus* abundance at the outer coast was significantly cross-correlated with positive alongshore wind stress and negative upwelling indices (Table III.4), suggesting that *Pagurus* megalopae returned to the outer coast site after an upwelling relaxation or downwelling event.

Discussion

Relative Abundance

The data presented here provide evidence for temporal coupling between arrival at the outer coast and estuarine ingress for juvenile *Engraulis mordax* and *Sardinops*

sagax and *Cancer magister* megalopae. For these species, abundance in the estuary consistently peaked at the same time or shortly after (0 to -4 d lag) abundance at the outer coast. There were not enough *Pagurus* megalopae collected in the estuary to draw any conclusions regarding the relationship between shoreward transport and estuarine ingress.

For most taxa, the total abundance at the outer coast was greater or not different than that in the estuary. *Cancer magister* megalopae were the exception. In this case, estuarine collections were exceptionally large, > 4x larger than outer coast collections. This remarkable difference may indicate a preferential use of estuaries in this species.

Extensive research on estuarine use by late-stage larval and juvenile *Cancer magister* has occurred in Washington (Stevens & Armstrong 1984, McConnaughey et al. 1992, Eggleston et al. 1998). Only one study, however, directly compared abundance at the outer coast and in the estuary (Gunderson et al. 1990). Population estimates of *C. magister* juveniles, based on 5 years of trawl surveys from the Washington coast and two adjacent estuaries, were highly variable. There were typically more 0+ juveniles (i.e. those < 1 year old) along the outer coast than in the estuaries and more 1+ juveniles (i.e. those > 1 year old) within the estuary than along the outer coast (Gunderson et al. 1990). It is difficult to make further comparisons between their study, which used bi-monthly beam trawls to collect juveniles, and ours, which used light-trap collections of megalopae.

The other notable difference in species composition is that the average size of *Engraulis mordax* in the estuary (38.8 mm SL) was significantly smaller than at the outer

coast (57.2 mm SL) (Table III.3). Given that the size range of individuals in the estuary (21 – 71 mm) was similar to the size range at the outer coast (28 – 80 mm), size-dependent estuarine immigration may have occurred (i.e. proportionally more, smaller individuals entered the estuary). This fits an observed pattern of size dependent depth distribution in certain species where smaller fish are found in, and presumably moved to, shallower waters (Deegan 1990, Beck et al. 2001). Alternatively, larger individuals may have migrated back out of the estuary. The size range of *Sardinops sagax*, however, was also similar at both sites but the average size in the estuary (60.1 ± 7.3 mm SL) was greater than at the outer coast (50.9 ± 6.9 mm SL) (Table III.3). The significantly larger average size of *S. sagax* in the estuary is contrary to such a model and is less easily explained as an average of nearly 10 mm of growth is unlikely to occur in 2 d.

One concern with the light trap deployment in this study is that the outer coast traps were tethered to buoys whereas the estuarine traps were attached to floating docks. Fishes and invertebrates at all life history stages have been shown to congregate around docks, pilings, and other floating objects (Hunter 1967, Kingsford 1999). Although we cannot rule out a possible dock effect in our study, we note that if it did occur, then it occurred only in *Cancer magister,* as all other species were collected in similar or greater numbers at the outer coast site. We know of no reason why such an effect would occur preferentially in *C. magister.*

Transport mechanisms

Tidal transport

Evidence for transport driven by the tides was found in all taxa except *Pagurus* spp. For both *Engraulis mordax* and *Cancer magister*, abundance at the outer coast tended to peak around spring tides while abundance in the estuary peaked between spring and neap tides. The outer coast abundance of *C. oregonensis* and *productus* megalopae peaked between spring and neap tides and no tidal signal was evident in the estuary. What can explain these patterns? Modeling efforts have shown that net horizontal displacement of zooplankton may occur in the presence of oscillatory tidal currents and daily vertical migrations (Hill 1998). However, if shoreward transport occurred solely due to tidal-stream transport, abundance patterns would more likely be proportional to water flux, and therefore tidal range. We did not see evidence of this in our data (e.g. Fig. III.3A). Rather, we saw relatively large, discrete peaks in abundance, which suggests that shoreward transport in these species was probably not promoted solely by tidal-stream transport. Another potential mechanism of shoreward transport, possibly in conjunction with tidal-stream transport, is non-linear internal tides and bores. Increased concentrations of larval fish and invertebrates (Shanks 1983, Shanks & Wright 1987, Shanks 1988, Pineda 1991, 1994, Shanks 1995, 1998), juvenile fish (Kingsford & Choat 1986), and small adult fish (Rogachev et al. 1996) have been observed in slicks associated with internal waves and bores. Tidal frequencies have also been identified in the near-shore abundance of larval invertebrates and fish observed in surface slicks

associated with internal waves (Shanks 1983, Shanks & Wright 1987, Shanks 1998). Therefore, it is possible that enhanced shoreward transport of organisms via internal waves and bores, in combination with tidal-stream transport, could have generated the abundance patterns that we observed.

Wind-driven transport

We present evidence for wind-driven transport in *Engraulis mordax*, *Cancer magister*, *C. oregonensis* and *productus*, and *Pagurus* spp. Peaks in species abundance occurred during upwelling-favorable winds, during downwelling-favorable winds, or with no relation to prevailing wind stress. The abundance of *C. magister* megalopae was significantly cross-correlated with upwelling-favorable winds, colder water, and positive upwelling indices at both the outer coast and estuarine site. For *C. oregonensis* and *productus* megalopae, abundance at the outer coast was significantly cross-correlated with colder water temperatures. Juvenile *E. mordax* abundance in the estuary was also related to indicators of upwelling, including upwelling-favorable winds and positive upwelling indices. The only evidence for transport to the outer coast during downwelling was found in the *Pagurus* spp., whose outer coast abundance was significantly cross-correlated with northward alongshore wind stress and negative upwelling indices. In the estuary, post-larval *C. oregonensis* and *productus* showed some, although weak, relationships with indicators of downwelling. Overall, these data indicate that shoreward transport and estuarine ingress may occur during both upwelling and downwelling.

However, we found more evidence for transport during periods of upwelling rather than downwelling conditions.

The cyclic nature and commercial value of *Cancer magister* populations have resulted in a considerable amount of research on their settlement and recruitment (Peterson 1973, Hatfield 1983, Johnson et al. 1986, Wing et al. 1995a, Wing et al. 1995b, Johnson and Shanks 2002, Roegner et al. 2003). Numerous attempts to relate physical conditions during various life history stages to adult harvest have yielded equivocal results. Cross-correlations between adult harvest and upwelling winds were found at a variety of lags, from 6 mos to 5 years (Peterson 1973, Johnson et al. 1986, McConnaughey et al. 1992, Wing et al. 1995a, Wing et al. 1995b). Johnson et al. (1986), for example, found significant correlations between upwelling favorable wind stress and adult harvest at lags of 4 and 5 years along northern California, Oregon, and Washington. The authors note that the observation may result from "onshore transport during the late larval phase" although "the exact mechanisms are unknown." Our data suggest that the shoreward transport of post-larval *C. magister* and *C. oregonensis* and *productus* can occur during active upwelling.

How might shoreward transport be promoted during a period of predominantly offshore surface transport? Huyer (1976) found that during upwelling-favorable winds on the Oregon coast, offshore flow occurred in a shallow surface layer less than 20 m thick. Onshore flow was strongest immediately below that surface layer and decreased with depth in the lower portion of the water column. Furthermore, the direction of movement

of the very near surface waters (upper centimeters) is typically less than the 45° shift from the prevailing wind direction predicted by Ekman theory and can be much closer to the actual wind direction (Brown et al. 1989). Thus, the northwesterly winds that generate upwelling could push very near surface waters and associated neustonic organisms shoreward and can result in the shoreward movement of water below the Ekman layer. Shoreward transport could occur during upwelling if organisms were below the surface layer or in the neuston.

The abundance of post-larval *Cancer oregonensis* and *productus* in the estuary and *Pagurus* spp. at the outer coast were significantly cross-correlated with indicators of downwelling. The shoreward transport of *Pagurus* spp. may be related to relaxation of the upwelling front and associated shoreward movement of water (Roughgarden et al. 1988, Shanks et al. 2000). The estuarine ingress of *C. oregonensis* and *productus* may be related to downwelling winds forcing surface waters into the estuary after individuals entered near-shore waters (Johnson & Shanks 2002).

We found tidal periodicities and evidence for wind driven transport, both upwelling- and downwelling-related, in the abundance of juvenile fish and crab megalopae at the outer coast and estuarine sites. It has been proposed that, in upwelling regions, species with pelagic larvae and relatively long dispersal periods, should reproduce primarily during the downwelling season to avoid advection offshore due to upwelling generated Ekman transport (Parrish et al. 1981). Numerous species, including those in this study, have larvae in coastal waters during the upwelling season, i.e. from

late April-May through September off the Oregon coast. There has been an emphasis on the importance of upwelling relaxations, which allow waters associated with the upwelling front to move towards shore, in returning individuals to shore (Roughgarden et al. 1988, Wing et al. 1995a, Wing et al. 1995b, Shanks et al. 2000). We suggest, and our data support, that successful shoreward transport can also occur during periods of active upwelling. Organisms, depending on their depth distribution, may be transported on- or offshore during active upwelling. Emphasis on only one mechanism may be insufficient to consistently explain shoreward transport and successful settlement.

The delivery of material to the coast and its exchange between outer coastal and estuarine areas are key components of coastal, estuarine, and population ecology. Mechanisms of larval transport are under investigation due to their importance in the determination of population size and structure. This study, which is one of the first to simultaneously document post-larval crab and juvenile fish abundance at an outer coastal and adjacent estuarine site, identified strong coherence in the peak abundance of *Engraulis mordax*, *Sardinops sagax*, and *Cancer magister* at the two sites. We also found evidence for tidal and wind-driven transport at both locations. These data support the idea that estuarine ingress is a two-stage process and indicate that both wind-driven and tidal transport mechanisms contributed to the shoreward transport and estuarine ingress of post-larvae and juveniles. Further investigation on individual behaviors, including depth distribution and vertical migrations, is needed to determine more specifically how such

behaviors interact with physical processes to regulate shoreward transport and estuarine ingress.

Bridge

The following chapter, Chapter IV, "Evidence for limited larval dispersal in black rockfish (*Sebastes melanops*): implications for population structure and marine reserve design," presents a different technique for examining larval dispersal, otolith elemental microchemistry. This technique, in conjunction with otolith microstructure analysis, was used to provide information on the relative movements of black rockfish larvae. The study presented in Chapter IV is published in the *Canadian Journal of Fisheries and Aquatic Sciences*, authored by myself and A. L. Shanks. I completed all of the field and laboratory work, data analysis, and writing for the manuscript.

Chapter IV

Evidence for limited larval dispersal in black rockfish (*Sebastes melanops*): implications for population structure and marine reserve design

Introduction

Information on larval dispersal distances is rare for marine species (Shanks et al. 2003). Yet dispersal distances of marine larvae affect gene flow and the geographic range and persistence of populations and species (Jablonski 1986; Sinclair 1988; Strathmann et al. 2002). The concept of a population, or "a group of individuals of the same species that live together in an area of sufficient size to permit normal dispersive and/or migration behavior," is integral to ecology and essential for effective conservation and management (Berryman 2002). However, the data currently available on "normal dispersive and migratory behavior" are insufficient to define realistic spatial scales for nearly all marine populations.

Accurate, empirical estimates of larval dispersal distances have been hampered by inadequate analytical techniques. Individual tagging studies are expensive, logistically difficult, and typically not feasible for larval stages, during which mortality often exceeds 90% (but see Jones et al. 1999). Although genetic techniques can underestimate the

extent of population structure and offer only indirect information on larval sources and dispersal distances (Kinlan and Gaines 2003; Palumbi 2003), there is evidence for population structure in some *Sebastes* (rockfish) species on relatively small spatial scales, i.e. from 200 km to 900 km apart (Buonaccorsi et al. 2002; Roques et al. 2002; Withler et al. 2001). Such studies hypothesize that limited larval dispersal may be one mechanism contributing to the genetic divergence observed (Buonaccorsi et al. 2002; Roques et al. 2002; Withler et al. 2001).

Assumptions regarding larval dispersal in marine populations include that (1) dispersal is primarily passive, (2) dispersal distances are typically long, (3) recruitment into a population comes from outside sources, and, therefore, (4) populations are primarily open (Cowen et al. 2000). Recent empirical evidence suggests that larval retention around islands and reefs may be more common in species with planktotrophic larvae than previously believed (Scheltema et al. 1996; Swearer et al. 2002; Taylor and Hellberg 2003). The extent of self-recruitment in species with extended pelagic larval periods that reside along continental margins, however, is not known. Current management efforts, such as the establishment of marine protected areas (MPAs) for both the maintenance of biodiversity and population recovery efforts, are hampered by the "current paucity of information regarding meroplanktonic larval transport processes" (Lockwood et al. 2002).

Black rockfish (*Sebastes melanops*) range from the Aleutian Islands, Alaska to southern California. Commercial and recreational harvest began in the late 1800s and

continues today. *S. melanops*, combined with blue rockfish (*S. mystinus*), comprised over 90% of Oregon's recreational harvest in 2001 and 2002 (Oregon Department of Fish and Wildlife catch statistics). However, new restrictions were recently placed on both recreational and commercial harvest to minimize harvest impacts on Oregon populations (PMCC 1999; ODFW 2003). These long-lived (≤ 50 years), viviparous fish commonly occur in waters < 55 m in depth and reach sexual maturity between 3 and 9 years old (Cailliet et al. 2001; Love et al. 2002). Larvae and juveniles are pelagic for 3 - 6 months, although areas of parturition are unknown. Benthic juveniles initially settle in shallow waters and move into deeper waters as they grow (Love et al. 2002).

Teleost otoliths grow by continuous deposition of calcium carbonate with no evidence of resorption. At the time of deposition, certain trace elements accumulate within otoliths in proportion to seawater concentrations (Bath et al. 2000; Campana 1999; Elsdon and Gillanders 2003). Therefore, otolith elemental composition can reflect ambient water conditions at the time of deposition. Laser ablation inductively coupled plasma mass spectrometry (LA-ICPMS) allows elements to be measured along the otolith growth axis to provide a chronological record of trace-element deposition. Comparisons of trace elements along the growth axis of fish collected in different areas may yield information about the relative distances larvae dispersed.

Unique geochemical signatures have been documented in otoliths of marine fish collected from estuaries and along cross-shelf gradients (Gillanders 2002a; Swearer et al. 1999; Thorrold et al. 1998). Similarly, studies on coastal water chemistry typically focus

within estuaries or along cross-shelf and depth gradients (Chester 1990; Flegal et al. 1991; Munksgaard and Parry 2001). Although there is some evidence of alongshore gradients in certain trace metals (Sanudo Wilhelmy and Flegal 1991), it is not yet clear whether, or how, otolith elemental composition varies on alongshore gradients. Trace-metal concentrations in seawater vary depending on external inputs (atmosphere and river), physical factors (upwelling, wind mixing), and biological processes (uptake and regeneration) (Cotte-Krief et al. 2002). These factors, i.e. riverine inputs, upwelling intensity, and biological community composition, vary alongshore in marine environments. Therefore, I hypothesized that there would be variation in the otolith chemistry of *S. melanops* collected along the Washington and Oregon coast.

Otolith microchemistry studies typically employ one of two approaches when examining population structure, or connectivity (Thresher 1999). One approach typically samples adults across a relatively broad region and searches for geographic groupings based on otolith geochemical signatures and, in many ways, is similar to a genetic approach. The other approach attempts to characterize geographic source signatures in otoliths of larvae or juveniles, collect dispersed adults at a later time, and then identify the source of those adults by matching the chemical signatures at their otolith cores, which represent natal origins, with those previously observed in larvae and juveniles. These efforts are based on a number of assumptions. A primary and relatively well established assumption is that otolith growth is continuous with no evidence of resorption, and thus provides a permanent chronological record (Campana 1999;

Campana and Thorrold 2001; Thresher 1999). The other major assumption, although not as well-verified, is that if fish reside in water masses with different chemical properties, those properties will be reflected in otolith microchemistry (Campana and Thorrold 2001; Thresher 1999).

In this study, I combined aspects of the two common approaches described above. I used otolith elemental composition as a relative indicator of larval and juvenile movement. I did not attempt to identify specific larval sources. Rather, I used otolith elemental composition of black rockfish (*Sebastes melanops*), a northeast Pacific species with an extended (3 - 6 months) pelagic larval and juvenile period, in conjunction with microstructure analyses, to determine if I could generate relative estimates of alongshore dispersal distance. To do this, I compared otolith geochemical signatures at three discrete positions along the otolith growth axis throughout the early life history of fish from different geographic locations.

The varied geology of the Washington and Oregon coast may contribute to alongshore differences in the elemental composition of otoliths in coastal fishes. Sediments from the Columbia River dominate coastal waters from Grays Harbor, Washington to Tillamook Head, Oregon (Komar 1997) (Fig. IV.1). Oregon's Coast Mountain Range extends from the Columbia River southward to the Klamath Mountain Range (Orr et al. 1992). These mountains have different geologies, and the volcanic rocks are of different age and mineralogy. Alongshore differences in salinity and silicate concentrations, primarily due to freshwater discharge from the Columbia River, occur

between Oregon's north and south coast (Landry et al. 1989). In this study, I determined if the trace-element composition of *S. melanops* otoliths varied alongshore and throughout the ontogeny.

Sebastes melanops larvae and pelagic juveniles are found associated with upwelling fronts but are also found landward and seaward of such fronts (Larson et al. 1994). In Oregon, larval release typically occurs between February and May and juveniles are found nearshore, and occasionally, in estuaries beginning in June (Love et al. 2002). Hence, early in black rockfish larval development, alongshore flow in the California Current system is predominantly poleward due to the Davidson Inshore Counter Current. The subsequent 3 to 6 month pelagic phase extends throughout the spring transition and the initiation of the upwelling season when dominant flow over the shelf is equatorward (Strub et al. 1987). If larval dispersal is widespread with extensive (> 1 month) periods near the upwelling front, I predicted that otolith elemental signatures from discrete life history periods would not be useful for discriminating fish based on collection locations. If otolith elemental signatures from discrete periods classify fish to their collection location, then fish most likely stayed together relative to the other collection locations (i.e. did not mix), did not move appreciable distances alongshore, or both. Alternatively, fish collected at the same location may have followed similar dispersal pathways. Otolith microstructure analysis provided information on the timing of parturition, individual age, and otolith growth to aid interpretation of otolith geochemical signatures.

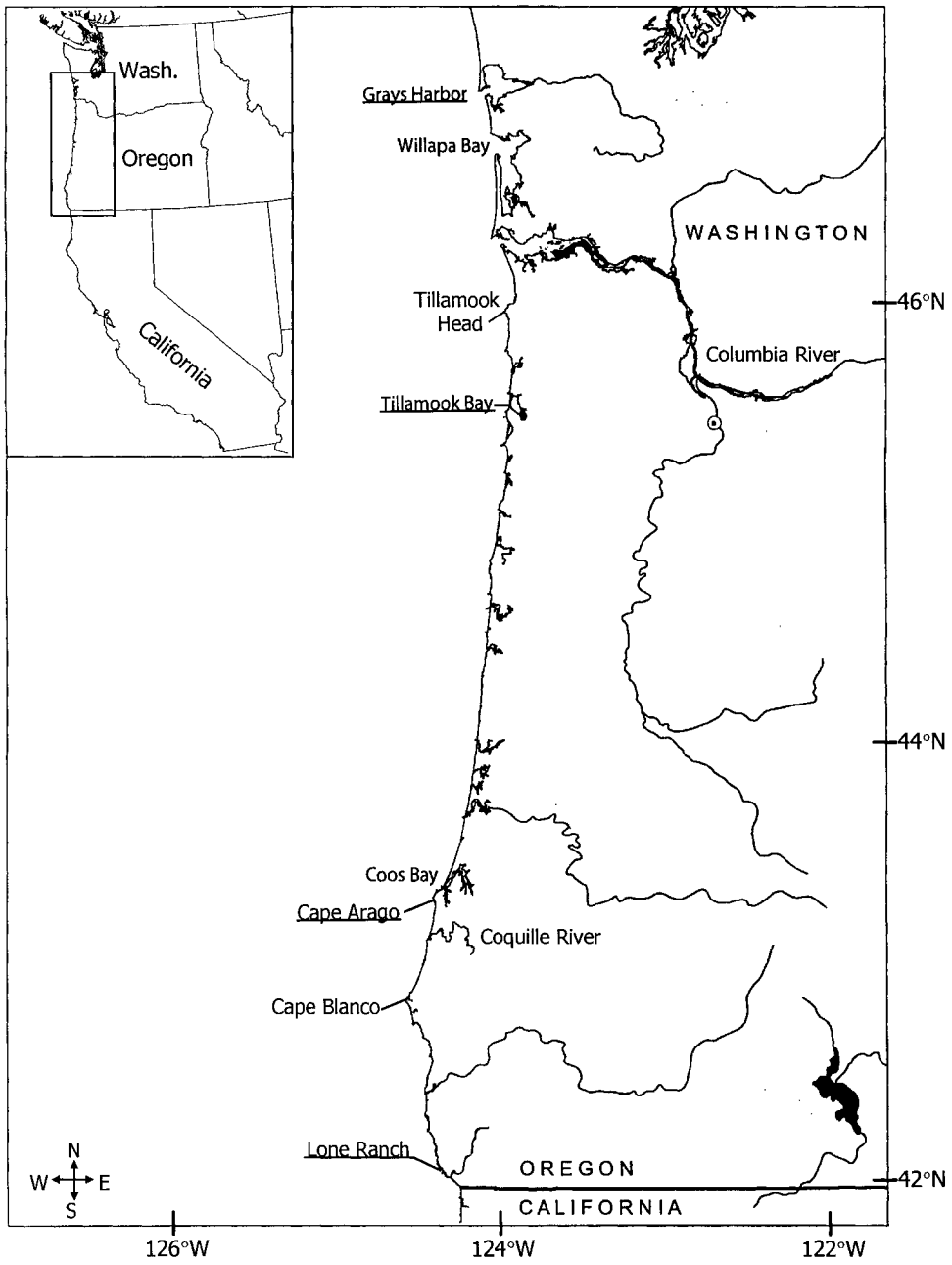

Fig. IV.1. Geographic locations (underlined) where juvenile black rockfish (*Sebastes melanops*) were collected. In 2001, juveniles were collected from 1) the mouth of Grays Harbor, Washington (46° 53'25"N, 124° 06'10"W), 2) Cape Arago, Oregon (43° 18'10"N, 124° 23'45"W), and 3) Lone Ranch Beach, Oregon (42° 05'55"N, 124° 20'30"W). In 2002, juveniles were collected from 1) the mouth of Tillamook Bay, Oregon (45° 33'36"N, 123° 54'35"W), 2) Cape Arago, and 3) Lone Ranch Beach. The closest sites, Cape Arago and Lone Ranch, were 120 km apart and the most distant were 460 km and 330 km apart, in 2001 and 2002, respectively.

Methods

The hypotheses that 1) the elemental signatures of *S. melanops* otoliths vary geographically alongshore and 2) the elemental signatures of fish collected within sites are more similar than between sites were tested with juveniles collected at three locations ranging from 120 – 460 km apart in 2001 and 120 – 330 km apart in 2002 (Fig. IV.1). To compare elemental signatures from various periods in the fish's life, I examined, on each otolith, three laser ablation transects. These transects were located at 1) the otolith core, 2) its outer edge, and 3) midway between the core and edge. The transect at the otolith core was 25 μm while the transects at the outer edge and midway between the core and edge were 120 μm. Daily otolith-increment width ranged from 1 μm to 11 μm (average 6 μm), with smaller increment widths located in the core region. The 25 μm transect represented, on average, the maternal incubation period plus 7 d post-parturition while each 120 μm long transect represented, on average, a 20 d period. Due to the viviparous nature of this species, the core transect is laid down during incubation of the embryo within the mother (mean otolith radius of 11.3 μm; see **Fish collection and otolith preparation** below) and very early larval stages (an average of 13.7 μm). The otolith core transect is hereafter referred to as the "early larval" elemental signature. The pelagic larval period, or "larval" elemental signature, was characterized by the transect midway between the early larval and edge signatures. The edge transect characterized the juvenile stage, or "juvenile" elemental signature.

At each sampling location, all fish were collected on the same day. Individuals collected within a site were exposed to the same water immediately prior to collection. Hence, the juvenile elemental signatures within a site may be the most similar and are most likely to yield accurate geographic classifications. If elemental signatures from the early larval and larval periods also classify a high percentage of fish to collection location, it is probable that fish either stayed together, relative to the other collection locations, during the pelagic larval phase, did not move appreciable distances, or both. Alternatively, fish from the same collection locations may have followed similar dispersal pathways.

Fish collection and otolith preparation

Juveniles were collected by seine in nearshore kelp beds between 14 July and 3 August 2001 and 11 and 16 June 2002. Fish were immediately measured to nearest 0.1 mm. Sagittal otoliths were removed on the day of collection (2002) or fish were frozen (< 2 months) prior to otolith removal (2001). Otoliths were removed with acid-washed plastic forceps, cleaned, weighed (to the nearest 0.01 mg), measured (to the nearest 0.1 mm), embedded and ground to expose the otolith core. Otoliths were ultrasonically cleaned in NANOpure® water, dried, and stored in acid-washed plastic vials prior to embedding in resin. Otoliths were ground with 3M™ Tri-m-ite wetordry™ paper (240 to 1200 grit), polished with Buehler AlO_2 powder (12.5 µm and 3.0 µm), and again cleaned ultrasonically for 15 min.

Yoklavich and Boehlert (1987) validated daily otolith increment deposition in juvenile *S. melanops*. Therefore, I was able to determine individual ages with otolith microstructure analysis. Polished otoliths were examined under oil immersion at 1000x magnification with a Leitz Laborlux S compound microscope. Laidig and Ralston (1995) identified a dark check at the edge of the nuclear radius in juvenile otoliths of eight *Sebastes* spp. Check marks were located at species specific radii, ranging from 10.93 μm to 16.96 μm. Ralston et al. (1996) verified, for shortbelly rockfish (*S. jordani*), that the check mark was an extrusion, or parturition, check. I consistently observed a distinct check mark on *S. melanops* otoliths at a radius of 10.6 - 12.5 μm, with a mean of 11.3 μm. Therefore, I interpreted the check mark as a parturition mark and counted increments, each representing one day, from that mark to the otolith's distal edge. If a check mark was not visible, increment counts began at a radius of approximately 11 μm. Otolith counts were independently determined three times. Parturition dates were then determined for each individual. In some cases, fewer individuals were aged than were used in microchemistry studies due to the inability to adequately discern all growth increments.

Optimas image analysis software (version 6.0) and a Laborlux S compound microscope at 400x magnification were used to visualize and measure otolith increments within the larval and juvenile transects. A minimum of 15 otolith-increment widths were measured within each transect. No measurements were taken for the early larval transect because of its short length and poor increment resolution. Individual and site averages

were generated for the larval and juvenile transects in both 2001 and 2002. Analysis of variance (ANOVA) was used to determine if there were significant differences in increment width among locations within years.

Trace-element analysis

All LA-ICPMS work was completed at the Oregon State University's WM Keck Collaboratory for Plasma Spectrometry, Corvallis, Oregon. A VG PQ ExCell ICPMS with a New Wave DUV193 excimer laser was used for all analyses. The laser was set at a pulse rate of 15 Hz and a 45 μm and 40 μm spot ablation were used in 2001 and 2002, respectively. The small change in the ablation spot size between years was due to changes in the PlasmaLab® laser software. The high calcium content of otoliths can cause significant buildup inside the sample chamber and quadrupole. In order to avoid biased data collection, background levels of ^{43}Ca were monitored for accumulation in the spectrometer and skimmer cones and gas tubing were cleaned daily. I collected no data during a period with elevated background calcium levels.

Time-resolved software (PlasmaLab®) allowed analyte (i.e. ^{25}Mg, ^{43}Ca, etc.) measurements to be made at discrete positions on the otolith and integrated and averaged for each element collected. Preliminary data analyses indicated no difference in analyte concentrations between left and right otoliths (paired t-tests, $n = 5$, $p > 0.20$, df = 9). Only left otoliths, however, were used in all subsequent analyses. Further analyses indicated no difference in analyte concentrations between transects in the different otolith quadrants (paired t-tests, $n = 6$, $p > 0.10$, df = 9). All subsequent transects were located in the

anterior dorsal quadrant and extended from the core to the otolith edge. Preliminary analyses of otoliths indicated that the following ten analytes were at concentrations that were well above background levels: ^{25}Mg, ^{43}Ca, ^{48}Ca, ^{55}Mn, ^{66}Zn, ^{86}Sr, ^{87}Sr, ^{138}Ba, and ^{208}Pb. The average %RSD (relative standard deviation) for National Institute of Standards and Technology (NIST) glass plates during data collection were as follows : ^{25}Mg = 11.3%, ^{43}Ca = 5.6%, ^{48}Ca = 5.6%, ^{55}Mn = 6.4%, ^{66}Zn = 8.4%, ^{86}Sr = 7.7%, ^{87}Sr = 7.3%, ^{138}Ba =7.5%, ^{208}Pb = 9.2%. The variation in the average %RSD between the 25 μm and 120 μm transects was less than 1.5%. The VG PQ ExCell ICPMS minimum detection levels are 1-10 parts per trillion (ppt) for Mg, Ca, Mn, and Zn and < 0.1 – 1 ppt for Sr, Ba, and Pb.

Trace-element compositions in NIST glass standards are homogenous and elemental concentrations are reported in Pearce et al. (1997). A NIST standard was run with each otolith sample; this allowed all otolith transects to be standardized to account for instrument drift or day-to-day variations in instrument sensitivity across the atomic mass range. Background analyte levels were determined with an argon gas blank prior to each transect and subtracted from both mean otolith and NIST glass slides measurements. Elemental data (in counts per second) were standardized by ^{43}Ca to adjust for variability in instrument sensitivity and the amount of ablated material (Campana et al. 1997). Measured element to calcium ratios from NIST glass slides were then multiplied by known average NIST concentrations to generate a correction factor. Otolith element to calcium ratios were then multiplied by the NIST correction factor collected at the same

time as the otolith measurement. Standardized ratios were transformed to attain normality and homogeneity of variance. The only case in which the variance among collection sites could not be stabilized was for ^{25}Mg (Levene's test, $F_{2, 67} = 3.8$, $p = 0.02$) in the 2002 juvenile signatures. The removal of one outlier from Tillamook Bay (i.e. $^{25}Mg \bullet {}^{43}Ca^{-1} > 3$ standard deviations from the mean) stabilized the variance (Levene's test, $F_{2, 67} = 2.7$, $p > 0.07$).

Statistical analysis

ANOVA was used to compare the element to calcium ratios among sites within each otolith region in 2001 and 2002. Quadratic discriminant function analysis (DFA) was then used to group individuals based on their elemental signatures at each otolith region. Jackknifed classifications were calculated with the removal of one observation, a total of N times (N = 55 and 70, in 2001 and 2002, respectively) and averaged. The best validation of a discriminant function classification is the assignment of new cases (i.e. those not used in the development of the original classification algorithm). Jackknifed predictions are used to provide a more realistic estimate of the ability of the predictor variables to separate groups when sample sizes are not large enough to generate two independent datasets. I also used the classification algorithm based only on the early larval otolith signatures to predict collection location of individuals using either the larval or juvenile signatures. In this case, the larval and juvenile signatures were treated as new cases and, therefore, jackknifed classifications were not generated. Statistica® and Systat® statistical software programs were used for the above analyses.

Results

Otolith microstructure

There was no significant difference in the total length (TL) of juveniles among sites within years (ANOVA, 2001: $F_{2, 47} = 1.8$, $p = 0.18$; 2002: $F_{2, 69} = 0.23$, $p = 0.79$) (Table IV.1). The average age of individuals and thus parturition dates, however, varied significantly among sites (ANOVA, 2001: $F_{2, 47} = 13.3$, $p < 0.001$; 2002: $F_{2, 69} = 24.3$, $p < 0.001$) (Table IV.1). The differences in age within sites ranged from a minimum of 22 d to a maximum of 66 d. Therefore, each site included fish of a range of individual ages and parturition dates.

In 2001, average daily increment width was 7.5 ± 0.8 µm (± standard deviation) during the larval period and 4.8 ± 1.6 µm during the juvenile period (Table IV.2). In 2002, average daily increment width was 7.2 ± 0.2 µm during the larval period and 6.5 ± 0.1 µm during the juvenile period (Table IV.2). The only significant difference in average otolith-increment width occurred during the juvenile period in 2001; Grays Harbor increment width was significantly smaller than either Cape Arago or Lone Ranch (ANOVA, $F_{2, 35} = 24$, $p < 0.001$) (Table IV.2).

Table IV.1. Mean and range for size (mm), age (d), and parturition dates (± standard error) of juvenile black rockfish (*Sebastes melanops*). Age and parturition dates were determined from otolith microstructure. Date of collection, collection location, and sample sizes (*n*) are included. TL = total length.

2001	**Grays Harbor** (*n* = 11)	**Cape Arago** (*n* = 13)	**Lone Ranch** (*n* = 10)
Mean size (TL - mm)	61.0 ± 1.4	58.6 ± 0.9	61.4 ± 1.5
Size (range - mm)	58 – 66	51 – 68	51 – 70
Mean Age (d)	153.5 ± 3.2	117.8 ± 2.9	133.0 ± 3.3
Age (range - d)	131 - 173	105 - 143	108 - 174
Date of collection	3 August	14 July	26 July
Parturition date (mean)	4 March	18 March	12 March
Parturition date (range)	11 Feb. – 25 Mar.	21 Feb. – 31 Mar.	2 Feb. – 9 Apr.
2002	**Tillamook Bay** (*n* = 15)	**Cape Arago** (*n* = 24)	**Lone Ranch** (*n* = 23)
Mean size (TL - mm)	53.4 ± 0.6	53.2 ± 0.5	52.8 ± 0.6
Size (range - mm)	49 – 59	47 – 60	47 – 60
Mean Age (d)	113.0 ± 1.74	108.5 ± 1.38	98.4 ± 1.44
Age (range - d)	107 - 129	98 - 125	83 - 108
Date of collection	16 June	11 June	12 June
Parturition date (mean)	23 February	22 February	6 March
Parturition date (range)	7 Feb. – 1 Mar.	6 Feb. – 5 Mar.	24 Feb. – 21 Mar.

Table IV.2. 2001 and 2002 average otolith-increment width (μm) x 10^3 (± standard deviation) during the larval and juvenile life history period. ** indicates statistically significant difference at $p < 0.001$. CA = Cape Arago, LR = Lone Ranch, GH = Grays Harbor, and TB = Tillamook Bay.

Otolith-increment width (μm) x 10^3		
2001	**Larval**	**Juvenile**
GH	6.7 ± 1.3	3.0 ± 1.3**
CA	7.6 ± 1.2	6.2 ± 0.8
LR	8.2 ± 1.8	5.2 ± 1.6
2002		
TB	7.1 ± 1.5	6.4 ± 1.4
CA	7.1 ± 1.2	6.5 ± 1.4
LR	7.4 ± 1.3	6.5 ± 1.5

Otolith microchemistry

There were statistically significant differences in otolith elemental composition among sites in both years (Table IV.3). In both 2001 and 2002, ^{25}Mg and ^{208}Pb varied significantly among sites at all three otolith regions while ^{55}Mn varied only during the juvenile period. ^{66}Zn, ^{87}Sr, and ^{138}Ba varied significantly among sites at one or two otolith regions in 2001 (ANOVA, $F_{2, 52} > 5$, $p \leq 0.05$) (Fig. IV.2) and in 2002 (ANOVA, $F_{2, 67} > 7$, $p \leq 0.05$) (Table IV.3). Some elements displayed intra-annual variation among otolith regions (i.e. $^{138}Ba \bullet {}^{43}Ca^{-1}$ in 2001 and 2002) (Fig. IV.2 and IV.3).

The goal of discriminant function analysis (DFA) is to predict group membership from a set of predictors (Tabachnick and Fidell 2001). Ideally, the analysis identifies the fewest predictors that generate the greatest discrimination. In 2001, ^{25}Mg, ^{66}Zn, ^{87}Sr, ^{138}Ba, and ^{208}Pb generated the most accurate classification and, in 2002, ^{25}Mg, ^{66}Zn, ^{87}Sr, and ^{208}Pb. All elements included contributed significantly to the classification model ($F > 2.0$, $p < 0.01$).

Table IV.3. Elements used in discriminant function analyses and the statistical transformations (in parentheses) used to attain normality and homogeneity of variance. The year of collection and otolith region (i.e. early larval, larval, and juvenile) are included. * indicates statistically significant differences among collection location at $p \leq 0.05$, ** indicates $p \leq 0.01$, and ns = no statistical difference. Analysis of variance (ANOVA) was used to determine significance.

	2001 Otolith region			**2002 Otolith region**		
Element	**Early larval**	**Larval**	**Juvenile**	**Early larval**	**Larval**	**Juvenile**
^{25}Mg ($1/^{25}Mg$)	**	**	**	**	**	**
^{55}Mn ($\log_{10}{}^{55}Mn$)	ns	ns	**	ns	ns	*
^{66}Zn ($\log_{10}{}^{66}Zn$)	ns	*	ns	**	**	**
^{87}Sr ($\log_{10}{}^{87}Sr$)	**	**	ns	ns	**	*
^{138}Ba ($\log_{10}{}^{138}Ba$)	ns	ns	*	ns	**	**
^{208}Pb ($\log_{10}{}^{208}Pb$)	**	**	**	**	**	**

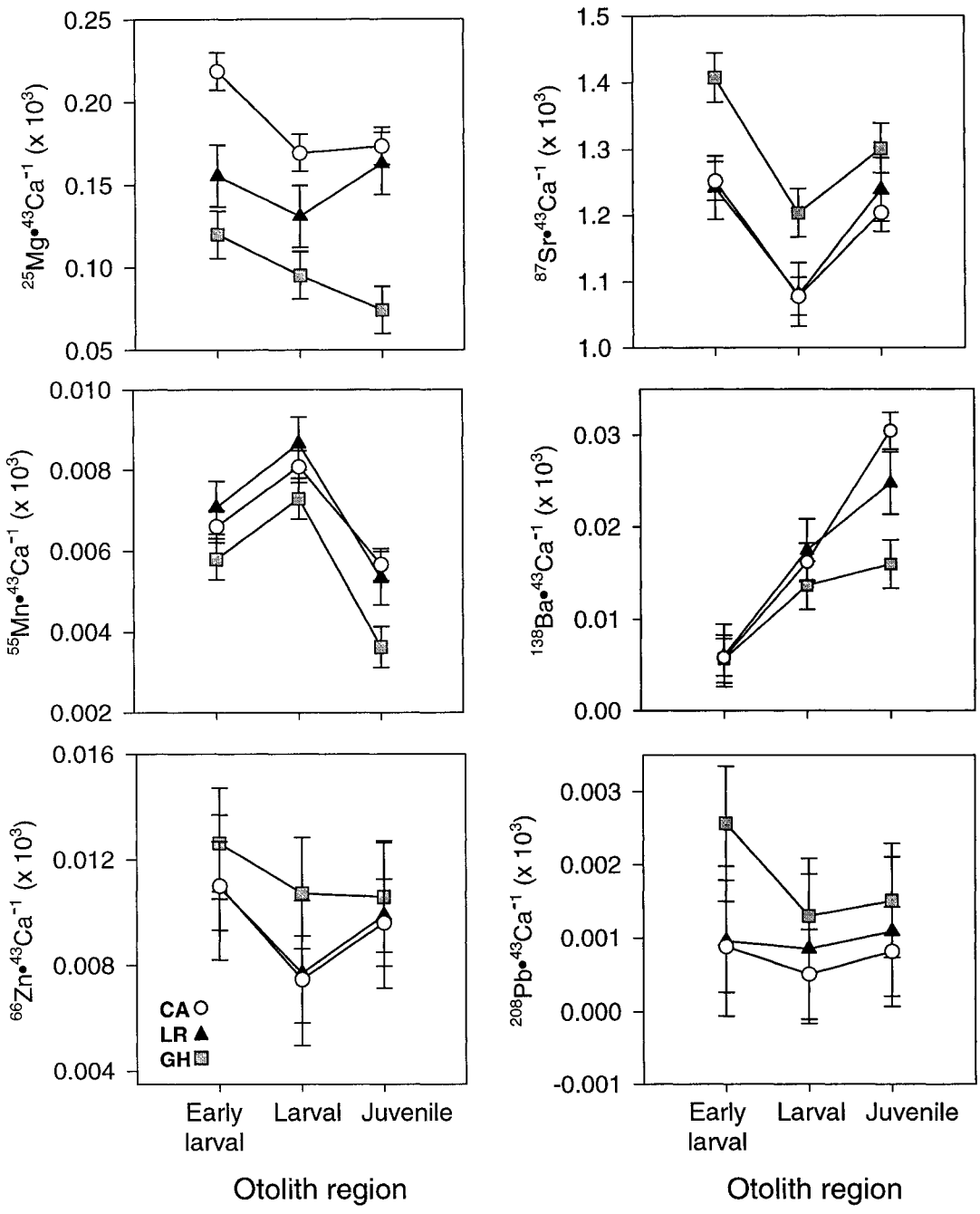

Fig. IV.2. The 2001 untransformed elemental ratios (10^3) measured in *Sebastes melanops* otoliths. ^{25}Mg, ^{55}Mn, ^{66}Zn, ^{87}Sr, ^{138}Ba, and ^{208}Pb are presented. Values are site averages (± standard error) for the early larval, larval, and juvenile otolith regions at Cape Arago (CA, open circles), Lone Ranch (LR, black triangles), and Grays Harbor (GH, gray squares).

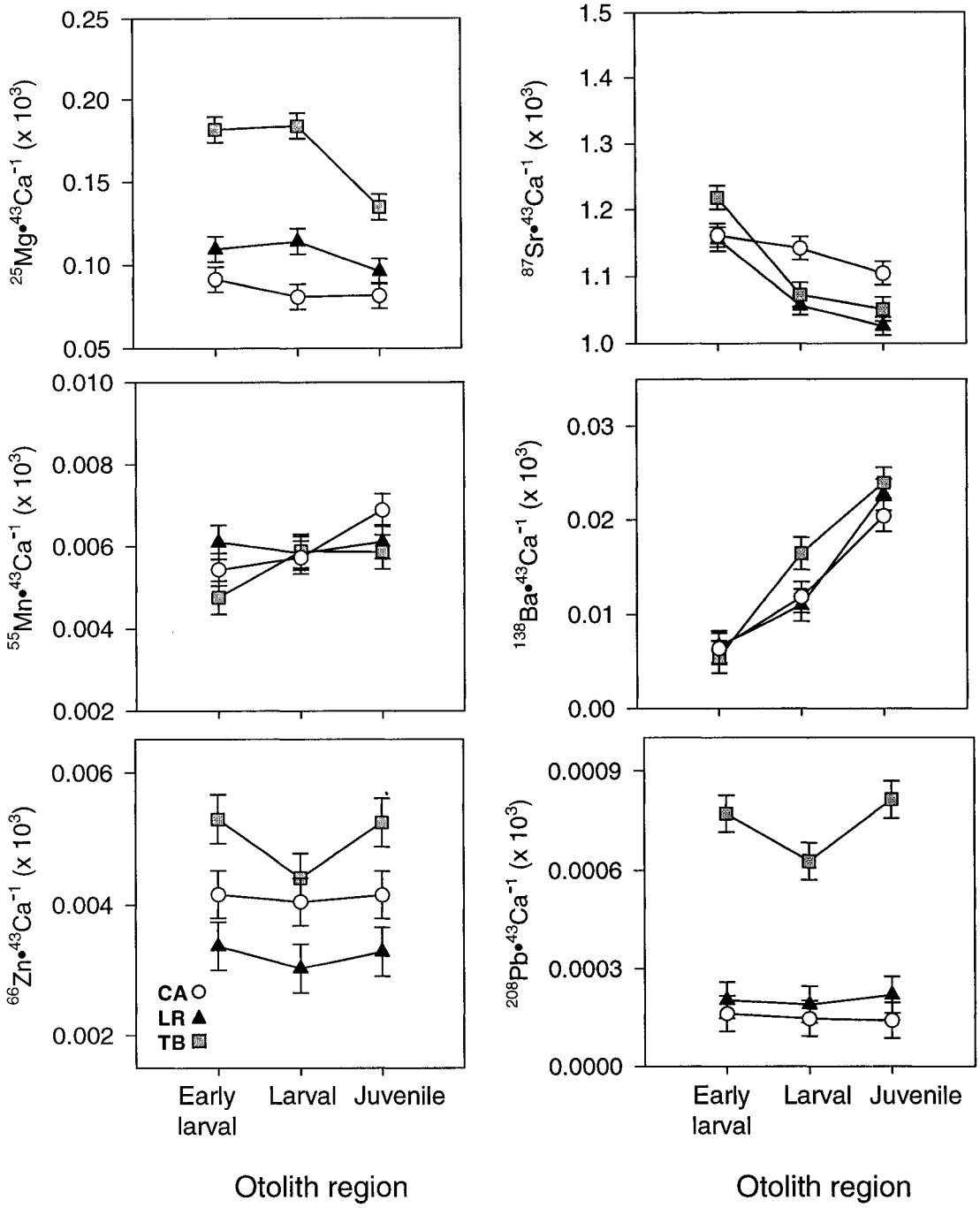

Fig. IV.3. The 2002 untransformed elemental ratios (10^3) measured in *Sebastes melanops* otoliths. ^{25}Mg, ^{55}Mn, ^{66}Zn, ^{87}Sr, ^{138}Ba, and ^{208}Pb are presented. Values are site averages (± standard error) for the early larval, larval, and juvenile otolith regions at Cape Arago (CA, open circles), Lone Ranch (LR, black triangles), and Tillamook Bay (TB, gray squares).

The DFA based on the juvenile otolith signatures grouped 88% of the fish by collection location in 2001 (jackknife = 74%) and 88% of the fish to collection location in 2002 (jackknife = 80%) (Table IV.4). The early larval and larval otolith signatures accurately grouped an average of 85% (jackknife = 64%) of the fish to collection location in 2001 and 86% (jackknife = 82%) in 2002 (Table IV.4). However, in both years, classification success was relatively good using only ^{25}Mg and ^{87}Sr in the DFA (2001 average = 68%; jackknife = 68% and 2002 average = 77%; jackknife = 76%). The additional elements improved the overall classification success by 17% in 2001 and 9% in 2002. Overall, 67 to 87% of the fish were grouped to their collection location based on the early larval, larval, or juvenile otolith signatures (Table IV.4), which is considerably better than the prior probabilities of 38 and 33%, for 2001 and 2002 respectively, based on sample size and chance alone.

For all otolith regions in both years, the first canonical factor accounted for > 75% of the discrimination (Fig. IV.4 and IV.5). ^{25}Mg was the most important element in the first factor (i.e. standardized canonical discriminant function (SCDF) > 0.90). Only variables with standardized canonical discriminant functions > 0.50 will be discussed. ^{208}Pb during the early larval period in both 2001 and 2002 and the juvenile period in 2002 also contributed substantially to the first canonical factor (SCDF > 0.52). ^{87}Sr during the early larval period in 2001 was the only other variable that contributed substantially to the first canonical factor (SCDF > 0.59). For the second canonical factor, which typically accounted for < 10% of the discrimination, ^{66}Zn was the dominant variable in all cases

(SCDF > 0.67) except during the early larval period in 2001 when ^{87}Sr and ^{138}Ba each had SCDF > 0.50. In 2001, ^{138}Ba contributed substantially during the larval period and ^{208}Pb in both the larval and juvenile periods (SCDF > 0.90).

Table IV.4. The percentage of *Sebastes melanops* accurately classified to collection location based on discriminant function analyses (DFA) using otolith elemental composition. The collection site, year of collection, otolith region (i.e. early larval, larval, and juvenile), percent correctly assigned, and the jackknifed percent correctly assigned (in parentheses) are included. GH = Grays Harbor, CA = Cape Arago, LR = Lone Ranch, and TB = Tillamook Bay.

Site	**DFA % Correct (jackknifed % correct)**			
2001	**Early larval**	**Larval**	**Juvenile**	**Site average**
GH	88 (59)	100 (76)	100 (94)	96 (76)
CA	89 (81)	89 (75)	93 (89)	90 (82)
LR	80 (40)	60 (50)	70 (40)	70 (43)
Average	86 (60)	83 (67)	88 (74)	85 (67)
2002				
TB	91 (87)	100 (91)	95 (86)	95(88)
CA	78 (78)	88 (88)	88 (83)	85 (83)
LR	83 (78)	74 (70)	83 (70)	80 (73)
Average	84 (81)	87 (83)	88 (80)	87 (81)

The majority of cases that were misclassified grouped with the closest geographic location. Seventy percent (33 out of 47) of the original misclassifications were placed with the closest collection location while 61% (51 out of 84) of the jackknifed

misclassifications grouped with the closest location. The second most common misclassification, in both years, was for fish from the more northern locations (GH and TB) to group with LR fish. In both the 2001 and 2002 DFA, LR fish were located intermediate to the other two collection locations (Fig. IV.4 and IV.5), this may account for the more frequent placement of misclassified individuals into the LR group. Furthermore, in 2001, the sample size for LR was only ten individuals and the 95% confidence ellipses for this group overlapped extensively with both GH and CA, which displayed very little overlap (Fig. IV.4). This would contribute to both the low classification rate for LR fish as well as GH and CA fish being misclassified to LR. In 2002, when sample sizes were larger and similar (i.e. 23 – 24 individuals per site), the 95% confidence ellipses displayed much less overlap and the classification success improved for all groups, especially LR (Fig. IV.5).

To further test the robustness of my classifications, I used a classification algorithm based on only the early larval otolith signatures to predict collection location of individuals based on either their larval or juvenile signatures. The elements used for those predictions were the same as the previous DFAs except for the removal of Ba in 2001 and Sr in 2002 because classification success was greater without them. The larval otolith signatures, using the early larval classification algorithm, grouped 66% of the 2001 and 87% of the 2002 individuals to their collection location. The juvenile otolith signatures, using the early larval classification algorithm, grouped 72% of the 2001 and 75% of the 2002 individuals to their collection location (Fig. IV.6). Misclassified individuals were

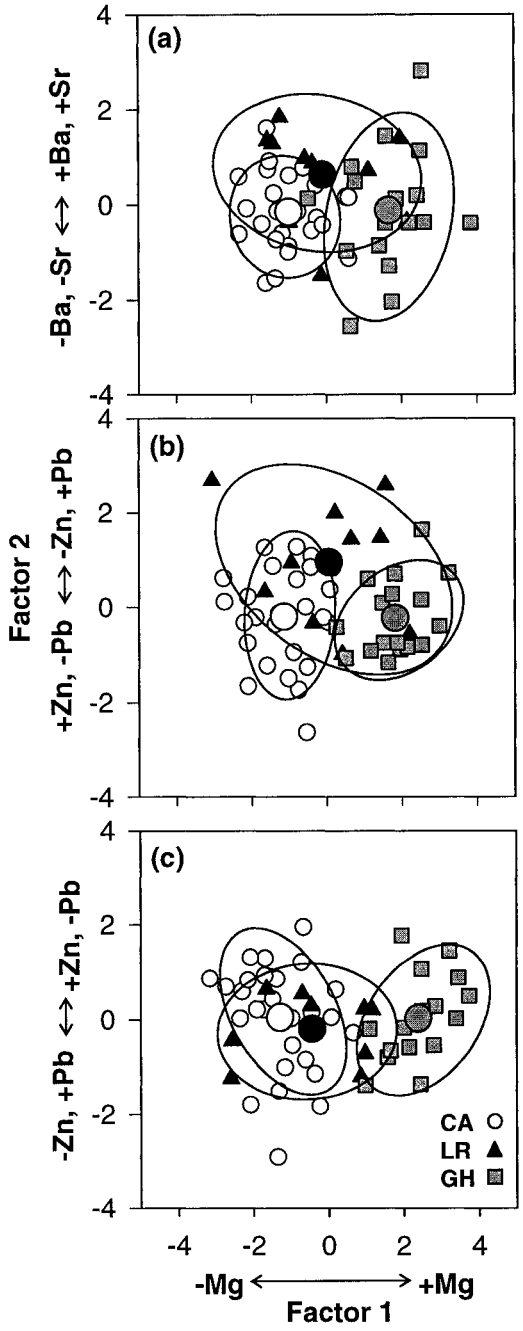

Fig. IV.4. Discriminant function classifications (DFA) based on (a) early larval, (b) larval, and (c) juvenile otolith elemental signatures of black rockfish (*Sebastes melanops*) collected in 2001 at Cape Arago (CA, open circles), Lone Ranch (LR, black triangles), and Grays Harbor (GH, gray squares). The elements responsible for the majority of discrimination within each factor are identified along the axes. Ellipses are 95% confidence intervals. Group centroids (larger circle symbols) are also plotted. Abbreviations and sample sizes are as follows: CA = Cape Arago (n = 28), LR = Lone Ranch (n = 10), and GH = Grays Harbor (n = 17).

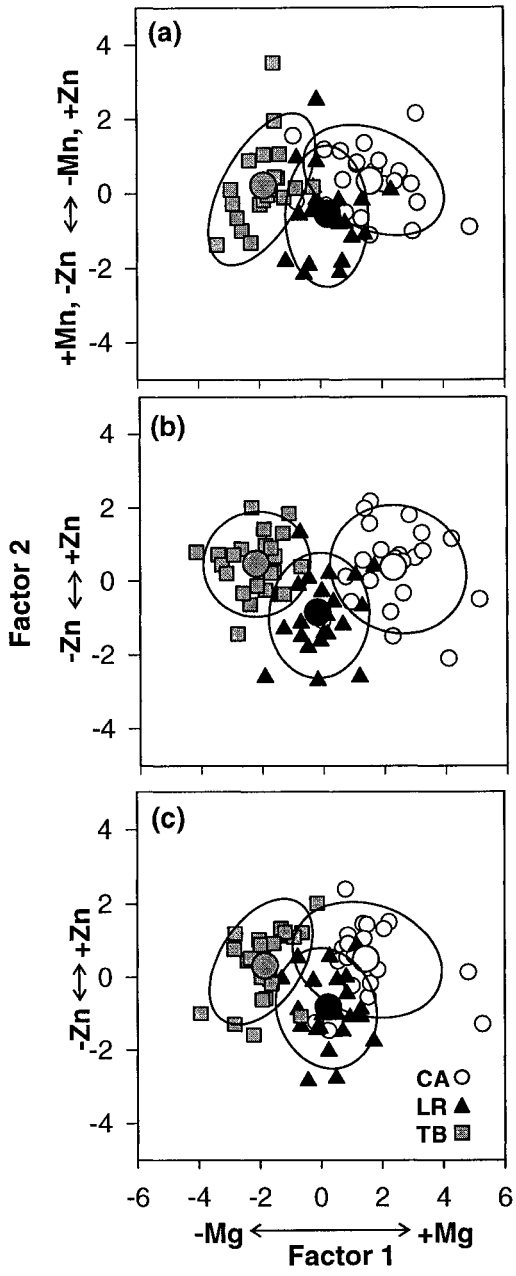

Fig. IV.5. Discriminant function classifications (DFA) based on (a) early larval, (b) larval, and (c) juvenile otolith elemental signatures of black rockfish (*Sebastes melanops*) collected in 2002 at Cape Arago (CA, open circles) , Lone Ranch (LR, black triangles), and Tillamook Bay (TB, gray squares). The elements responsible for the majority of discrimination within each factor are identified along the axes. Ellipses are 95% confidence intervals. Group centroids (larger circle symbols) are also plotted. Abbreviations and sample sizes are as follows: CA = Cape Arago (n = 24), LR = Lone Ranch (n = 23), and TB = Tillamook Bay (n = 23).

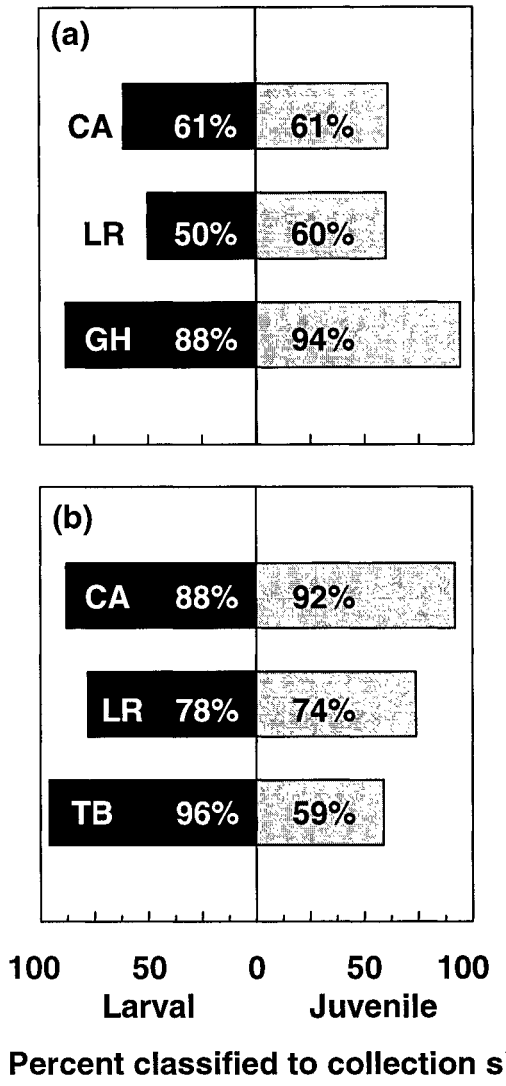

Fig. IV.6. Discriminant function classification of black rockfish (*Sebastes melanops*) larval and juvenile otolith elemental signatures based on the early larval classification algorithm for (a) 2001 and (b) 2002. Bars represent the percent of individuals grouped to their collection location based on each of the elemental signatures. Larval classifications are on the left, labeled "Larval," and the juvenile classifications are on the right, labeled "Juvenile." Collection locations and sample sizes (in parentheses) are listed. Abbreviations are as follows: CA = Cape Arago, LR = Lone Ranch, GH = Grays Harbor, and TB = Tillamook Bay.

most commonly placed with the nearest geographic location (i.e. 68% of the misclassifications in 2001 and 62% in 2002). In 2001, the remainder of the misclassifications involved LR fish being placed in GH (25% of the misclassifications). In 2002, the second most common misclassification was that TB fish were placed with LR fish (31% of the misclassifications).

Discussion

I found statistically significant differences in the otolith elemental composition, including Mg, Mn, Zn, Sr, Ba, and Pb, of juvenile *Sebastes melanops* collected on an alongshore gradient, 120 to 460 km apart, in both 2001 and 2002. Certain elements, such as Mg in 2001 and 2002 and Zn and Pb in 2002, varied significantly and consistently among collection locations throughout ontogeny, i.e. at all three otolith regions. The data suggest that the spatial variation in ambient water chemistry at these spatial scales is adequate to generate unique otolith geochemical signatures.

There are certain characteristics of the otolith geochemical signatures observed in this study that warrant further discussion. There were inter-annual differences in the otolith concentration of some elements (i.e. Mg and Zn) and the discriminatory power of some elements varied between 2001 and 2002 (e.g. Pb was more important in the second discriminant factor in 2001). Multi-year otolith chemistry studies have often found that inter-annual variation can exceed intra-annual variation and prevent accurate classification of fish based on algorithms developed from fish otoliths collected in previous years (Gillanders 2002b, but see Hamer et al. 2003). Given that various factors

affect coastal water chemistry, including riverine inputs and upwelling intensity, these findings are not surprising. They do, however, warrant further investigation.

Additionally, the elements most useful for discrimination varied somewhat throughout ontogeny (e.g. in 2002, Mn was more important during the juvenile life history period). Our data are insufficient to determine if the observed variation in elemental concentrations across the otolith represent ontogentic changes in elemental incorporation, actual changes in water chemistry, or some other unknown factor. However, such differences may be due to temporal changes in ambient water chemistry within locations. I cannot distinguish fish movement from temporal changes in ambient water chemistry within locations. However, the fact that the otolith geochemical signatures of the juvenile *S. melanops* grouped 60 to 80% of fish to their collection location throughout their early life history does indicate that fish from different collection locations did not mix earlier in their life history. Similarly, the fact that the early larval signatures grouped 69 and 81% of the fish, in 2001 and 2002 respectively, to their collection location further suggests that fish remained together relative to the other collection locations, did not move appreciable distances alongshore, and/or followed similar dispersal pathways.

Thresher (1999), in an extensive review on the use of otolith elemental chemistry for resolving population structure, identified an emerging consistency in such studies. He found that the Group IIA elements (Mg, Sr, and Ba) were routinely identified as stock delineators. In this study, I had relatively good jackknifed classification accuracy (68 to

76%) using only Mg and Sr. These results are consistent with Thresher's (1999) finding and indicate that otolith elemental chemistry may provide accurate information on the relative movements of individuals and groups of fish.

What transport mechanisms could have generated the geochemical otolith signatures seen in this study? I consider a number of possibilities: 1) fish stayed together relative to the other collection locations (i.e. did not mix); 2) fish did not move appreciable distances alongshore; 3) both 1) and 2); or 4) fish from the same collection location may have followed similar dispersal pathways. Parturition dates within each site were spread over a 22 - 66 d period. Therefore, larvae were not released at the same time. In order for fish from one location to remain together relative to other locations (#1), they would have not moved appreciable distances alongshore since parturition (#2) or followed similar dispersal pathways for indeterminate distances (#4). As stated by Warner et al. (2000), when individuals in groups that settle together differ by weeks in their larval ages, any physical processes associated with accumulation over the duration of larval life must be persistent for that long. As previously mentioned, the predominant sea surface flow over the continental shelf in the California Current system undergoes a seasonal reversal with predominantly poleward flow during fall and winter months and equatorward flow during spring and summer (Huyer et al. 1979; Strub et al. 1987). This transition typically occurs between mid-February and mid-May, occurring later in the year at more northerly locations (Strub et al. 1987). Parturition dates of fish used in this study, i.e. from 2 Feb – 9 Apr in 2001 and 6 Feb – 21 Mar in 2002, occurred prior to this

transitional period. It is difficult to imagine what physical pathway would persist for a 22 - 66 d period in such an oceanographic regime. A more parsimonious hypothesis may be that larvae do not move appreciable distances alongshore after parturition (#2).

If black rockfish larvae did not disperse appreciable distances alongshore during their 3 - 6 month pelagic larval period, they presumably experienced conditions conducive to reduced alongshore flow and/or have behaviors that minimize alongshore transport. Minimal alongshore transport may occur when advective forces that promote alongshore movement are minimized *in relation to* diffusive forces, e.g. in the nearshore coastal boundary, inshore of wind-driven "upwelling jets," and in coastal eddies. Modeling efforts indicate that coastal species that spawn over many years and have extended pelagic larval durations, two characteristics of most *Sebastes* species, are typically exposed to increased flow variability during larval stages which can, at times, result in greater diffusivity and reduced alongshore transport (Largier 2003). The reduction in alongshore transport due to physical factors could be enhanced by larval behavior (Shanks et al. 2003). Larvae may actively maintain nearshore positions with behaviors similar to those documented in intertidal fishes, including bottom orientation, rheotaxis, and schooling (Largier 2003; Marliave 1986; Montgomery et al. 1997).

Can I estimate larval dispersal distances for *S. melanops*? The closest collection locations in this study were 120 km apart. Given the rate of geographic classification at these two sites throughout ontogeny in both 2001 and 2002 (jackknifed average = 63% in 2001 and 78% in 2002), these data suggest that dispersal distances may be < 120 km for

the majority of individuals. This may represent the dominant dispersal pattern for *S. melanops* but does not preclude the possibility that > 10% of the individuals collected at a site came from distances greater than 120 km. Efforts to classify a population as "open," or one where recruits arrive from outside sources, or "closed," where recruits are locally derived, may not be appropriate if the long term success of a species and maintenance of its populations depend on a variety of dispersal outcomes over time (Largier 2003).

The lack of information on larval dispersal distances and the proportion of individuals within a population that disperse widely hinder current conservation and management efforts. The maintenance of genetic diversity within a population may not be in jeopardy if > 10% of the new recruits came from external sources. The recovery of a depleted population, however, depends not only on the size and proximity of adjacent populations but also on the proportion of larvae from those populations that disperse widely enough to provide new recruits to the depleted population. Therefore, the rate of recovery of such a population could be substantially slower in a species where typically 80%, compared with 20%, of the successful recruits are generated internally. Similarly, such principles apply in the design of marine reserves. Botsford et al. (2001), for example, conclude that successful reserve design requires knowledge of the mean dispersal distance as well as the proportion of successful recruits generated within the reserve. Much of the debate surrounding marine reserve design, i.e. are single, larger reserves more successful than networks of smaller reserves, will remain largely theoretical until more specific information on larval dispersal distance is generated.

Tools and techniques that provide information on larval dispersal distance and the proportion of successful recruits that are locally derived will be invaluable for the establishment of harvest regulations and conservation strategies, particularly the design and placement of marine protected areas. Otolith microchemistry has provided novel information on larval, juvenile, and adult fish movements. In this study, I found unique geochemical otolith signatures throughout ontogeny in juvenile *S. melanops* collected 120 – 420 km apart, which suggests that larval and juvenile movements may be relatively limited. Estimates of *S. melanops* dispersal distance based solely on pelagic duration range from 255 km to 570 km (Shanks et al. 2003), roughly two to five times farther than the 120 km estimated in this study. Although more information on the spatial and temporal variation in water chemistry and the relationship between ambient water and otolith chemistry is needed to fully interpret otolith geochemical signatures, the data presented here indicate that otolith chemistry holds further promise in studies on alongshore fish movement and larval dispersal in coastal environments.

Bridge

The following chapter, Chapter V, "Population structure in black rockfish (*Sebastes melanops*): a comparison between otolith microchemistry and DNA microsatellites," compares two relatively new techniques that can identify discrete groups of fish. The data presented in the preceding chapter, Chapter IV, indicate that *S. melanops* larvae have limited alongshore dispersal, which could lead to genetic divergence along the Oregon/Washington coast, particularly if there is minimal adult movement. Chapter V examines this possibility by examining both otolith microchemistry and DNA microsatellites in adult black rockfish.

Chapter V

Population structure in black rockfish (*Sebastes melanops*): a comparison between otolith microchemistry and DNA microsatellites

Introduction

Otolith microchemistry and DNA microsatellites are recent technological advances that allow for detailed investigations of population structure in fishes. Each has generated great expectations for discoveries that may provide insight into poorly understood biological and ecological processes. Both techniques have been touted as being among the most powerful means to distinguish among fish populations (Campana et al. 1994; O'Connell and Wright 1997). Briefly, the chemical composition of otoliths can be measured at discrete locations along an otolith's growth transect with laser ablation-inductively coupled plasma mass spectrometry (LA-ICPMS). This provides a chronological map of elemental concentrations that potentially enables researchers to reconstruct aspects of an individual fish's environmental history. Microsatellite markers are genomic DNA sequences consisting of tandem repeats of short, two-to-five base pair, motifs that are distributed throughout most eukaryotic genomes. These highly polymorphic, rapidly mutating regions provide previously unattainable genetic resolution

for population studies (Bentzen et al. 1996; Banks et al. 2000, 2003; Buonaccorsi et al. 2002).

Otolith microchemistry studies that investigate population structure typically employ one of two approaches (Thresher 1999). One approach attempts to characterize geographic source signatures in otoliths of larvae or juveniles, collect dispersed adults at a later time period, and then identify the source of those adults by matching the chemical signatures at their otolith cores, which represent natal origins, with those previously observed in larvae and juveniles. The other approach typically collects adults across a relatively broad region and searches for geographic groupings based on otolith geochemical signatures and, in ways, is similar to a genetic approach. These inferences rely on two primary assumptions. First, otolith growth is continuous with no evidence of resorption, and thus provides a permanent chronological record. This is reasonably well established (Campana 1999; Campana and Thorrold 2001; Thresher 1999). Second, if fish reside in water masses with different chemical properties, those properties will be reflected in otolith microchemistry. However, because the mechanistic control of elemental incorporation is not thoroughly understood, this assumption has yet to be fully verified (Campana and Thorrold 2001; Thresher 1999).

Primary methods of trace-metal incorporation into the otolith include ion substitution of calcium with other divalent ions, inclusion in interstitial spaces, or in association with the protein matrix. Certain elements, such as magnesium (Mg), strontium (Sr), and barium (Ba), may be substituted for calcium in the aragonitic matrix

whereas other metals may to "get stuck" in the crystalline structure (Campana 1999). When examined in laboratory settings, these events, for certain trace elements, occur in some proportion to ambient water chemistry, although often in a species-specific manner (Bath et al. 2000; Geffen et al. 1998; Milton and Chenery 2001).

Marine species often have relatively long pelagic larval periods (weeks to months) and the potential for long distance dispersal (Palumbi 2003; Shanks et al. 2003). Therefore, estimates of genetic structure among marine populations are typically low (Waples 1998). DNA microsatellite markers, due to their high level of genetic variation, may be able to differentiate among populations with higher rates of exchange than previous genetic techniques (Banks et al. 2000). The primary assumptions associated with microsatellites are that they are neutral and rapidly mutating markers. Current limitations to the technique include the lack of agreement on the underlying mutation model (i.e. stepwise mutation model vs. infinite allele model), a fairly common occurrence of null alleles (i.e. alleles that fail to amplify), and the inability to determine if two identical alleles share ancestry (Jarne and Lagoda 1996). Numerous studies, however, have documented relatively high levels of genetic divergence in marine fishes with microsatellite analysis (Bentzen et al. 1996; Buonaccorsi et al. 2002; Withler et al. 2001).

The *Sebastes* complex is comprised of over 90 species with relatively unique life histories, the majority of which are found in the Pacific Ocean. They are typically long-lived and at least some are viviparous (Love et al. 2002; Yoklavich and Boehlert 1987).

The black rockfish, *Sebastes melanops*, ranges in distribution from the Aleutian Islands, Alaska to southern California. Commercial and recreational harvest began in the late 1800s and continues today. Although *S. melanops* has traditionally comprised a large portion of Oregon's recreational fishery, new restrictions were recently placed on both recreational and commercial harvest to minimize harvest impacts on Oregon populations (PMCC 1999; ODFW 2003). Adults typically reach sexual maturity between 3 and 7 years (Love et al. 2002). Larvae typically spend 3 to 6 months in the plankton, although areas of parturition, or larval release, are unknown. Benthic juveniles initially settle in shallow waters and move into deeper waters as they grow and adults commonly occur in waters < 55 m in depth (Laroche and Richardson 1980).

Movement patterns of *Sebastes melanops* adults, juveniles, and larvae are not well known. In a mark and recapture study on adult *S. melanops*, Mathews and Barker (1983) recaptured between 63 and 69% of their tagged adults within their release site over a two year period. A few adults, however, moved > 300 km. A previous study on *S. melanops* (Miller & Shanks, in press) examined the otolith elemental composition of juveniles collected from locations 120 to 460 km apart. Otolith elemental composition was measured at three discrete locations on the otolith growth axis, including the otolith core, its edge, and halfway between its core and edge. Using the otolith elemental signatures, juveniles grouped together by their collection location at all three otolith regions an average of 74% of the time. A possible explanation for these data is limited larval dispersal, which may result in relatively low levels of exchange among populations. Such

limited larval dispersal with minimal adult movements may lead to genetic structure along the Oregon/Washington coast.

Attempts to quantify the level of connectivity, or exchange, among marine populations have increased recently (Botsford et al. 2001; Lockwood et al. 2002; Warner et al. 2000). Many of these efforts are related to theoretical, practical, and biological considerations associated with the design and establishment of marine protected areas (MPAs). The majority of marine populations probably represent a continuum between fully open, where new recruits come primarily from external sources, and closed, where immigration and emigration of individuals are negligible. Fisheries science, however, currently has few tools to accurately determine the extent of larval dispersal and adult migration among marine populations. This is particularly true on ecological time scales that are useful for management and conservation efforts. Otolith microchemistry has the potential to provide information on individual movements and exchange among populations within a generation whereas microsatellite data can provide information on population connectivity over longer periods. These two techniques work at different time scales but are theoretically linked, i.e. limited dispersal within each generation should lead to population structure and may be able to provide independent but complementary estimates of population connectivity.

In this study, I completed both otolith microchemistry and DNA microsatellite analyses on adult *Sebastes melanops* to determine if there was evidence of population structure along the Oregon/Washington coast. The primary questions were: 1) Are there

unique geochemical signatures in adult otoliths? 2) Do those geochemical signatures vary ontogenetically, i.e. at the otolith core vs. otolith edge? 3) Do otolith elemental signatures provide discriminatory power to predict the collection location of *S. melanops* along the Oregon/Washington coast? 4) Do DNA microsatellites provide evidence for genetic population structure in *S. melanops* collected along the Oregon/Washington coast? 5) Do DNA microsatellite data provide discriminatory power to predict the collection location of *S. melanops* along the Oregon/Washington coast? 6) Are data generated with otolith microchemistry and DNA microsatellite data complementary and corroborative?

Methods

Fish collection

Adult *Sebastes melanops* were collected from recreational fishing vessels at four geographic locations, Grays Harbor, Washington, and Cape Arago, Gold Beach, and Brookings, Oregon, during summer 2001 (Fig. V.1). All fish from each location were collected on the same day. In the field, fish were measured to the nearest 0.5 cm (TL) and caudal fin clips (approx. 1 cm^2) were stored in 95% ethanol in plastic vials. Fish heads were removed from carcasses and otoliths were either immediately removed (Cape Arago samples) or heads were frozen (< 1 month) prior to otolith removal (all other samples). A total of 149 fish were used for DNA microsatellite analyses, 93 of which were also used for otolith microchemistry analyses. Fewer fish were analyzed for otolith microchemistry due to the relatively high cost per sample.

Otolith preparation and aging

Both sagittal otoliths were removed with acid-washed plastic forceps, cleaned, weighed (to the nearest 0.01 g), and measured (to the nearest 0.1 cm). Otoliths were ultrasonically cleaned in NANOpure® water, dried, and stored in acid-washed plastic vials. Left otoliths were embedded in resin and ground to expose the otolith core. Otoliths were ground with 3M™ Tri-m-ite wetordry™ paper (240 to 1200 grit), polished with Buehler AlO_2 powder (12.5 and 3.0 μm), and again cleaned ultrasonically for 15 min. Right sagittal otoliths were stored in plastic vials for increment, i.e. age, analysis. Annual formation of increments in *Sebastes melanops* otoliths was validated by the Committee of Age Reading Experts (C.A.R.E. 2000). Increments were visualized with the break-and-burn protocol (C.A.R.E. 2000) and a Leitz dissecting microscope at 65 to 250x magnification. Immersion oil was used to further clarify increments. Three independent counts (i.e. separated by at least one d) were made for each otolith and averaged (and rounded to the nearest whole year). Fish size (TL) was regressed against both otolith weight and estimated increment number to evaluate the strength of those relationships.

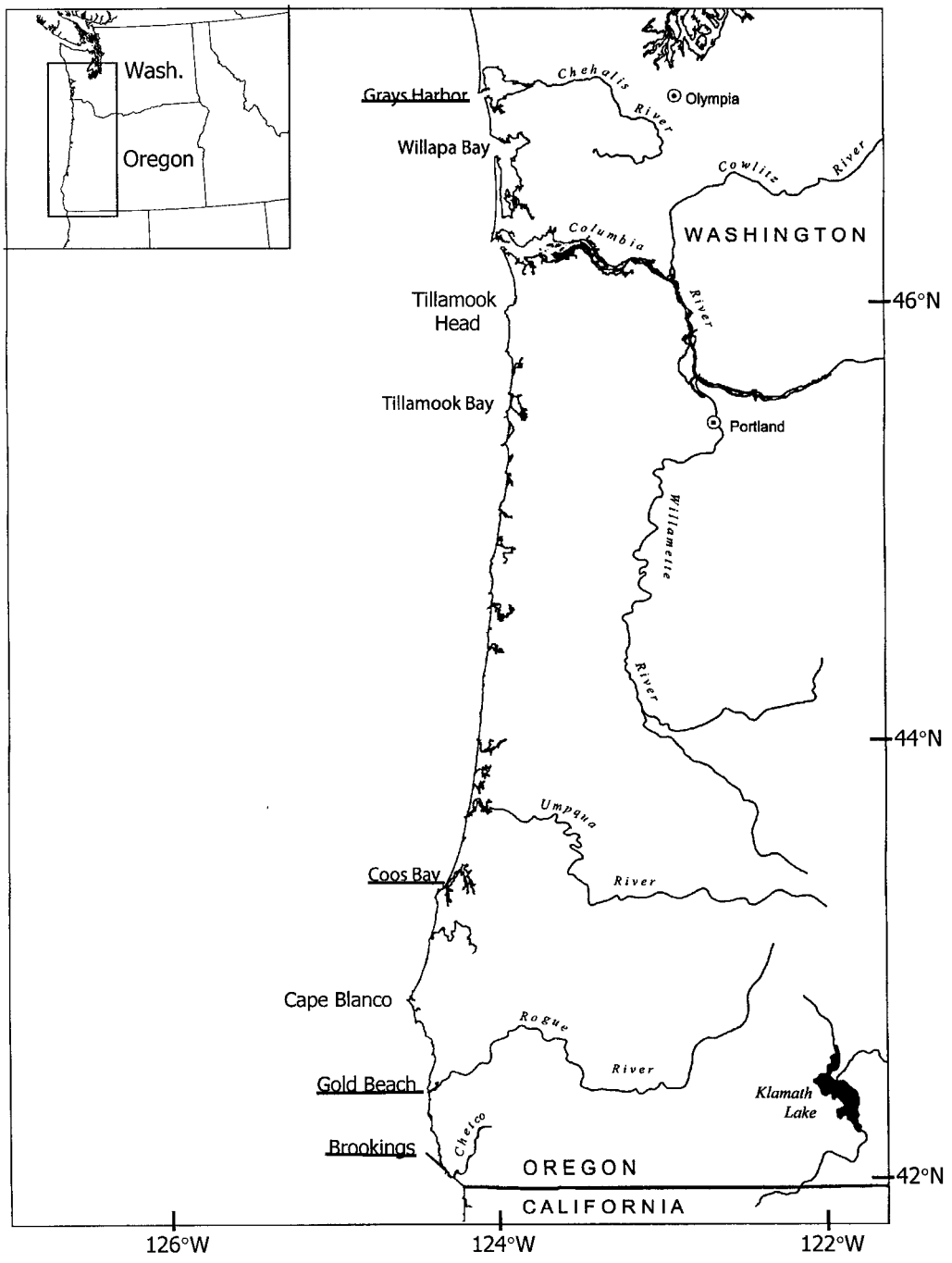

Fig. V.1. Geographic locations (underlined) where adult black rockfish (*Sebastes melanops*) were collected. In 2001, adults were collected from 1) north of Grays Harbor, Washington, 2) south of Cape Arago, Oregon, 3) Gold Beach, Oregon, and 4) between Chetco and Brookings, Oregon.

Otolith microchemistry analysis

Otolith elemental composition was measured with a laser ablation-inductively coupled plasma mass spectrometer (LA-ICPMS); all laser work was completed at the Oregon State University's WM Keck Collaboratory for Plasma Spectrometry, Corvallis, Oregon. A VG PQ ExCell ICPMS with a New Wave DUV193 excimer laser was used for all analyses. The laser was set at 10 Hz with a 50 μm ablation spot size and traveled at 30 μm sec^{-1}. The high calcium content of otoliths can cause significant calcium buildup inside the sample chamber and quadrupole. In order to avoid biased data collection, background levels of ^{43}Ca were monitored for accumulation in the spectrometer and skimmer cones and gas tubing were cleaned daily. I collected no data during periods with elevated background calcium levels.

Only left otoliths were used in microchemical analyses. Preliminary analyses indicated that the following nine analytes were consistently at concentrations in otoliths that were well above background levels: ^{25}Mg, ^{43}Ca, ^{48}Ca, ^{55}Mn, ^{66}Zn, ^{86}Sr, ^{87}Sr, ^{138}Ba, and ^{208}Pb. The %RSD for National Institute of Standards and Technology (NIST) glass plates during data collection were as follows: ^{25}Mg = 10.8%, ^{43}Ca = 4.3%, ^{48}Ca = 6.6%, ^{55}Mn = 4.3%, ^{66}Zn = 6.6%, ^{86}Sr = 5.7%, ^{87}Sr = 4.8%, ^{138}Ba = 4.6%, ^{208}Pb = 6.0%. Multiple transects within the anterior-dorsal quadrant were collected to determine if there were significant differences between replicate transects. The anterior-dorsal quadrant was chosen because it most consistently had the clearest increments. Preliminary analyses indicated no significant difference in transformed analyte concentrations between

multiple transects in the anterior-dorsal quadrant (paired t-tests, N = 6, $t > 0.10$, $p > 0.05$, df = 9).

Trace-element compositions in National Institute of Standards and Technology (NIST) glass standards are homogenous and average elemental concentrations are reported in Pearce et al. (1997). A NIST standard was run with each otolith sample. Background analyte levels were determined with an argon gas blank prior to each transect and subtracted from mean otolith isotope counts. Elemental data (in counts per second) were divided by ^{43}Ca to adjust for variability in instrument sensitivity and the amount of ablated material (Campana et al. 1997). Measured otolith element to calcium ratios were then multiplied by a correction factor determined by dividing the measured NIST ratio by the mean metal•Ca^{-1} ratios as reported in Pearce et al. (1997). This allowed all otolith transects to be standardized relative to NIST concentrations to account for instrument drift or day-to-day variations in instrument sensitivity across the atomic mass range.

Time-resolved software (PlasmaLab®) allows analyte (i.e. ^{25}Mg, ^{43}Ca, etc.) measurements to be made at discrete positions on the otolith and integrated and averaged for each element collected. This sampling technique can average otolith element measurements over a distinct period in the life of each individual. Therefore, I collected data from two portions of every otolith. One transect, 300 µm in length, was located within the otolith core, inside of the 1st annulus. A second 300 µm transect was located at the outer edge of the otolith and represented the collection year (2001). These do not

represent equivalent periods of time. The core transect, which originated at the otolith primordial, is located completely within the 1st annual increment and represents, on average, a 4 month period. The edge transect always terminated at the outermost otolith edge and integrated over the last year of life. This resulted in two average element measurements for each individual, one that represented the initial portion of Year 1 and one that represented the period just prior to collection. The purpose of this was to make comparisons of otolith geochemical signatures from different collection locations at the different otolith regions in order to examine how elemental composition varied over time and among collection locations.

Standardized elemental data were transformed to attain normality and homogeneity of variance. My initial hypothesis was that there were no significant differences in otolith elemental composition due to fish age. The distribution of fish age among sites was skewed with older fish collected at Grays Harbor and Gold Beach, so all data could not be pooled to test this hypothesis without introducing a location bias. Therefore, I examined fish from only one location at a time. I also needed adequate numbers of individuals from each location. This resulted in four test groups; 1) Grays Harbor (GH) 7 to 10 years old, 2) Cape Arago (CA) 6 to 8 years old, 3) Gold Beach (GB) 6 to 8 years old, and 4) Brookings (BR) 6 to 9 years old. Because I collected otolith element data on each individual from the two otolith regions (i.e. the core and edge), repeated measures analysis of variance (ANOVA) was used to test whether otolith composition varied significantly due to age at each of the otolith regions. Although

repeated measures ANOVA is more typically used when the treatment effect, in this case otolith region, is of primary interest, it is also a valid test of differences among blocks, age in this case. Furthermore, as there are only two repeated measures, the assumption of sphericity does not apply. Blocks (random) were represented by age, treatments (fixed) were represented by otolith region (core and edge), and the elements (^{25}Mg, ^{55}Mn, ^{66}Zn, ^{87}Sr, ^{138}Ba, and ^{208}Pb) were dependent variables.

Repeated measures ANOVA was also used to examine otolith elemental composition among the four collection locations at the two otolith regions (core and edge). Blocks (random) were represented by collection location, treatments (fixed) were represented by otolith region, and the elements (^{25}Mg, ^{55}Mn, ^{66}Zn, ^{87}Sr, ^{138}Ba, and ^{208}Pb) were dependent variables. Scheffé's post-hoc test was used to identify homogeneous groups, by collection location, for each element at both the otolith core and edge. To further examine the magnitude of the relative differences in otolith chemistry among geographic locations, sequential pair-wise comparisons (N = 36) of the difference in average element concentration between collection locations were also made for each otolith region (i.e. GH average core $^{25}Mg \bullet ^{43}Ca^{-1}$ divided by BR average core $^{25}Mg \bullet ^{43}Ca^{-1}$, etc.)

Discriminant function analyses (DFA) was used to predict collection location based on both the core and edge otolith geochemical signatures using only those elements that varied significantly among collection location. The primary goals of DFA are to 1) find dimensions along which groups of interest differ and 2) to find classification

functions to predict group membership (Tabachnick and Fidell 2001). The assumptions of DFA, i.e. normality and linearity, were met. Tabachnick and Fiddell (2001) recommend the use of F_{max}, or the ratio of the largest cell variance to the smallest, to evaluate the homogeneity of variance-covariance matrices. If samples sizes are relatively equal, then $F_{max} = 10$ is adequate. In this case, F_{max} for all transformed variables was < 7.3. However, site classifications were determined with both linear DFA, which assumes equal covariances and pools the variance-covariance matrix, and quadratic DFA, which does not assume equal covariances and is based on individual within group covariances, and compared (Tabachnick and Fiddell 2001). Jackknifed classifications were calculated with the removal of one observation a total of N times (N = 93) and averaged. The best validation of a discriminant function classification is the assignment of new cases (i.e. those not used in the development of the original classification algorithm). Jackknifed predictions are used to provide a more realistic estimate of the ability of the predictor variables to separate groups when sample sizes are not large enough to generate two independent datasets.

DNA microsatellite analysis

A 5% Chelex solution was used for DNA extraction. An MJ Research™ Peltier Thermal Cycler was used for all reactions. A 5 µl volume reaction contained 1.5 µl of DNA template, 1x polymerase buffer (500 mM KCl, 100 mM Tris-HCL, 1% Triton® X-100), 1.5 mM $MgCl_2$, 200µM dNTP, 0.5 µM primer (forward primers were fluorescently labeled), and 0.1 µl of *Taq* DNA polymerase (Promega). Seven previously published

microsatellite primers that consistently amplified and displayed polymorphism in *Sebastes melanops* were used, including *Spi*4, *Spi*6, *Spi*10, *Spi*12 (Gomez-Uchida et al. 2003), *Sma*7 (Wimberger et al. 1999), *Sal*3 and *Sal*6 (Miller et al. 2000). Temperature profiles used were as reported in original primer descriptions. Amplified fragments were electrophoresed in a MJ Research™ BaseStation using 5% polyacrylamide gels and GENESCAN® 400HD (Applied Biosystems) size standard and scored with Cartographer™ software.

Summary statistics, including both observed (H_o) and unbiased expected heterozygosities (H_e), number of alleles (A), and exact tests of Hardy-Weinberg equilibrium (HWE) and population differentiation, were determined with GENEPOP (Markov-chain algorithm, 200,000 steps) (version 3.3; Raymond and Rousset 1995). Tests for genotypic disequilibrium (200 permutations) and the generation of unbiased estimates of *F* statistics (F_{ST} and F_{IS}; Weir and Cockerham 1984) and G_{ST} were completed with FSTAT (version 2.9.3.2; Goudet 2001). F_{ST}, or the fixation index, quantifies the distribution of genetic variation across populations (Hartl and Clark 1997). F_{ST} values can range from 0 to 1 and are often small in marine fish species; the mean value for 57 fish species was 0.062 and the median was 0.02 (Waples 1998). F_{IS} is an estimate of the heterozygosity deficit within populations and is considered an indicator of inbreeding. G_{ST} is an equivalent estimate of F_{ST}, independent of sample size (Nei 1987). Error estimates for F_{ST}, F_{IS}, and G_{ST} were generated by jackknifing over all loci. Permutation tests (1000 randomizations) were used to determine if the overall F_{ST} was

statistically greater than zero and if pair-wise comparisons were statistically significant. All probabilities were adjusted for multiple comparisons using a sequential Bonferroni correction. R_{ST} CALC (Goodman 1997) was used to generate estimates of R_{ST} (Slatkin 1995). R_{ST} is based on the assumption of a generalized stepwise model of mutation at microsatellite loci and may generate a less biased estimate of population differentiation than F_{ST}. R_{ST} CALC transforms microsatellite data by globally standardizing the data so alleles are expressed in terms of standard deviations from the global mean rather than repeat unit number. Permutation tests ($N = 1000$) were used to determine statistical significance and bootstrapping ($N = 1000$) provides variance estimates.

Multilocus estimates of the effective number of migrants (Nm) were determined according to Barton and Slatkin (1986) based on F_{ST} with GENEPOP and R_{ST} with R_{ST} CALC. The stepping stone model predicts that genetic divergence (F_{ST}) should increase linearly with distance (Wright 1943). The hypothesis of isolation-by-distance was tested with a regression of F_{ST} on geographic distance (Barton and Slatkin 1986). Statistical significance was determined with Spearman rank correlation coefficient test (500 permutations) in GENEPOP.

WHICHLOCI (version 1.0) was then used to predict collection location based on microsatellite data (Banks et al. 2003). WHICHLOCI re-samples populations based on allele frequencies to generate populations of user-defined sizes. Genotype data for each location (GH, CA, GB, and BR) were re-sampled to generate sample sizes of 1000. Group membership was then predicted for 10 independent re-sampling events, thus

generating 10 replicate classifications. This allowed average classification success to be compared with classification success estimated with otolith microchemistry.

Results

Otolith microstructure

Significant positive correlations ($R^2 > 0.70$, $p < 0.01$) were found between total fish length (TL) and otolith mass and increment number (Fig. V.2). Overall, ages ranged from 4 to 12 years. Ages, however, were not evenly distributed among sites (Fig. V.3). Grays Harbor and Brookings samples had more 9 and 10 year olds while Cape Arago and Gold Beach samples had more 7 and 8 year olds.

Otolith microchemistry

There was no significant difference in elemental composition due to age, although there were highly significant effects of otolith region (i.e. core vs. edge) for all elements at all sites (Table V.1). There were no significant interactions between age and otolith region. Given the lack of any significant age effects within collection locations, all ages within a site were pooled for statistical analyses of site effects on otolith elemental composition.

There were highly significant effects due to collection location and otolith region for all elements examined (Table V.2 and V.3). There was also a significant interaction between collection site and otolith region. The significant interaction, however, between collection location and otolith region was due solely to ^{55}Mn. When the repeated measure

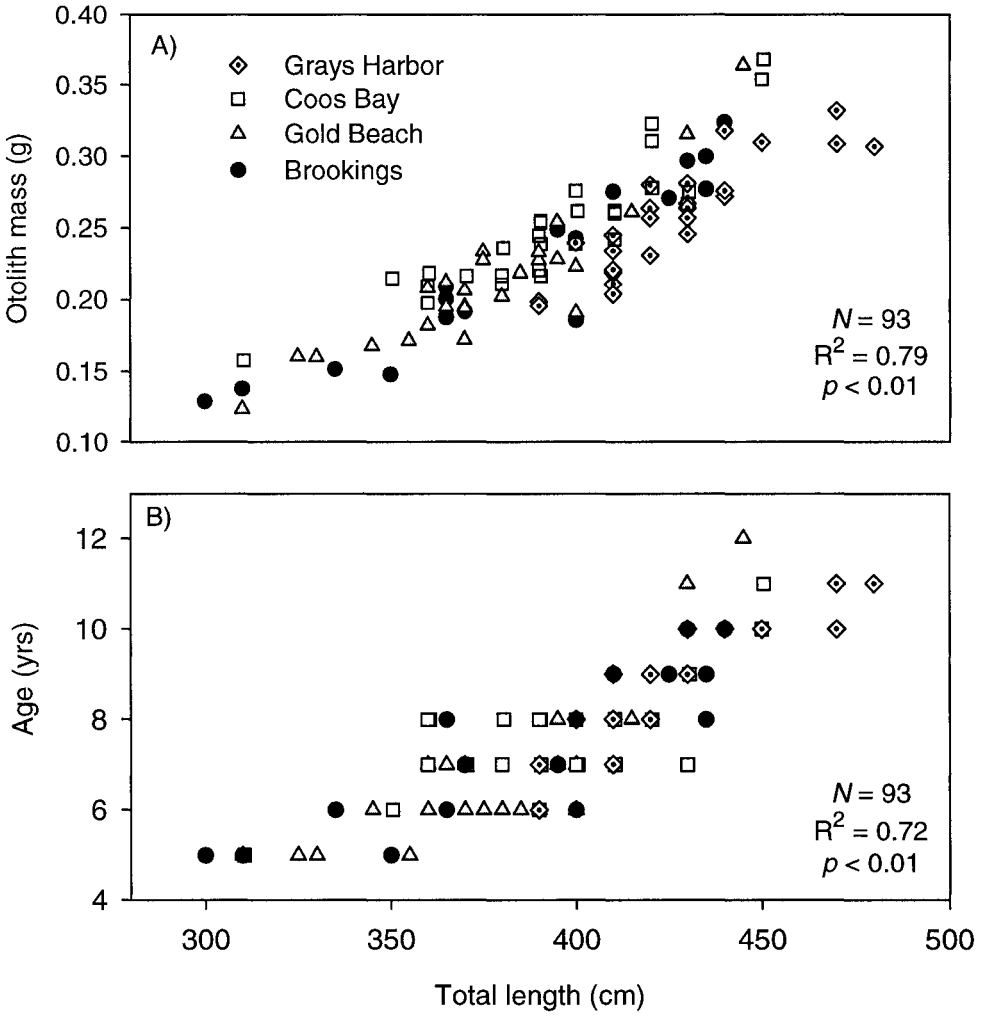

Fig. V.2. A) Otolith mass (g) and B) fish age (yrs) plotted against total fish length (cm) for the adult black rockfish (*Sebastes melanops*) used in this study. Grays Harbor fish are represented by diamonds, Cape Arago fish by squares, Gold Beach fish by gray triangles, and Brookings fish by black circles. The sample sizes, the correlation coefficients (R^2), and the significance values for each regression are reported.

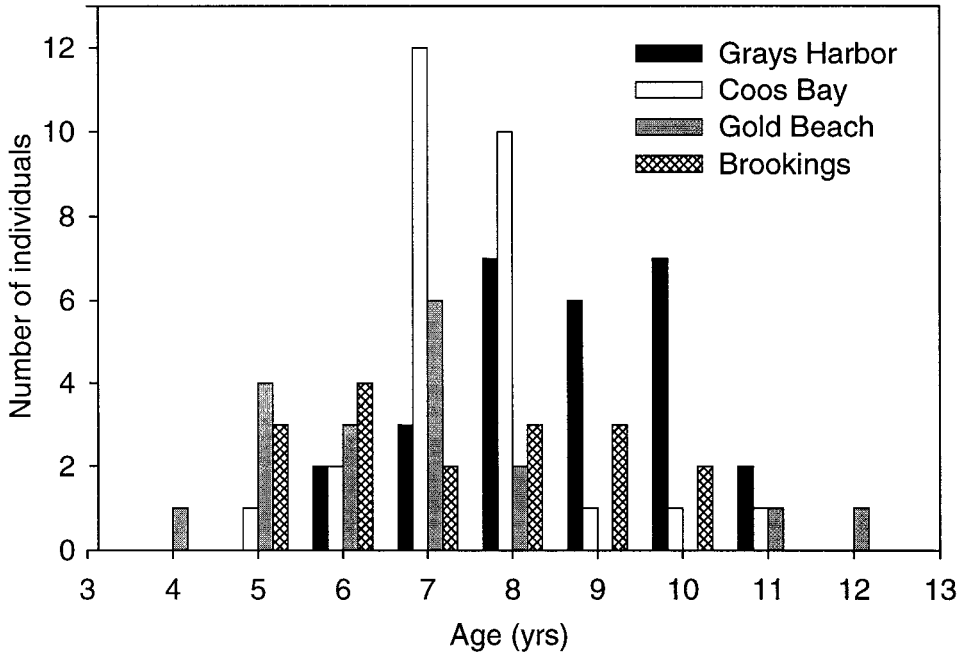

Fig. V.3. Age frequency of the black rockfish (*Sebastes melanops*) used in this study. The number of individuals is plotted against age (yrs). Grays Harbor fish are represented by black bars, Cape Arago fish by white hatched bars.

ANOVA was completed without ^{55}Mn, the interaction term was not significant (p = 0.32). Univariate results (Table V.4) indicate that all elements differed significantly among collection location at both otolith regions. There were also highly significant effects of otolith region on elemental composition. Mean ratios for ^{25}Mg, ^{66}Zn, ^{138}Ba and ^{208}Pb were about two times greater in the otolith core than at the edge (Table V.1). Mean ^{55}Mn ratios were nearly seven times greater in the

otolith core than at the edge while mean ^{87}Sr ratios were consistently lower in the otolith core than at the edge.

Another way to compare otolith elemental composition over the life history is to examine how relative site differences vary between otolith regions, i.e. the otolith core vs. edge. There were some site differences in otolith elemental composition that were similar at both the otolith core and edge. In other words, the same homogeneous groups occurred at both the otolith core and edge measurements (Table V.5). The highest elemental concentrations were typically found in Grays Harbor (GH) fish and the lowest were seen in Gold Beach (GB) fish. For example, ^{87}Sr to ^{43}Ca ratios were consistently greatest in Grays Harbor samples, at both the otolith core and edge (Table V.1 and V.5). The patterns for ^{25}Mg and ^{138}Ba were also similar, with GB samples consistently the lowest. GB samples also had the lowest mean ^{55}Mn to ^{43}Ca ratios, but it was not significantly so at the otolith edge. However, fewer and less consistent differences were observed in ^{66}Zn and ^{208}Pb (Table V.5).

The difference in average element to calcium ratios observed in 36 pair-wise comparisons between collection locations ranged from < 1 to 70%, depending on the element and otolith region. The average error associated with sequential NIST measurements was 3%. If this error is subtracted from the average difference between sites, six of the 36 pair-wise comparisons are negative, indicating that the error was

Table V.1. Results from multivariate repeated measures ANOVA to test for the effect of otolith region (core vs. edge) and fish age on otolith elemental composition within each collection location. Wilk's lambda, *F*-statistic, the degrees of freedom (df), the significance value (*p*), and the number of fish used for each test (*N*) are reported.

Effect	**Wilk's**	***F***	**df**	***p***
Grays Harbor: 7 to 10 yrs (*N* = 20)				
Age	0.27	1.0	18	0.47
Region	0.05	39.15	6	<0.0001
Age x Region	0.42	0.64	18	0.84
Cape Arago: 6 to 8 yrs (*N* = 22)				
Age	0.35	1.6	12	0.14
Region	0.08	27.0	6	<0.0001
Age x Region	0.55	0.80	12	0.64
Gold Beach: 6 to 8 yrs (*N* = 23)				
Age	0.72	0.44	12	0.93
Region	0.09	24.03	6	<0.0001
Age x Region	0.57	0.80	12	0.64
Brookings: 6 to 9 yrs (*N* = 14)				
Age	0.03	1.95	18	0.10
Region	0.04	19.41	6	0.003
Age x Region	0.17	0.69	18	0.77

Table V.2. Mean otolith element ratios (10^3) for *Sebastes melanops* from four geographic locations. All elements were divided by ^{43}Ca. Mean values ± standard error for otolith core and edge are presented.

Element	**Collection location**			
Otolith Core	**Grays Harbor**	**Cape Arago**	**Gold Beach**	**Brookings**
$log_{10}{}^{25}Mg$	0.111 ± 0.004	0.093 ± 0.004	0.073 ± 0.004	0.109 ± 0.005
$log_{10}{}^{55}Mn$	0.019 ± 0.0009	0.014 ± 0.001	0.008 ± 0.0008	0.013 ± 0.001
$log_{10}{}^{66}Zn$	0.016 ± 0.002	0.015 ± 0.002	0.0009 ± 0.002	0.015 ± 0.002
$log_{10}{}^{87}Sr$	1.37 ± 0.060	1.13 ± 0.056	1.09 ± 0.054	1.18 ± 0.069
$log_{10}{}^{138}Ba$	0.024 ± 0.003	0.015 ± 0.002	0.011 ± 0.002	0.017 ± 0.003
$log_{10}{}^{208}Pb$	0.0015 ± 0.0002	0.002 ± 0.0002	0.0008 ± 0.0002	0.0014 ± 0.0003
Otolith Edge				
$log^{25}Mg$	0.042 ± 0.005	0.040 ± 0.004	0.030 ± 0.004	0.051 ± 0.005
$log_{10}{}^{55}Mn$	0.0027 ± 0.001	0.0015 ± 0.001	0.0013 ± 0.0008	0.0031 ± 0.001
$log_{10}{}^{66}Zn$	0.006 ± 0.002	0.005 ± 0.002	0.004 ± 0.002	0.008 ± 0.002
$log_{10}{}^{87}Sr$	2.19 ± 0.062	1.75 ± 0.056	1.66 ± 0.054	1.72 ± 0.069
$log_{10}{}^{138}Ba$	0.010 ± 0.003	0.009 ± 0.002	0.006 ± 0.002	0.011 ± 0.003
$log_{10}{}^{208}Pb$	0.0006 ± 0.0002	0.0004 ± 0.0002	0.0007 ± 0.0002	0.0009 ± 0.0003

Table V.3. Results from multivariate repeated measures ANOVA to test for the effect of otolith region (core vs. edge) and collection location on otolith elemental composition. Wilk's lambda, *F*-statistic, the degrees of freedom (df), the significance value (*p*), and the number of fish used for each test (*N*) are reported.

Effect	**Wilks' lambda**	***F***	**df**	***p***
Site	0.21	9.59	18	<0.0001
Region	0.07	185.40	6	<0.0001
Site x Region	0.58	2.81	18	0.002

Table V.4. Univariate results from the repeated measures ANOVA to test the effect of site on the otolith elemental composition at the otolith core and edge.

		Otolith Core			Otolith Edge		
Effect	**df**	**MS**	**F**	***p***	**MS**	**F**	***p***
log ^{25}Mg							
Site	3	0.18	14.6	<0.001	0.20	12.0	<0.001
Error	89	0.01			0.02		
log ^{55}Mn							
Site	3	0.01	16.9	<0.001	0.002	11.8	<0.001
Error	89	<0.01			<0.01		
log ^{66}Zn							
Site	3	0.35	3. 6	0.018	0.23	5.5	0.002
Error	89	0.10			0.04		
log ^{87}Sr							
Site	3	0.05	17.0	<0.001	0.06	9.1	<0.001
Error	89	<0.01			0.007		
log ^{138}Ba							
Site	3	0.33	6.2	<0.001	0.29	17.6	<0.01
Error	89	0.05			0.02		
log ^{208}Pb							
Site	3	0.78	6.0	<0.001	0.30	2.7	0.05
Error	89	0.13			0.11		

greater than the site differences in mean element concentrations. Thirty of the comparisons were positive, indicating that the otolith elemental differences between sites were greater than the estimated error. The average difference (± standard deviation), minus the 3% error estimate, between collection locations for each element was: ^{25}Mg = 30.9% (± 24.8); ^{55}Mn = 74.8% (± 19.4); ^{66}Zn = 40.8% (± 28.1); ^{87}Sr = 12.6% (± 10.8); ^{138}Ba = 52.9% (± 27.7); and ^{208}Pb = 54.8% (± 37.5). Overall, there were relatively large site differences.

Discriminant function analysis (DFA) was used to predict collection location based on otolith geochemical signatures. Quadratic DFA resulted in slightly greater classification success, i.e. 5%, than linear DFA. For the otolith core signatures, the most accurate classification of fish (average = 82%) occurred using ^{25}Mg, ^{55}Mn, ^{66}Zn, ^{87}Sr, ^{138}Ba, and ^{208}Pb, which all varied significantly among collection location and were significant variables in the model ($F > 2.5$, $p < 0.01$) (Table V.6). ^{55}Mn, ^{66}Zn, and ^{208}Pb were the most important in discriminating between collection locations and the two canonical discriminant functions explained 92% of the variation (Table V.7). Jackknifed classifications were a bit lower (average = 72%) (Table V.6). For the otolith edge signatures, classification success was greatest with fewer elements, including ^{25}Mg, ^{55}Mn, were the most important in discriminating between collection locations and the two canonical ^{87}Sr, and ^{138}Ba, which all varied significantly among collection location and were significant variables in the model ($F > 3.3$, $p < 0.05$) (Table 6). The average was 71% with a jackknifed average of 63% (Table V.6). The two canonical discriminant

functions explained 94% of the variation. Low levels of Zn and Pb in the otolith cores of Gold Beach (GB) samples discriminated those fish from the other three locations, as evident in canonical coefficients of CV1 for the otolith core (Table V.7). No such differences were evident at the otolith edge and, therefore, Zn and Pb were not significant variables in the model.

Prior probabilities, based on random chance and sample sizes, predict that an average of 25.9% of the fish would be correctly classified based on chance alone. An average of 77% and a jackknifed average of 68%, which is probably more representative of the true discriminatory ability, is a significant improvement over chance alone. Misclassifications, however, were typically not to the nearest geographic neighbor but were spread relatively equally among other locations.

DNA microsatellites

Table V.8 summarizes the genetic statistics calculated for each sample. Across loci, the number of alleles ranged from 3 to 16 and the expected heterozygosities varied between 0.154 and 0.856. There was no evidence of genotypic disequilibrium for any pair of loci within samples. Deviations from Hardy-Weinberg equilibrium proportions occurred in the Brookings (BR) sample, which failed to meet the assumption of random mating at *Spi*10 and *Spi*4. I approached this problem in two ways. First, I completed subsequent analyses with all four collection locations using only the five loci that did meet the assumption of random mating (HW exact test, $p > 0.05$). Secondly, I completed

Table V.5. Results of the repeated measures ANOVA Scheffé's post-hoc test for homogeneous groups. Separate results for otolith core and edge are presented. GH = Grays Harbor, CA = Cape Arago, GB = Gold Beach, and BR = Brookings. ND indicates no statistically significant difference.

	Otolith core	**Otolith edge**
^{25}Mg	GB CA = BR = GH	GB CA = GH GH = BR
^{55}Mn	GB CA = BR BR = GH	GB = CA GH = BR
^{66}Zn	GB = BR = GH BR = GH = CA	GB = CA = GH CA = GH = BR
^{87}Sr	GB = CA = BR GH	GB = CA = BR GH
^{138}Ba	GB = CA CA = BR = GH	GB CA = GH = BR
^{208}Pb	GB = BR = GH GH = CA	ND

Table V.6. Site classification success based on both otolith microchemistry and DNA microsatellites. Collection site and sample size (*N*) are presented. For otolith microchemistry, the % correct, jackknifed % correct (in parentheses), and total average are presented. For DNA microsatellites, site classification success was based on re-sampled allele frequencies ($N = 1000$). Ten iterations per population were generated and averaged for 5 and 7 loci. The % correct (± standard deviation) and the total average are included.

Site (*N*)	**% correct (jackknife % correct)**			**% correct classified**	
	1st year	**Collection Year**	**Average**	**5 loci**	**7 loci.**
Grays Harbor (*22*)	77 (59)	67 (62)	70 (61)	59.7 ± 2.1	68.9 ± 1.0
Cape Arago (*26*)	81 (73)	50 (46)	66 (60)	72.7 ± 1.4	86.2 ± 0.7
Gold Beach (*28*)	100 (89)	89 (89)	95 (89)	43.5 ± 1.2	68.4 ± 2.1
Brookings (*17*)	71 (65)	76 (53)	74 (59)	79.5 ± 1.5	N/A
Total average	82 (72)	71 (63)	77 (68)	63.1 ± 0.6	74.6 ± 0.6

Table V.7. Standardized canonical coefficients for canonical discriminant functions (CDF) 1 and 2 for the six elements from the otolith core and the four elements from the otolith edge used to classify fish to collection location.

	Core		Edge	
Element	**CDF 1**	**CDF 2**	**CDF 1**	**CDF 2**
^{25}Mg	0.17	0.37	0.51	0.53
^{55}Mn	0.80	-0.44	0.35	-0.60
^{66}Zn	-1.1	0.59	NA	NA
^{87}Sr	0.62	0.52	0.36	-0.78
^{138}Ba	0.40	-0.29	0.63	0.42
^{208}Pb	0.84	-1.2	NA	NA

the same analyses with all seven loci but without the Brookings sample, leaving three collection locations (HW exact test, $p > 0.05$). Results from analyses with all four locations and the five loci that meet the assumption of random mating are presented; results from the analyses with three locations and seven loci are only presented when they differ.

F_{IS} values, or inbreeding coefficients, were comparable in both analyses, ranging from 0.00 to 0.078. The largest F_{IS} values were found in the Grays Harbor sample (i.e. 0.059 for 5 loci; 0.078 for 7 loci). Overall, $F_{ST} = 0.018 \pm 0.004$ and was statistically greater than zero ($p < 0.001$). Excluding Brookings from the analysis did not change significantly the parameter value ($F_{ST} = 0.017 \pm 0.004$). Pair-wise comparisons of F_{ST}

identified Grays Harbor, Washington fish as significantly different from all Oregon samples (Table V.9). There were no significant differences observed among Oregon samples. G_{ST} estimates were similar to F_{ST}. R_{ST} (0.010 ± 0.001) was statistically greater than zero ($p = 0.027$) (Table V.8). However, the only significantly different pair-wise comparison determined with R_{ST}, once corrected for multiple comparisons, was between GH and CA ($p = 0.009$). There was no evidence for isolation-by-distance ($p = 0.20$). The estimate for *Nm*, adjusted for sample size in GENEPOP, was 11.2 and, in R_{ST} CALC, averaged 15.7 ± 8.3 (Table V.9).

Classification success by WHICHLOCI based on re-sampled populations ($N = 1000$) varied with the number of loci and collection locations. The average success rate for all four collection locations and the five loci that met the assumption of random mating was 63.1% ± 0.6 SD. Classification success with only three collection locations (GH, CA, and GB) and all seven loci, however, averaged 74.6 ± 0.6% SD (Table V.6).

Table V.8. The collection location, sample sizes (*N*), 2001 collection dates, total (A_T) and mean (A) number of alleles per population, the observed (H_{ob}) and unbiased expected (H_{exp}) heterozygosities, and probability of heterozygote deficiency (*p*) are presented for all 7 loci [*p* (7)] and the 5 loci [*p* (5)] that met the assumption of random mating (*Spi*6, *Spi*12, *Sal*3, *Sal*6, *Sma*7).

Site	*N*	Collection Date	A_T	A	H_{ob}	H_{exp}	*p* (7)	*p* (5)
Grays Harbor	50	August 3	60	8.6	0.535	0.578	0.09	0.49
Cape Arago	33	June 3	47	6.7	0.484	0.485	0.49	0.41
Gold Beach	49	July 3	55	7.9	0.577	0.577	0.21	0.18
Brookings	17	June 16	41	5.9	0.512	0.557	0.003	0.30

Table V.9. Significance tests for pair-wise comparisons of F_{ST} and *Nm*. F_{ST} (in bold) is on the upper diagonal and *Nm* is on the lower diagonal. Adjusted nominal level (5%) for multiple comparisons = 0.0083. * is significant at $\alpha = 0.05$. See text for collection location abbreviations.

	GH	CA	GB	BR
GH		**0.032***	**0.011***	**0.021***
CA	6.7		**0.015**	**0.026**
GB	17.4	29.3		**0.008**
BR	11.7	8.4	30.6	

Discussion

Data on *Sebastes melanops* collected with otolith microchemistry and DNA microsatellites yielded corroborative and complementary information. Otolith microchemistry differed significantly among geographic regions at both the otolith core and edge for all elements examined, except Pb at the otolith edge region. Otolith chemistry also differed significantly throughout ontogeny (i.e. between core and edge otolith regions). However, using the elemental chemistry of both otolith regions, I was able to correctly classify an average of 68% of fish to collection location. Using DNA microsatellite data, I identified significant divergence between the Washington and

Oregon samples but not within Oregon samples. Site classification success based on microsatellite data averaged 63.1 and 74.6%, with five and seven loci, respectively. Overall site classification success was similar with both methods and significantly greater than that expected by chance alone (i.e. 25%). The Oregon and Washington collection locations were between approximately 340 and 460 km apart. Therefore, taken together, these data indicate that there is population structure in *S. melanops* at scales < 500 km and that otolith microchemistry and DNA microsatellites may prove useful in providing corroborative information on population structure in marine fishes.

These results raise some interesting questions regarding the information provided by otolith microchemistry. Numerous studies, see Gillanders (2002) for review, have documented interannual variation in otolith chemistry that matches or exceeds relative differences within years. Why, in this study, were there no statistically significant differences in otolith chemistry due to age within the otolith core region? This region represents otolith material laid down in the 1^{st} year of life, which was spread over numerous years from 1990 to 1998. One possibility is that I had low statistical power (β typically < 0.50) to detect differences among years due to many comparisons with relatively small sample sizes. Alternatively, some of the elemental differences among geographic regions may be stable over time. Currently, there are not enough data on ambient water chemistry to adequately address this question. However, even with fish of various ages, the observed variation in otolith core elemental signatures among

geographic locations was still significantly greater than that within locations, and thus provided relatively good discriminatory power.

Mean elemental ratios for ^{25}Mg, ^{66}Zn, ^{138}Ba and ^{208}Pb at the otolith core were in general two times greater than at the otolith edge and mean ^{55}Mn ratios were seven times greater at the core. On the other hand, mean ^{87}Sr ratios at the otolith core were about 70% of edge measurements. The core otolith ratios observed in this study are similar in range to those observed in juvenile *Sebastes melanops* otolith chemistry data collected in 2001 and 2002 (Miller and Shanks, in review) and thus are probably representative of the 1st year of life. These differences suggest that either 1) there are ontogenetic differences in otolith elemental incorporation in *Sebastes melanops* or 2) larvae and juveniles resided in waters with different chemical characteristics than adults.

Although there are studies that document changes in elemental otolith concentrations of fish held under relatively constant environmental conditions (Fowler et al. 1995; Hoff and Fuiman 1995), it is unclear if any consistent ontogenetic changes occur in otolith elemental concentrations. Kalish (1989) suggests that changes in otolith Sr/Ca ratios may be related to changes in the amount of free Ca in the endolymph due to changes in the level of Ca-binding proteins in the blood plasma, which has been shown to be proportional to Ca levels in the endolymph (Mugiya 1966). Reductions in the Ca levels in both the plasma and endolymph, which can be related to changes in reproductive status, could lead to relative increase in Sr levels in the endolymph, and hence the otolith matrix. It is unlikely, however, that such a mechanism can explain both the increase in Sr

and Ca ratios and the decrease in Mg, Mn, Sr, and Ba. Alternatively, larvae and juveniles may reside in waters with different chemical characteristics than adults. This is a reasonable possibility because *Sebastes* larvae have a relatively long pelagic duration (> 3 month) and juveniles initially settle very nearshore, at times in estuaries, and progressively move deeper as they grow (Love et al. 2002). Given that concentrations of various elements is often greater in nearshore and estuarine areas (Sanudo Wilhelmy and Flegal 1991; Swearer et al. 1999), this may be reflected in the otolith microchemistry. More research is required to determine the underlying causes of the relatively large differences in otolith elemental composition between otolith core and edge regions in *Sebastes melanops*.

Given the lack of a thorough understanding regarding the mechanistic processes regulating otolith elemental incorporation, there is concern that observed elemental compositions may reflect differences in temperature, salinity, or growth rate rather than differences in ambient water chemistry. Most studies have found that salinity effects most commonly occur in a range of 10 to 30 (Elsdon and Gillanders 2002; Thresher 1999). As all of my locations are nearshore marine waters where salinity exceeds 30, this is likely not a concern. There was no evidence for significant differences in size-at-age among these collection locations ($F = 1.5$, error $df = 92$, $p = 0.25$), reducing the probability of growth rate effects. If oceanographic factors, such as temperature, altered the incorporation of trace elements into otoliths, these factors would most probably represent real differences in water quality among locations and thereby support the premise that

these fish were in different water masses. It is clear, however, that more information on the relationship between otolith elemental composition and ambient water chemistry would aid the interpretation of otolith elemental composition.

Why was classification success greater for otolith core signatures, which represented a diversity of years, than for edge signatures, which all represent the same year? There were significantly lower levels of Zn and Pb in the otolith core signatures for Gold Beach (GB) samples, which contributed to the greater classification accuracy of core signatures. Alternatively, as previously mentioned, increases in the level of Ca-binding proteins can decrease the endolymph calcium, thereby altering the ratios of other elements incorporated into the otolith. Edge measurements were from adult fish that may have been in different reproductive states, and thereby displayed more variation in their otolith composition. However, the mean variances were not significantly greater for the edge, compared to core, measurements, as one would expect if this were the case. Additional sample collection over multiple years and made comparisons between otolith regions that represent more similar time periods may address these questions.

The 68% jackknifed site classification accuracy observed with otolith geochemical signatures at both the otolith core and edge supports the idea that there are significant alongshore differences in marine water chemistry that result in identifiable geochemical otolith signatures. The fact that fish which range in age from 4 to 12 years group together by collection location based on their otolith elemental core signatures suggests that these fish have remained, relative to the other collection locations, in their

respective geographic regions throughout their life. Furthermore, it suggests that at least some regional differences in water chemistry may be consistent over time.

Microsatellite data provide evidence, based on genotype frequencies, for population structure between Washington and Oregon samples. Based on allele frequencies, there were significant differences among all samples > 90 km apart. R_{ST} values were more variable than F_{ST} and identified divergence only between Grays Harbor, Washington and Cape Arago, Oregon. This may be due, in part, to differences in how these estimates perform under variable sample sizes and different levels of population subdivision as reported in Bentzen et al. (1996). Although there was no evidence for isolation-by-distance, I only examined four geographic locations within 500 km, a sampling protocol which reduced my ability to identify such a pattern. Related work on juvenile black rockfish collected from five geographic locations within this same geographic region displayed weak evidence for isolation-by-distance using the same seven microsatellites reported in this study ($R^2 = 0.50$, $p = 0.05$, for 10 replicate data sets with N per population = 1000).

The level of genetic divergence observed in this study ($F_{ST} = 0.017 \pm 0.004$) over a range of 500 km is remarkably similar to previous reports for *Sebastes* spp. For example, Withler et al. (2001) examined five microsatellites of Pacific ocean perch (*S. alutus*) from 14 sites in British Columbia, Canada. They report a mean pair-wise F_{ST} of 0.015 ± 0.008 (± standard deviation) over an 800 km geographic range. Buonaccorsi et al. (2002) examined six microsatellites of copper rockfish (*S. caurinus*) along the West

Coast of North America and found significant population subdivision among coastal samples with significant pair-wise F_{ST} comparisons observed in sites < 900 km apart. Roques et al. (2002) examined eight microsatellites of North Atlantic redfish (*S. mentella*) across a 6000 km geographic range. Although they found large variation in the level of population subdivision across this range, there was significant population division between samples from Newfoundland and the Grand Banks (F_{ST} = 0.015) that were < 200 km apart. Roques et al. (2002) note that this level of genetic divergence is high for marine fish in such close geographic proximity with no apparent barriers to dispersal. These studies indicate that the establishment of population structure in *Sebastes* spp., even with their extended pelagic larval durations, may occur on relatively small spatial scales.

The only other empirical data available on the movement of individual *Sebastes melanops* are reported in Mathews and Barker (1983). Their studies on the recapture of tagged *Sebastes melanops* adults found that 63% (based on 8 recaptures) and 69% (based on 77 recaptures) of the fish were collected within 300 m of their release site. Interestingly, these estimates of site fidelity, or philopatry, are remarkably similar to those generated with otolith microchemistry (jackknifed average = 70%) and DNA microsatellites (63.1 and 74.6%, with five and seven loci, respectively).

So how much exchange occurs among *Sebastes melanops* "populations" along the Oregon/Washington coast? Based on classification success, otolith microchemistry and microsatellite data suggest that 30% of the individuals within a "population" came from

outside that "population". The number of migrants per generation, *Nm*, estimated from microsatellite data was 11 to 16. Similarly, related work on juvenile black rockfish indicated that > 70% of the juveniles may move < 120 km within their first year (Miller & Shanks, in review). Overall, the combined evidence based on otolith microchemistry and DNA microsatellites indicate that about 70% of black rockfish may move very little throughout their entire life.

Are these results biologically meaningful? Black rockfish are part of the *Sebastes* complex, which is a diverse species assemblage that has been compared to the African cichlids (Johns and Avise 1998). Although some speciation events are most probably due to allopatry (i.e. speciation with geographic separation), sympatric (i.e. without geographic separation) speciation has likely occurred many times. Characteristics that may promote sympatry include mate recognition, species-specific courtship rituals, and internal fertilization. Limited larval dispersal in conjunction with minimal adult movements would aid the segregation of populations and subsequent divergence. Similar mechanisms may have aided the development and maintenance of sympatric *Sebastes* species.

The number of migrants per generation (*Nm*) that is theoretically adequate to maintain genetic diversity would vary if fishing effort is considered in addition to highly variable larval recruitment. Harvest effects on long-lived species with variable recruitment success would be dramatically different in populations with larval export of 20% vs. 80%. The recovery of a depleted population depends not only on the size and

proximity of adjacent populations but also on the proportion of larvae from those populations that disperse widely enough to provide new recruits to the depleted population. Therefore, the rate of recovery of such a population could be substantially slower in species with 80% vs. 20% self-recruitment. The design and establishment of successful marine protected areas (MPAs) for both the species recovery and conservation requires knowledge of larval dispersal distance and the fraction of natural reproduction required for population persistence (Botsford et al. 2001). Techniques that can provide such information will be invaluable for both harvest regulations and conservation strategies, particularly in the design and placement of MPAs.

The increased resolution associated with current technologies, such as otolith elemental and DNA microsatellite analyses, is rapidly increasing the amount of information available for understanding population ecology of marine organisms. Comparative approaches such as this study provide: 1) independent verification of two relatively new techniques and 2) information useful for both population ecology and fisheries management. In particular, otolith microchemistry can be combined with DNA microsatellites to generate information on both ecological and evolutionary time scales, and thus provide comparative information on population structure as well as potential isolating mechanisms.

Bridge

Chapter VI, "Spatial and temporal variation in the otolith microchemistry of staghorn sculpin (*Leptocottus armatus*)," further examines the potential of otolith microchemistry to provide information on individual movements in coastal fish. The following chapter takes a detailed look at the scales of variation in the otolith microchemistry of a marine species often found within estuaries during its early life history. This study provides information on variation in otolith microchemistry among as well as within estuaries in Oregon and California.

Chapter VI

Spatial and temporal variation in otolith microchemistry of the staghorn sculpin (*Leptocottus armatus*)

Introduction

Otolith microchemistry is increasingly used in fisheries research to address questions about stock identification, sources of larvae, and migratory pathways. This type of research is typically based on a number of assumptions. One major assumption, although not yet fully validated, is that if fish reside in water masses with different chemical properties, those properties will be reflected in otolith microchemistry (Campana and Thorrold 2001; Thresher 1999). Another primary and well supported assumption is that otolith growth is continuous with no evidence of resorption. Thus, the otolith provides a permanent chronological record that can be used to reconstruct aspects of an individual's environmental history (Campana 1999; Campana and Thorrold 2001; Thresher 1999). The primary interest of this study is to evaluate the potential for otolith microchemistry to provide information on the movement patterns of individuals.

In laboratory validation studies, certain trace elements, when standardized by calcium, are consistently incorporated in otoliths in proportion to ambient water chemistry, including strontium (Sr), barium (Ba) (Bath et al. 2000; Elsdon and Gillanders

2003; Milton and Chenery 2001), mercury (Hg), and lead (Pb) (Geffen et al. 1998). However, in studies using juvenile black bream (*Acanthopagrus butcheri*), otolith manganese (Mn) to calcium ratios were not related to water chemistry (Elsdon and Gillanders 2003). Furthermore, water temperature and salinity can alter the otolith incorporation of Sr and Ba (Elsdon and Gillanders 2002; Fowler et al. 1995). Numerous studies have reported significant variation in certain trace elements, including Mg, Mn, Sr, and Ba, in the otoliths of fish collected from different geographic regions, and such differences led to relatively good discrimination among those groups (Gillanders 2002; Hamer et al. 2003; Miller and Shanks in review, Thresher 1999, for review).

Studies have documented significant differences in the otolith elemental composition of fishes collected from areas with distinct seawater chemical signals, such as along salinity gradients (Secor et al. 1995; Secor et al. 2001) or in coastal versus open ocean environments (Forrester and Swearer 2002; Swearer et al. 1999). Less information, however, is available on how otolith elemental composition varies within more similar environments and over time within the same environment (but see Gillanders 2002; Gillanders and Kingsford 2003; Hamer et al. 2003). There is a need for studies that quantify variation in otolith elemental composition at various scales, i.e. among and within bays and estuaries, throughout ontogeny, and between years.

As understanding of the spatial and temporal scales of variability in otolith microchemistry increases, the potential of otolith microchemistry to provide novel insights in the biology, ecology, and behavior of fishes will also expand. The usefulness

of otolith chemistry in addressing questions of stock structure, the sources of new recruits, and the relative movements of larvae, juvenile, and adult fishes requires knowledge of the spatial and temporal variation in otolith elemental composition, the mechanisms that regulate that variation, and our ability to detect and quantify such variation. For example, some knowledge of variation, both spatial and temporal, in otolith elemental composition is necessary to accurately identify larval and/or juvenile source signatures. Furthermore, detailed information on the movements of individuals, such as migratory or dispersal pathways, can be gained with a greater understanding of the environmental and biological variation associated with otolith elemental incorporation. Specifically, the intent of this study is to quantify variation in the otolith elemental chemistry of staghorn sculpin (*Leptocottus armatus*) in order to assess its potential to provide information on the movement of individuals.

The life history characteristics of the staghorn sculpin (*Leptocottus armatus*) make it an ideal candidate to address certain questions about otolith microchemistry. Estuarine waters are typically enriched in terms of metal concentrations in comparison with offshore waters. There are also differences in watershed characteristics, such as geology and precipitation patterns, that can lead to differences in water chemistry among estuaries. These differences have proved useful for classifying fish to their collection estuary based on the chemical composition of their otoliths (Forrester and Swearer 2002; Gillanders and Kingsford 2003; Thorrold et al. 1998). Therefore, distinct otolith elemental signatures are likely to occur in *L. armatus* collected from different estuaries.

Furthermore, strontium, due to its positive relationship with salinity, has been used to successfully chart migration patterns of anadromous fishes (Limburg 1995; Secor et al. 1995; Secor et al. 2001). If *L. armatus* larvae spend extended periods in coastal waters outside of estuaries, there is a high probability of elevated strontium to calcium ratios in their otoliths during that period. Finally, spatial differences at comparatively small scales, i.e. within estuaries, can be examined due to the large abundance of juvenile *L. armatus* within estuaries along the west coast of the United States.

The staghorn sculpin (*Leptocottus armatus)* is a ubiquitous NE Pacific coastal species, ranging from the Bering Sea to Baja California. Adults are found in shallow waters, typically between 0 and 156 m in depth. Larvae, juveniles, and at times adults, are found in estuaries where they can dominate the community both numerically and in biomass (Bottom et al. 1987). *L. armatus* are classified as a non-dependent marine fish, i.e. those commonly found in lower reaches of estuaries but do not depend on them to complete their life cycle (Moyle and Cech 1996). These demersal, oviparous fishes typically reach maturity at sizes > 10 cm and usually spawn in late fall through winter in bays and estuaries, and possibly along the open coast (Jones 1962; Tasto 1975). Hatching can occur within 10 d and is followed by a four to six week larval period. Larvae have been reported to remain in brackish waters during their development (Jones 1962) but their movements are not well described. Although larvae can survive across a range of salinities, the greatest larval survival was reported to occur at salinities from 17

to 26 (Jones 1962). Adults, it is assumed, migrate back into coastal waters after spawning (Tasto 1975).

In order to quantify spatial and temporal variation in otolith microchemistry, I examined staghorn sculpin (*Leptocottus armatus*) collected within estuaries from the Columbia River at the Washington/Oregon state border to Humboldt Bay, California. I addressed a number of questions: 1) Are there significant differences in the otolith chemistry of *L. armatus* collected from different estuaries and from different sites within those estuaries? 2) At what spatial scales are such differences detectable? 3) Do otolith elemental concentrations, whether due to intrinsic or extrinsic factors, vary throughout ontogeny? 4) Is there interannual variation in otolith elemental composition? And, if so, how large is that variation and how does it compare to spatial and intra-annual variation? 5) Which, if any, elements provide discriminatory information on the collection location among and within bays?

Methods

I tested five hypotheses. 1) The null hypothesis that the otolith elemental composition of *Leptocottus armatus* otoliths does not vary among estuaries was tested with juveniles collected from three locations, the Columbia River estuary (CR) and Cape Arago (CA), Oregon and Humboldt Bay (HB), California (Fig. VI.1). 2) The null hypothesis that the otolith elemental composition of *L. armatus* does not vary between sites within estuaries was tested with juveniles collected from two sites in the Columbia River and Humboldt Bay estuaries. Bays were located between approximately 285 km

and 610 km apart. Sites within the Columbia River and Humboldt Bay were < 5 km apart. Both hypotheses were tested with juveniles collected in 2002. 3) The null hypothesis that the elemental composition of *L. armatus* otoliths within a site are stable (i.e. do not vary significantly) over time (two years) was tested with juveniles collected in 2001 and 2002 from the South Slough National Estuarine Research Reserve in Cape Arago. 4) The null hypothesis that the elemental composition of *L. armatus* otoliths does not vary during ontogeny (i.e. across the otolith growth axis) was tested by examining multiple transects at discrete locations along the otolith growth axis (i.e. otolith core, middle, and edge) of all juveniles collected in 2002. 5) The null hypothesis that otolith elemental composition is not useful in predicting collection location was tested with juveniles collected from five sites in three bays: Columbia River Channel (CRC) (46°12'28"N; 123°55'45"W); Columbia River Old Young's Bridge (CR-OYB) (46°09'59"N; 123°54'05"W); Coos Bay South Slough (CB-SS) (43°16'36"N; 124°19'05"W); Humboldt Bay South Bay (HB-SB) (40°43'40"N; 123°13'20"W); and Humboldt Bay South Jetty (HB-SJ) (40°44'40"N; 123°13'36"W) (Fig. VI.1). Predictions were made based on otolith elemental composition at three discrete otolith regions (i.e. otolith core, middle, and edge), each representing a different life history period.

Fish collection and otolith preparation

Juveniles were collected by seine on 24 May 2001 and between 23 March and 15 June 2002. Fish were measured to the nearest 0.1 m prior to otolith removal. Sagittal otoliths were removed within 2 d of collection for all except the Columbia River Channel

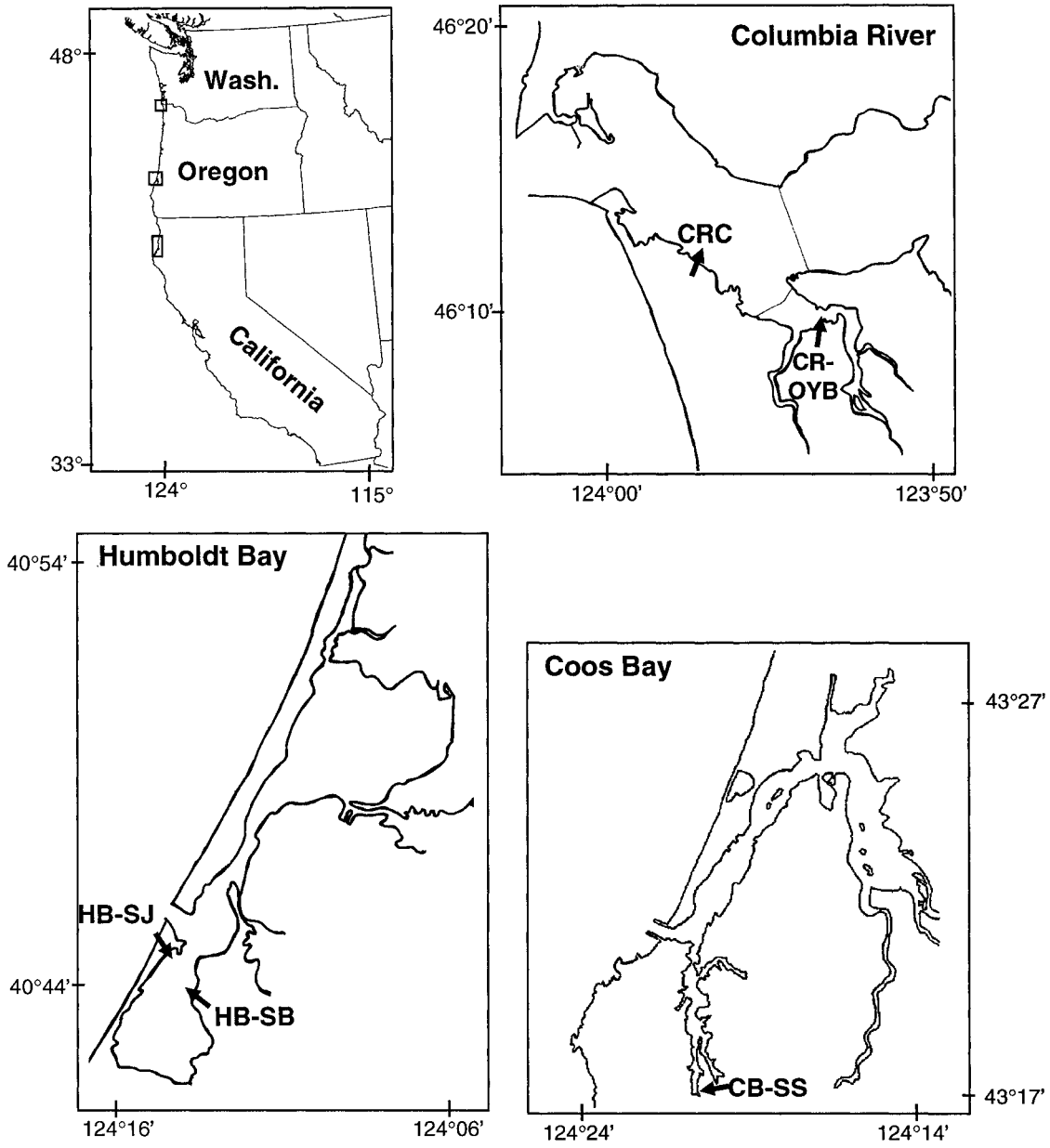

Fig.VI.1 Collection locations of staghorn sculpin (*Leptocottus armatus*) used in the otolith microchemistry study. a) the region of study; b) the Columbia River Channel (CRC) and Old Young's Bridge (CR-OYB) sites; c) Humboldt Bay's South Jetty (HB-SJ) and South Bay (HBSS) sites; and d) Coos Bay's South Slough (CB-SS) sites.

samples which were briefly (< 2 mos.) frozen. Otoliths were removed with acid-washed plastic forceps, cleaned, measured (to the nearest 0.1 mm), weighed (to the nearest 0.01 mg), embedded in resin, and ground to expose the otolith core. Otoliths were ultrasonically cleaned in NANOpure® water, dried, and stored in acid-washed plastic vials prior to embedding in resin. Otoliths were ground with 3M™ Tri-m-ite wetordry™ paper (240 to 1200 grit), polished with Buehler AlO_2 powder (12.5 µm and 3.0 µm), and again cleaned ultrasonically for 15 min.

Trace-element analysis

A laser ablation–inductively coupled plasma mass spectrometer (LA–ICPMS) was used for otolith elemental analyses. The work was completed at Oregon State University's WM Keck Collaboratory for Plasma Spectrometry in Corvallis, Oregon using a VG PQ ExCell ICPMS with a New Wave DUV193 excimer laser. The laser was set at a pulse rate of 15 Hz with a 40 µm spot ablation size. The high calcium content of otoliths can cause significant buildup inside the sample chamber and quadrupole. To avoid biased data collection, background levels of ^{43}Ca were monitored for accumulation in the spectrometer, and skimmer cones and gas tubing were cleaned daily. I collected no data during a period with elevated background calcium levels.

Time-resolved software (PlasmaLab®) allowed analyte (i.e. ^{25}Mg, ^{43}Ca, etc.) measurements to be made at discrete positions on the otolith and integrated and averaged for each element collected. Only left otoliths were used in all analyses. All transects were located in the anterior dorsal quadrant and extended from the otolith core to the edge.

Preliminary analyses indicated no difference in analyte concentrations between multiple transects in the anterior dorsal quadrant (paired t-tests, $n = 9$, $p > 0.20$, df = 16). Further preliminary analyses of otoliths indicated that the following ten analytes were at concentrations that were well above background levels: ^{25}Mg, ^{43}Ca, ^{48}Ca, ^{55}Mn, ^{66}Zn, ^{86}Sr, ^{87}Sr, ^{138}Ba, and ^{208}Pb. The average %RSD (relative standard deviation) for National Institute of Standards and Technology (NIST) glass plates during data collection were as follows : ^{25}Mg = 11.1 %, ^{43}Ca = 3.7%, ^{48}Ca = 3.4%, ^{55}Mn = 4.4%, ^{66}Zn = 8.2%, ^{86}Sr = 6.3%, ^{87}Sr = 5.4%, ^{138}Ba =5.2%, ^{208}Pb = 7.6%. The minimum detection levels for the VG PQ ExCell ICPMS are 1-10 parts per trillion (ppt) for Mg, Ca, Mn, and Zn and < 0.1 – 1 ppt for Sr, Ba, and Pb.

Trace-element composition in NIST glass standards is homogenous and elemental concentrations are reported in Pearce et al. (1997). A NIST standard was run with each otolith sample; this allowed all otolith transects to be standardized to account for instrument drift or day-to-day variations in instrument sensitivity across the atomic mass range. Background analyte levels were determined with an argon gas blank prior to each transect and subtracted from both mean otolith and NIST glass slide measurements. Elemental data (in counts $second^{-1}$) were standardized by ^{43}Ca to adjust for variability in instrument sensitivity and the amount of ablated material (Campana et al. 1997). Measured element to calcium ratios from NIST glass slides were then multiplied by known NIST concentrations to generate a correction factor. Otolith element to calcium

ratios were then multiplied by the NIST correction factor collected at the same time as the otolith measurement.

I examined, on each otolith, three 120 μm laser ablation transects. These transects were located at 1) the otolith core, 2) its outer edge, and 3) midway between the core and edge transects. The transect in the otolith core began at the primordium and extended 120 μm, providing information from the egg and early larval periods. The edge transect encompassed the final 120 μm of otolith material, providing information on the juvenile period just prior to field collection of the fish. The intermediate transect was also 120 μm long and was located mid-way between the core and the edge transects, providing information on the larval period. There was no spatial overlap of transects on an individual otolith. Otolith-increment width averaged 7.6 μm ± 2.1 μm and ranged from 4 μm to 13 μm. Therefore, each transect represented, on average, 16 d. This sampling protocol provided information on otolith elemental composition at the time of collection (the otolith edge transect) as well as during ontogeny (the otolith core and middle transects).

Statistical analysis

Spatial and temporal variation

Analysis of variance (ANOVA) was used to examine spatial and temporal differences in otolith chemistry. A one-way ANOVA was used to examine the spatial differences in *Leptocottus armatus* otolith chemistry 1) among bays and 2) between sites within bays. Two separate analyses were completed to examine differences within 1) the

Columbia River, between the Channel and Old Young's Bridge sites, and 2) Humboldt Bay, between the South Jetty and South Bay sites. To determine if there were significant effects of otolith region (i.e. the core, middle, and edge) on otolith chemistry, all fish collected in 2002 were combined. A one-way ANOVA was then used to test for differences in elemental composition among otolith regions. The interannual variation in otolith chemistry (2001 vs. 2002) was examined with a two–factor ANOVA, with otolith region and year as fixed factors, using the samples collected in Coos Bay at the South Slough site.

Otolith element data required transformation to attain normality and homogeneity of variance. Following transformation, however, the homogeneity of variance was still not met in all cases (i.e. $Mg{\bullet}Ca^{-1}$, $Zn{\bullet}Ca^{-1}$, and $Ba{\bullet}Ca^{-1}$, Levene's test, $p < 0.01$). ANOVA was still used in these cases because 1) the differences between the smallest and largest variances were not excessively large (i.e. $F_{max} < 7.0$), 2) non-parametric alternatives such as the Kruskal Wallis test also require homogeneity of variance, and 3) ANOVA is fairly robust to such deviations when sample sizes are relatively large, i.e. > 10 (Quinn and Keough 2002). In this study, $N > 15$ in all cases except Humboldt Bay South Bay ($N = 7$). When significant differences among means were observed, pair-wise comparisons were made with Scheffé's post-hoc comparison test. The Type I error rate is increased in cases with heterogeneous variances (Day and Quinn 1989). Therefore, the significance level for multiple comparisons of the $Mg{\bullet}Ca^{-1}$, $Zn{\bullet}Ca^{-1}$, and $Ba{\bullet}Ca^{-1}$ ratios was adjusted ($p = 0.01$) to reduce the probability of Type I errors.

Quadratic discriminant function analysis (DFA) was used to group individuals based on their otolith elemental signatures. The primary goals of DFA are to 1) find dimensions along which groups of interest differ, and 2) to find classification functions to predict group membership (Tabachnick and Fidell 2001). Quadratic DFA does not assume equal variance-covariance matrices. Two classifications were completed; 1) fish were classified to an estuary (i.e. Columbia River estuary, Coos Bay, or Humboldt Bay) and 2) to a site within an estuary (i.e. Columbia River Channel, Columbia River Old Young's Bridge, Coos Bay South Slough, Humboldt Bay South Bay, or Humboldt Bay South Jetty). The best validation of a discriminant function classification is the assignment accuracy of new cases (i.e. those not used in the development of the original classification algorithm). When sample sizes are not large enough to generate two independent datasets, jackknifed predictions are typically used to provide a more realistic estimate of the ability of the predictor variables to separate groups. Jackknifed classifications represent the average of N classifications, where N = sample size, in which one observation was removed each time. In this study, sample sizes were large enough at all sites except Humboldt Bay's South Bay (HB-SB) to split samples in half. Therefore, in all analyses that did not include HB-SB, I generated classifications for jackknifed data and "new", or previously unassigned, individuals in order to evaluate the accuracy of the jackknifed classifications. Statistica® and Systat® statistical software programs were used for these analyses.

Scales of variation

Two measures were used to quantify the scales of variation in otolith elemental composition observed in the study; 1) coefficients of variation (CV) (100 * (standard deviation•mean^{-1})) and 2) the maximum percent difference for pair-wise comparisons of mean metal•Ca^{-1} ratios (100 * (the largest metal•Ca^{-1} ratio divided by the smallest metal•Ca^{-1} ratio)). The CVs were calculated for the metal•Ca^{-1} ratios of Mg, Mn, Zn, Sr, Ba, and Pb at the scale of bay, site, and otolith region. The maximum percent difference in mean metal•Ca^{-1} ratios was determined for bays, sites, otolith regions, and years. All calculations were completed on transformed data. These measures provide information on the magnitude of elemental differences in *L. armatus* otoliths and provide insight into how each element varied at the spatial and temporal scales examined. Such information aids the identification of spatial and temporal patterns in otolith elemental chemistry and will help assess its utility for tracking the movement of individuals within and among estuaries.

Results

The collection date, sample size (N), size range, and mean size ± standard deviation of the *Leptocottus armatus* used in the study are reported in Table VI.1. In 2002, mean size ± standard deviation (standard length, mm) was 52.9 (± 15.0), and ranged from 41.7 (± 7.02) at the Humboldt Bay South Jetty (HB-SJ) site to 71.8 (± 9.8) at the Columbia River Old Young's Bridge site (CR-OYB). Mean size of Coos Bay South Slough (CB-SS) fish was 60.6 (± 4.3) in 2001 and 44.9 (± 7.0) in 2002. Otolith length

(mm) was positively and significantly correlated with fish length ($R^2 = 0.96$, $p < 0.001$, N = 93).

Table VI.1. The collection site, day and year of collection, sample size (*N*), size range and average size ± standard deviation (standard length, in mm) for *Leptocottus armatus* juveniles used in otolith microchemistry study.

Collection site	Collection date	Year	*N*	Size range (mm)	Average size (mm)
Columbia River, Channel	15 May	2002	17	39-77	52.9 ± 12.1
Columbia River, Old Young's Bridge	15 June	2002	22	54-96	71.8 ± 9.8
Coos Bay, South Slough	24 May	2001	15	53-72	60.6 ± 4.3
Coos Bay, South Slough	24 March	2002	23	38-63	44.9 ± 6.9
Humboldt Bay, South Jetty	23 March	2002	17	27-58	41.7 ± 7.02
Humboldt Bay, South Bay	23 March	2002	7	27-66	50.0 ± 14.8

Bays

Otolith elemental composition varied significantly among bays for nearly all elements examined. The metal to calcium ratios were different for Mg, Mn, Sr, Ba, and Pb but not for Zn (Table VI.2). The statistically significant differences in Mg, Mn, Sr, and Ba were due to differences in the Columbia River estuary samples compared with the other two bays, Coos and Humboldt Bays, which were not statistically different. The Columbia River estuary samples had the highest metal to calcium ratios of Mg, Mn, and

Ba and the lowest of Sr (Scheffé post-hoc comparison, df = 242, $p < 0.001$) (Fig.VI. 2). Relatively high ratios of $Pb \bullet Ca^{-1}$ distinguished Humboldt Bay (Scheffé post-hoc comparison, df = 242, $p < 0.001$) from the Columbia River estuary and Coos Bay, where ratios of $Pb \bullet Ca^{-1}$ were not different (Fig. VI.2).

Sites within bays

Otolith elemental composition varied significantly between sites in both the Columbia River estuary and Humboldt Bay. Significant site variation in the Columbia River occurred in the metal to calcium ratios of Mg, Ba, and Zn (Table VI.3). In Humboldt Bay, significant site variation occurred in the metal to calcium ratios of Mn, Ba, and Pb (Table VI.4). Data transformation did not remove the heterogeneity of variance in the $Mg \bullet Ca^{-1}$ ratios. When a conservative significance level ($p = 0.01$) was applied to the analysis, the difference in the $Mg \bullet Ca^{-1}$ ratios between Humboldt Bay sites ($p = 0.04$) is not significant. The significant differences between the Columbia River sites were due to larger ratios of $Mg \bullet Ca^{-1}$ and $Zn \bullet Ca^{-1}$ and smaller ratios of $Ba \bullet Ca^{-1}$ in Channel samples compared with Old Young's Bridge samples (Scheffé post-hoc comparison, df = 109, $p < 0.001$) (Fig. VI.3). In Humboldt Bay, the South Jetty samples had smaller $Mn \bullet Ca^{-1}$ and $Ba \bullet Ca^{-1}$ and larger $Pb \bullet Ca^{-1}$ ratios than South Bay samples (Scheffé post-hoc comparison, df = 69, $p < 0.001$). The only ratio that varied significantly between sites in both bays was $Ba \bullet Ca^{-1}$.

Table VI.2. The results of the ANOVA used to test for the effect of bay on the otolith elemental composition of *Leptocottus armatus*. The Columbia River estuary, Coos Bay, and Humboldt Bay were included in analysis.

Bay effect	**MS**	**df**	**F**	**p**
log ^{25}Mg				
Bay	1.12	2	42.15	<0.001
Error	0.03	248		
log ^{55}Mn				
Bay	6.58	2	157.66	<0.001
Error	0.04	248		
sqrt ^{66}Zn				
Bay	<0.001	2	0.71	0.49
Error	<0.001	248		
log ^{87}Sr				
Bay	0.36	2	85.69	<0.001
Error	0.004	248		
log ^{138}Ba				
Bay	7.17	2	43.35	<0.001
Error	0.17	248		
log ^{208}Pb				
Bay	11.41	2	82.02	<0.001
Error	0.14	248		

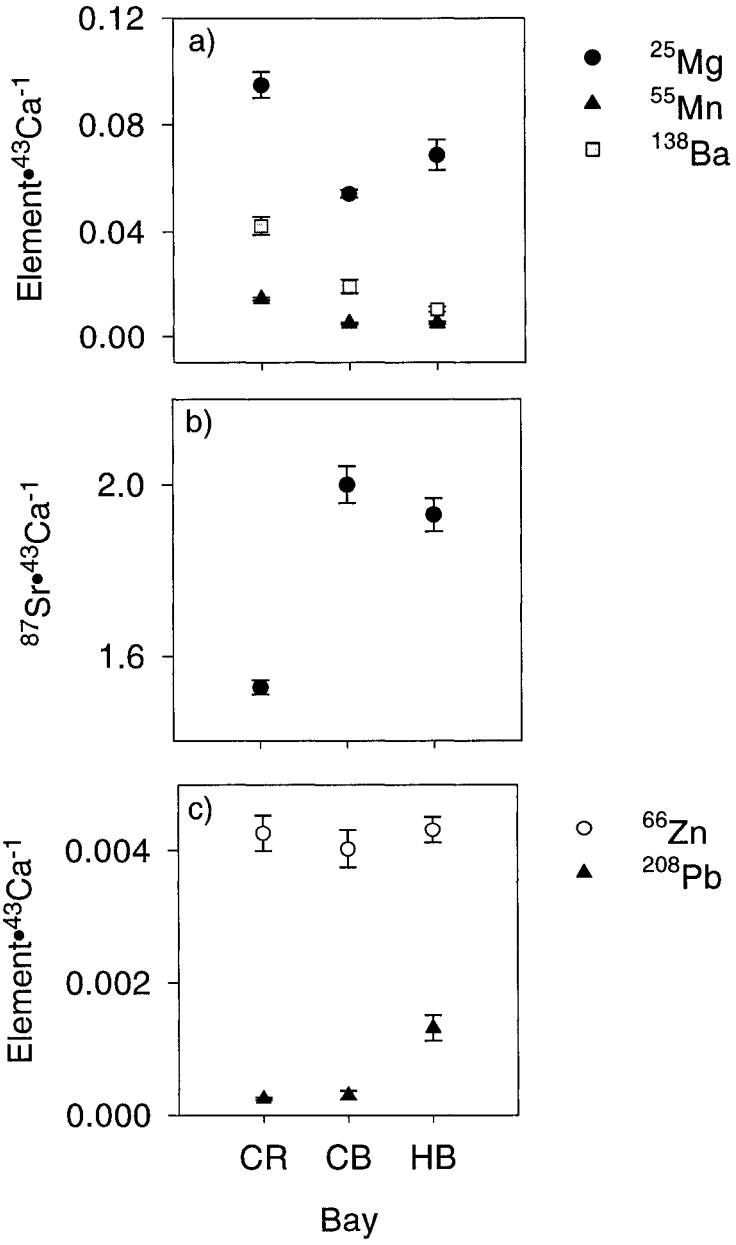

Fig. VI.2. The 2002 bay average otolith metal•Ca-1 ratios for staghorn sculpin (*Leptocottus armatus*) collected from Columbia River estuary (CR), Coos Bay (CB), and Humboldt Bay (HB). Bay averages (± standard error) are for a) $^{25}Mg•Ca^{-1}$ (black circles), $^{55}Mn•Ca^{-1}$ (black triangles) and $^{138}Ba•Ca^{-1}$ (gray squares), b) $^{87}Sr•Ca^{-1}$, and c) $^{66}Zn•Ca^{-1}$ (open circles) and $^{208}Pb•Ca^{-1}$ (black triangles). Sample sizes are CR = 39, CB = 23, HB = 24.

Otolith region

There were significant differences in elemental composition among otolith regions (i.e. core, middle, and edge). These data are presented in two ways: 1) the metal to calcium ratios for each otolith region averaged over all samples (Fig. VI.4) and 2) the metal to calcium ratios for each otolith region averaged by bay (Fig. VI.5). In order to test the effect of otolith region independent of collection location, all fish were pooled for statistical analyses. Highly significant differences among otolith regions were observed in the metal•Ca^{-1} ratios of Mn, Sr, and Ba. No significant differences were detected in Mg•Ca^{-1} or Pb•Ca^{-1} ratios (Table VI.5). The significant differences among otolith regions were primarily due to elevated ratios of Mn•Ca^{-1}, Sr•Ca^{-1}, and Ba•Ca^{-1} at the otolith edge (Scheffé post-hoc comparison, $df = 248$, $p < 0.001$) (Fig. IV.4 and IV.5). There were no significant differences in Mn•Ca^{-1} and Sr•Ca^{-1} between the otolith middle and core transects. The relative amount of barium was significantly different at all three otolith regions; the Ba•Ca^{-1} ratios increased consistently from the otolith core to the edge (Scheffé post-hoc comparison, $df = 248$, $p < 0.001$).

Table VI.3. The results of the ANOVA used to test for the effect of site on the otolith elemental composition of *Leptocottus armatus* collected from the Columbia River estuary, Oregon. Sites were the Channel and Old Young's Bridge.

Site effect Columbia River	**MS**	**df**	**F**	**p**
log ^{25}Mg				
Site	1.16	1	53.02	<0.001
Error	0.02	109		
log ^{55}Mn				
Site	0.06	1	1.93	0.17
Error	0.03	109		
sqrt ^{66}Zn				
Site	0.004	1	14.63	<0.001
Error	<0.001	109		
log ^{87}Sr				
Site	0.002	1	0.80	0.37
Error	0.003	109		
log ^{138}Ba				
Site	10.58	1	117.65	<0.001
Error	0.09	109		
log ^{208}Pb				
Site	<0.001	1	<0.001	0.99
Error	0.12	109		

Table VI.4. The results of the ANOVA used to test for the effect of site on the otolith elemental composition of *Leptocottus armatus* collected from Humboldt Bay, California. Sites were the South Jetty and South Bay.

Site effect Humboldt Bay	**MS**	**df**	**F**	**p**
log ^{25}Mg				
Site	0.15	1	4.54	0.04
Error	0.03	69		
log ^{55}Mn				
Site	0.47	1	8.75	0.004
Error	0.05	69		
sqrt ^{66}Zn				
Site	<0.001	1	0.09	0.77
Error	<0.001	69		
log ^{87}Sr				
Site	0.01	1	2.16	0.15
Error	0.005	69		
log ^{138}Ba				
Site	1.70	1	35.83	<0.001
Error	0.05	69		
log ^{208}Pb				
Site	1.69	1	12.94	<0.001
Error	0.13	69		

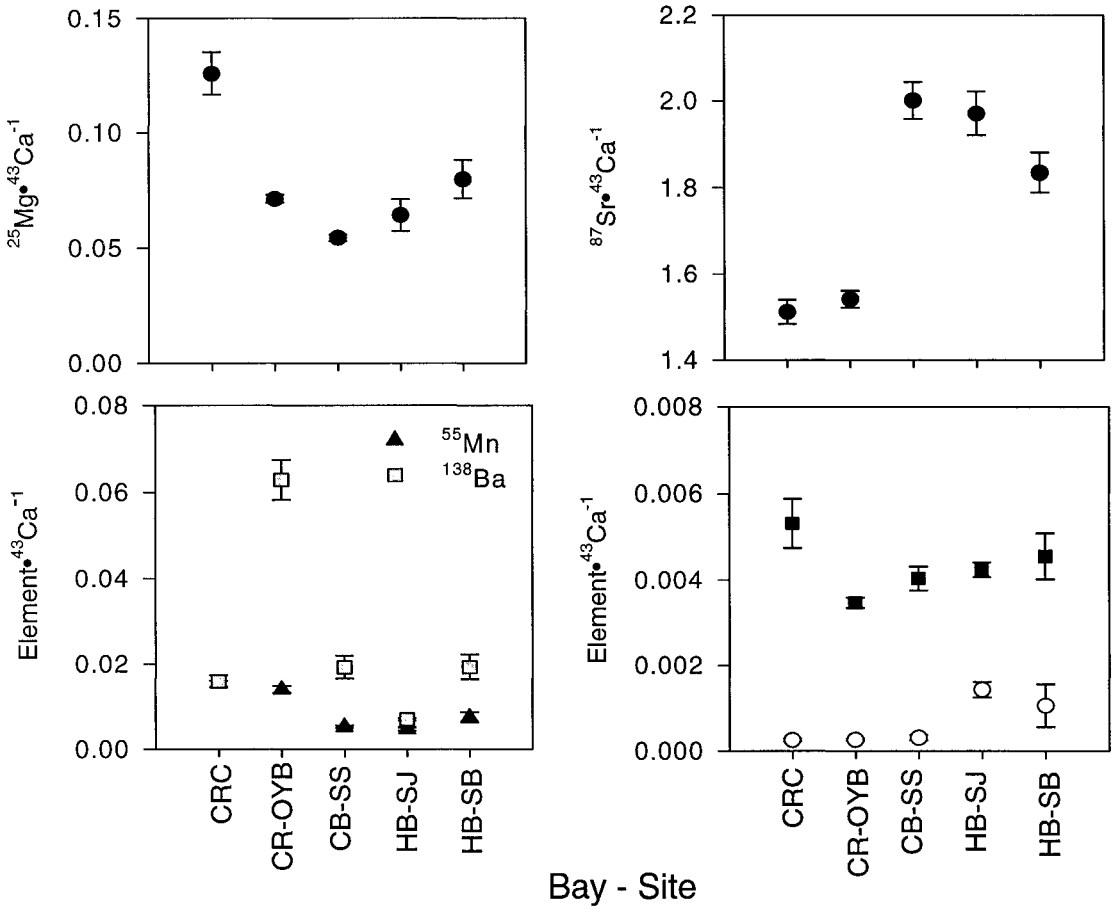

Fig. VI.3. The 2002 site average otolith metal•Ca^{-1} ratios for staghorn sculpin (*Leptocottus armatus*) collected from the Columbia River estuary Channel (CRC) and Old Young's Bridge (CR-OYB) sites, Coos Bay South Slough (CB-SS), and Humboldt Bay South Jetty (HB-SJ) and South Bay (HB-SB) sites. Site averages (± standard error) are for a) $^{25}Mg•Ca^{-1}$, b) $^{55}Mn•Ca^{-1}$ (black triangles) and $^{138}Ba•Ca^{-1}$ (gray squares), c) $^{87}Sr•Ca^{-1}$, and d) $^{66}Zn•Ca^{-1}$ (black squares) and $^{208}Pb•Ca^{-1}$ (open circles). Sample sizes are CRC = 17, CR-OYB = 22, CB-SS = 23, HB-SJ = 17, HB-SB = 7.

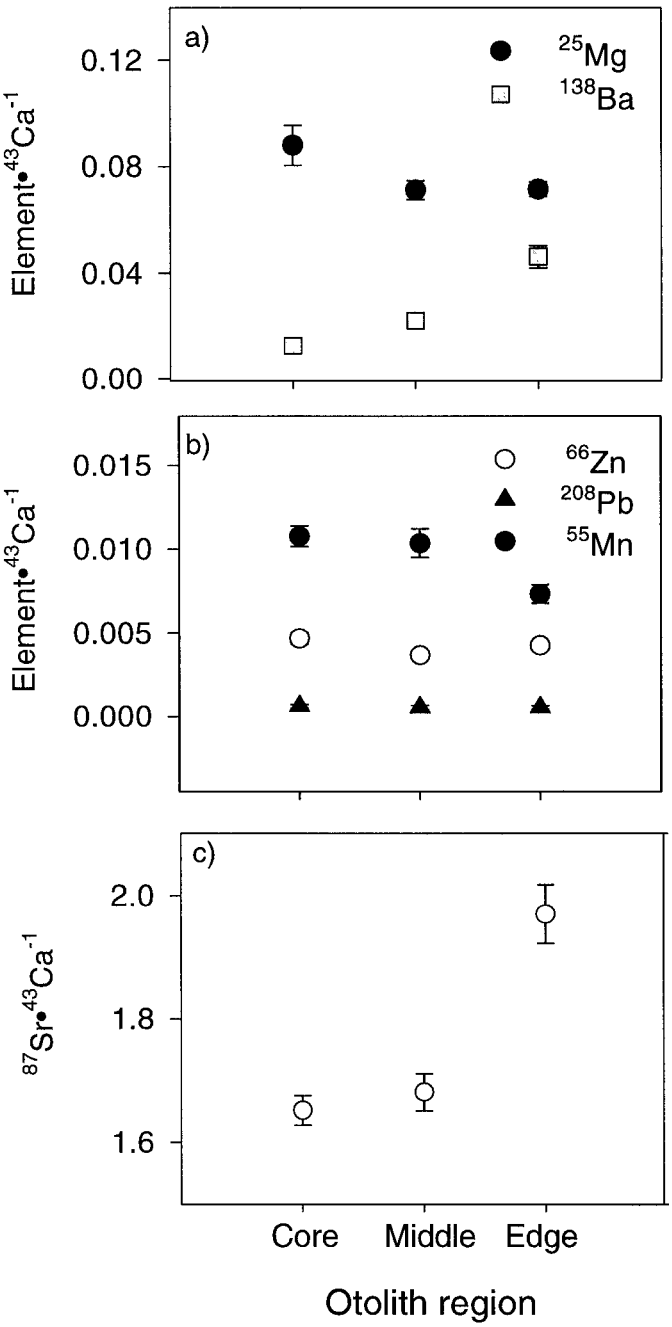

Fig. VI.4. The 2002 average metal•Ca^{-1} ratios for otolith regions (i.e. core. middle, and edge) in staghorn sculpin (*Leptocottus armatus*) collected from the Columbia River estuary, Coos Bay, and Humboldt Bay. All fish were grouped to generate averages (± standard error): a) $^{25}Mg•Ca^{-1}$ (black circles) and $^{138}Ba•Ca^{-1}$ (gray squares); b) $^{66}Zn•Ca^{-1}$ (open circles), $^{208}Pb•Ca^{-1}$ (black triangles), and $^{55}Mn•Ca^{-1}$ (black triangles); and c) $^{87}Sr•Ca^{-1}$. Sample size = 73 for each otolith region.

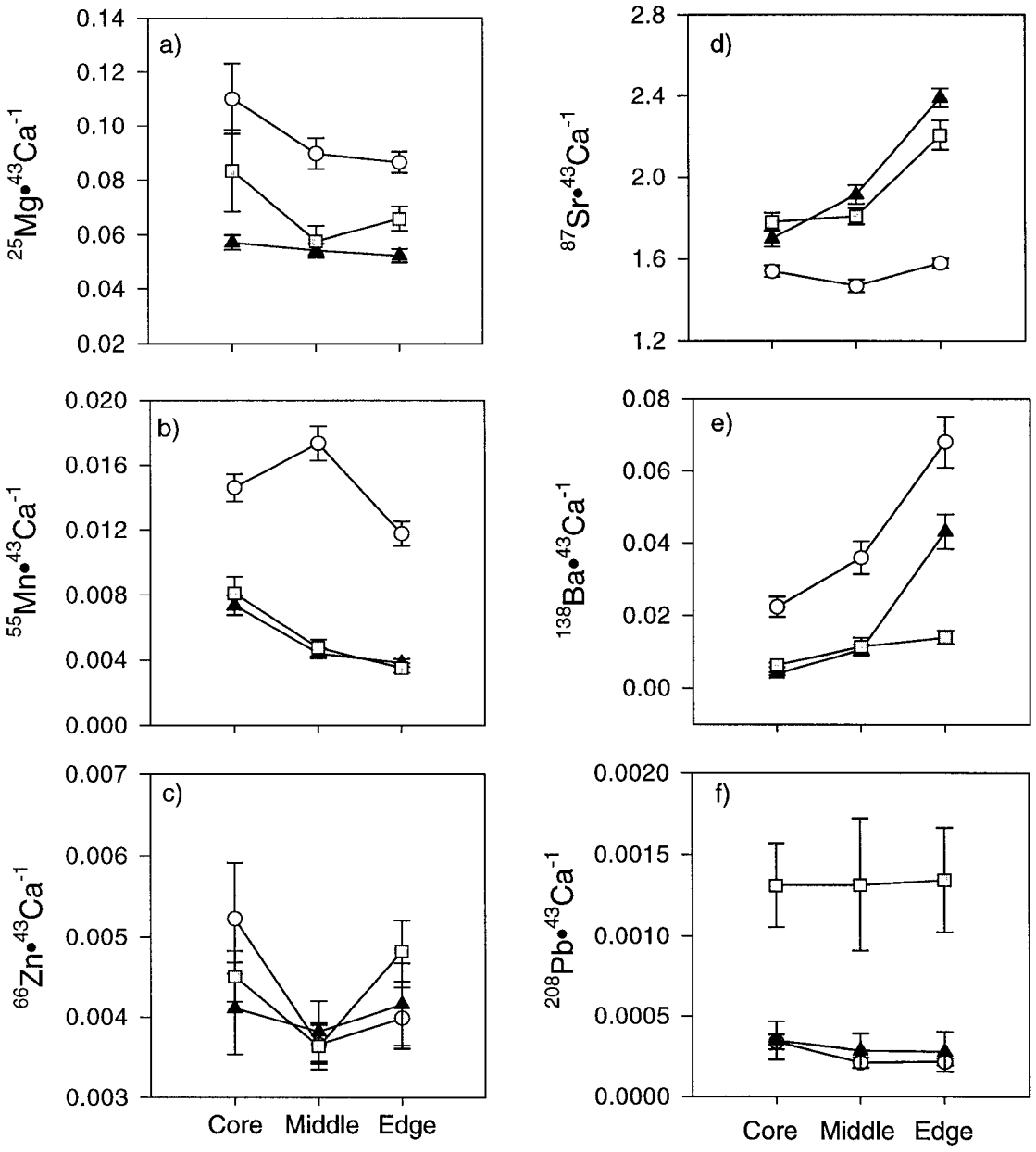

Fig. VI.5. The 2002 average metal•Ca^{-1} ratios for otolith regions (i.e. core. middle, and edge) in staghorn sculpin (*Leptocottus armatus*) separated by collection bay, i.e. the Columbia River estuary (N = 39, open circles), Coos Bay (N = 23, black triangles), and Humboldt Bay (N = 24, gray squares). Averages (± standard error) are presented for a) $^{25}Mg•Ca^{-1}$, b) $^{55}Mn•Ca^{-1}$, c) $^{66}Zn•Ca^{-1}$, d) $^{87}Sr•Ca^{-1}$, e) $^{138}Ba•Ca^{-1}$, and e) $^{208}Pb•Ca^{-1}$.

When all samples were pooled to generate averages for each otolith region, the ratios of $Sr•Ca^{-1}$ and $Ba•Ca^{-1}$ were found to increase from the otolith core to the edge while $Mn•Ca^{-1}$ decreased (Fig. VI.4). If comparisons among otolith region are made bay-by-bay, however, it is evident that changes in the $metal•Ca^{-1}$ ratios were quite different among bays (Fig. VI.5). Although the trends are similar and statistically significant, each element in one bay displays much less variation in the $metal•Ca^{-1}$ ratios across the otolith (i.e. $Mg•Ca^{-1}$ in Coos Bay, $Sr•Ca^{-1}$ in Columbia River, and $Ba•Ca^{-1}$ in Humboldt Bay) (Fig. VI.5a, VI.5d, VI.5e).

Interannual variation

Interannual variation in otolith element composition was examined with Coos Bay fish collected in March 2001 and May 2002. Differences between years (2001 vs. 2002) and among otolith regions were examined with a two-factor ANOVA. Highly significant differences between years and among otolith regions were observed in $metal•Ca^{-1}$ ratios for Mg, Mn, Sr, and Ba (Table VI.6). $Zn•Ca^{-1}$ and $Pb•Ca^{-1}$ ratios did not vary significantly between years. The general trend was for larger otolith $metal•Ca^{-1}$ ratios in 2001 (i.e. Mg, Mn, Zn, and Pb) (Fig. VI.6). The only ratios that were significantly larger in 2002 than in 2001 were $Sr•Ca^{-1}$ and $Ba•Ca^{-1}$ at the otolith edge. The majority of the significant pair-wise comparisons between years (four out of five) occurred in the otolith core or edge transects (Fig. VI.6). The only ratio that was significantly different between years at all three otolith regions was $Mg•Ca^{-1}$. In 2001, $Mg•Ca^{-1}$ ratios were greater than 2002 at the otolith core, middle, and edge (Fig. VI.6). Significant interactions between year and $metal•Ca^{-1}$ ratios were observed in Mn ($p = 0.02$) and Ba ($p = < 0.001$). However, these were due to the lack

of significant differences at one or two otolith regions not a reversal of the relationship in metal•Ca^{-1} between years or regions (Fig. VI.6).

Table VI.5. The results of the ANOVA used to test for the effect of otolith region (i.e. core, middle, and edge) on the otolith elemental composition of *Leptocottus armatus*. All 2002 collections from the Columbia River estuary, Coos Bay, and Humboldt Bay were combined for the analysis.

Effect of otolith region	MS	df	F	p
log ^{25}Mg				
Otolith region	0.07	2	2.1	0.13
Error	0.04	248		
log ^{55}Mn				
Otolith region	0.90	2	10.34	<0.001
Error	0.09	248		
sqrt ^{66}Zn				
Otolith region	0.001	2	4.18	0.02
Error	<0.001	248		
log ^{87}Sr				
Otolith region	0.13	2	22.11	<0.001
Error	0.006	248		
log ^{138}Ba				
Otolith region	7.79	2	48.49	<0.001
Error	0.16	248		
log ^{208}Pb				
Otolith region	0.40	2	1.77	0.17
Error	0.23	248		

Table VI.6. The results of the factorial ANOVA used to test for the effect of year (2001 vs. 2002) and otolith region (core, middle, and edge) on otolith elemental composition of *Leptocottus armatus* collected at the same location in Coos Bay, Oregon

Effect	MS	df	F	*p*
log ^{25}Mg				
Year	1.60	1	119.13	<0.001
Region	0.08	2	5.72	0.004
Year x Region	0.03	2	2.00	0.14
Error	0.013	108		
log ^{55}Mn				
Year	0.22	1	8.57	0.004
Region	1.22	2	48.15	<0.001
Year x Region	0.10	2	3.99	0.02
Error	0.03	108		
sqrt ^{66}Zn				
Year	<0.001	1	2.40	0.12
Region	<0.001	2	0.54	0.59
Year x Region	<0.001	2	0.83	0.44
Error	<0.001	108		
log ^{87}Sr				
Year	0.02	1	10.58	0.002
Region	0.20	2	118.39	<0.001
Year x Region	0.002	2	1.034	0.36
Error	0.002	108		
log ^{138}Ba				
Year	1.28	1	31.91	<0.001
Region	5.32	2	132.63	<0.001
Year x Region	0.64	2	15.89	<0.001
Error	0.04	108		
log ^{208}Pb				
Year	0.07	1	0.49	0.49
Region	0.14	2	1.00	0.37
Year x Region	0.02	2	0.14	0.87
Error	0.14	108		

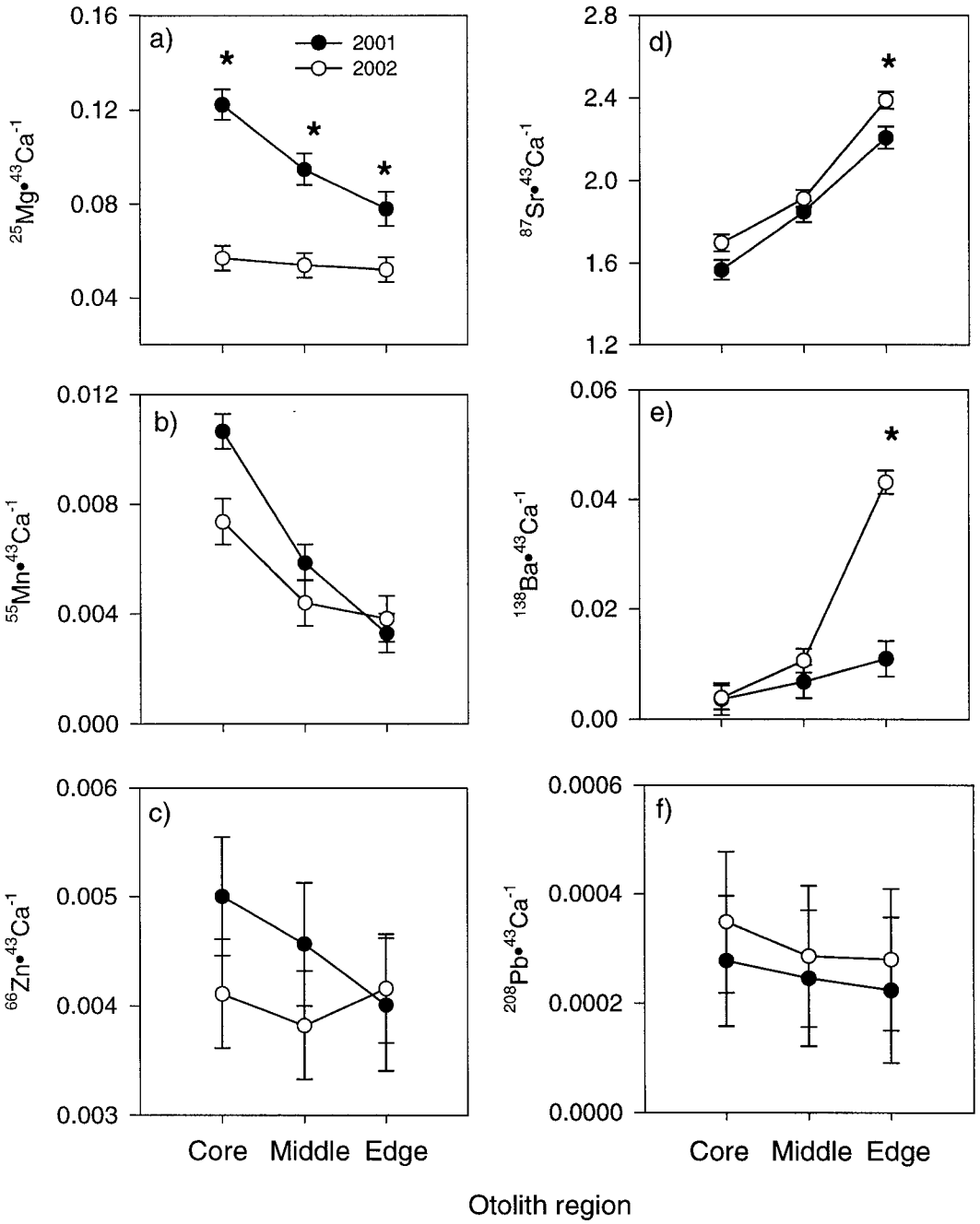

Fig. VI.6. The 2001 and 2002 average metal•Ca^{-1} ratios for staghorn sculpin (*Leptocottus armatus*) collected in Coos Bay South Slough at the otolith edge, middle, and core transects. Averages (± standard error) are presented for a) $^{25}Mg•Ca^{-1}$, b) $^{55}Mn•Ca^{-1}$, c) $^{66}Zn•Ca^{-1}$, d) $^{87}Sr•Ca^{-1}$, e) $^{138}Ba•Ca^{-1}$, and e) $^{208}Pb•Ca^{-1}$. 2001 is represented by black circles (N = 15); 2002 by open circles (N = 23). * denotes a statistically significant difference between years (Scheffé post-hoc comparison, $p \leq 0.01$).

Classification

The goal of discriminant function analysis (DFA) is to predict group membership from a set of predictors (Tabachnick and Fidell 2001). Ideally, the analysis identifies the fewest predictors that generate the greatest discrimination. Classification models were developed for bays and sites at each of the three otolith regions (i.e. otolith core, middle and edge transects). The metal•Ca^{-1} ratios of Mn, Sr, Ba, and Pb contributed significantly to the bay and site classification models at all otolith regions ($F > 5.0$, $p < 0.01$) with three exceptions; 1) Sr•Ca^{-1} in the otolith-core models for bay ($F = 2.4$, $p = 0.10$) and 2) site ($F = 2.2$, $p = 0.08$) and 3) Ba•Ca^{-1} in the models for the middle otolith transect ($F = 2.2$, $p = 0.12$). Although the ratios of Sr•Ca^{-1} and Ba•Ca^{-1} did not contribute significantly to the model in these three out of 24 cases (i.e. four elements and six classification models), the overall models were still highly significant ($F > 15.0$, $p < 0.001$). Therefore, in order to generate consistent and comparable classification models, the four elements (Mg, Mn, Sr, and Ba) were used in all of the classification models.

For bays (N = 3), classification success of individuals based on elemental signatures at the otolith edge was very high, with an average of 96% (jackknifed = 96%) (Table VI.7). For sites (N = 5), classification success of individuals based on elemental signatures at the otolith edge was also very high, with an average of 99% (jackknifed = 94%) (Table VI.8). The average classification success at the core and middle otolith regions was lower but still quite accurate, with a bay average of 87% (jackknifed = 84%) and a site average of 85% (jackknifed = 75%) (Table VI.7 and VI.8).

Cross-validation of classification models was completed with the classification of "new" cases, which were generated by splitting existing samples in half. The classification algorithms were generated with half of the original data and then the remaining data were classified with that algorithm. Overall, classification accuracies of "new" cases were similar to jackknifed estimates. Bay classification success of "new" cases was 93% for the otolith edge, 81% for the middle, and 79% for the core transects (Table VI.9). Due to the small sample size at the Humboldt Bay South Bay site (N = 7), the sample could not be split in half for classification of "new" cases. Therefore, the site classifications of "new" cases are based on the four remaining sites (i.e. Columbia River Channel, Columbia River Old Young's Bridge, Coos Bay, and Humboldt Bay South Jetty). Site classification success of "new" cases was 98% for the otolith edge, 93% for the middle, and 79% for the core (Table VI.10). Although cross-validation of "new" cases is often considered a more robust test of the discriminatory ability of classification algorithms than jackknifed estimates, both methods generated very similar results in this study. Jackknifed estimates were never more than 5% greater, and at times were less, than cross-validation estimates. Because cross-validation analyses could not be completed on all data due to the small sample size at the Humboldt Bay South Bay site, further discussion will be limited to the jackknifed estimates.

Table VI.7. The bay classification results for the discriminant function analysis of *Leptocottus armatus* juveniles based on the elemental composition of the otolith core, middle, and edge transects. $Mn•Ca^{-1}$, $Sr•Ca^{-1}$, $Ba•Ca^{-1}$, and $Pb•Ca^{-1}$ were included in the model. The collection bay, sample size (*N*), percent of individuals correctly classified, and the jackknifed percent correctly classified (in parentheses) are included.

Bay (*N*)	**% Correct (jackknifed %)**		
	Core	**Middle**	**Edge**
Columbia River (*38*)	89 (83)	97 (95)	100 (100)
Coos Bay (*23*)	83 (78)	87 (83)	96 (96)
Humboldt Bay (*23*)	79 (79)	79 (75)	91 (91)
Total	84 (81)	89 (86)	96 (96)

Table VI.8. The site classification results for the discriminant function analysis of *Leptocottus armatus* juveniles based on the elemental composition of the otolith core, middle, and edge transects. $Mn•Ca^{-1}$, $Sr•Ca^{-1}$, $Ba•Ca^{-1}$, and $Pb•Ca^{-1}$ were included in the model. The collection bay, sample size (*N*), percent of individuals correctly classified, and the jackknifed percent correctly classified (in parentheses) are presented.

Site (N)	**% Correct**		
	Core	**Middle**	**Edge**
Columbia River Channel (*17*)	75 (56)	94 (88)	100 (100)
Columbia River OYB (*21*)	90 (90)	95 (95)	100 (100)
Coos Bay South Slough (*23*)	83 (70)	74 (70)	96 (71)
Humboldt Bay South Jetty (*17*)	94 (76)	94 (88)	100 (100)
Humboldt Bay South Bay (*7*)	29 (0)	86 (57)	100 (83)
Total	81 (67)	88 (82)	99 (98)

Overall, the highest classification accuracies for both bays and sites were attained using elemental signatures at the otolith edge (jackknifed average = 97%) while the lowest classifications occurred using elemental signatures at the otolith core (jackknifed average = 74%). Average site classifications were consistently the highest (≥ 90%) at the Columbia River Old Young's Bridge and the lowest at Humboldt Bay South Bay, the site with the fewest fish, where the average jackknifed classification success was 47% (Table VI.8). On average, using the jackknife technique, 88% of individuals were classified to the bay in which they were collected throughout their early life history (i.e. at the otolith core, middle, and edge). Similarly, on average, 82% of the individuals were classified to their collection site within the bays throughout their early life history.

The $Ba•Ca^{-1}$ and $Mn•Ca^{-1}$ ratios were consistently significant components of factor 1 (standardized canonical discriminant function > 0.50) in the discriminant function analysis for both the bay and site classification models. The $Sr•Ca^{-1}$ and $Pb•Ca^{-1}$ ratios were significant components of factor 2 in the bay model while the $Pb•Ca^{-1}$, $Ba•Ca^{-1}$, and $Mn•Ca^{-1}$ ratios were significant components of factor 2 in the site classification model. In the bay classification model, factor 1 was responsible for ≥ 80% of the cumulative total dispersion. In the site classification model, factor 1 was responsible for ≥ 75% of the total dispersion and factor 2 accounted for an additional 10 – 15% of the dispersion.

Scales of variation

Two measures, the coefficients of variation (CV) and the maximum mean difference of pair-wise comparisons, were used to quantify the scales of variation in

otolith elemental composition observed in this study. The maximum differences in mean otolith elemental composition and the coefficients of variation (CV) are presented in Table VI.11 and VI.12. Across the spatial and temporal scales examined, the maximum differences in mean otolith metal•Ca^{-1} ratios averaged 124% (± 19.9% SD) (Table VI.11). The smallest differences occurred in Pb•Ca^{-1} ratios (i.e. 101% for interannual variation) and the largest occurred in the Ba•Ca^{-1} ratios (169% for inter-site variation). On average, however, the largest differences in mean metal•Ca^{-1} ratios were observed in Sr and Ba. The smallest differences were seen in Zn and Pb, with Mg and Mn intermediate. If the

Table VI.9. The bay classification results for the discriminant function analysis of *Leptocottus armatus* juveniles based on the elemental composition of the otolith core, middle, and edge transect. Mn•Ca^{-1}, Sr•Ca^{-1}, Ba•Ca^{-1}, and Pb•Ca^{-1} were included in the model. The collection bay, sample size (*N*), and the percent of individuals correctly classified are presented. Samples were split in half to generate an initial classification algorithm that was used to classify the remaining individuals. The results presented are the percentage of the "new," or previously unclassified, individuals that were correctly classified.

Bay (*N*)	**% Correct**		
	Core	**Middle**	**Edge**
Columbia River (*38*)	83	90	92
Coos Bay (*23*)	75	82	100
Humboldt Bay (*23*)	75	67	83
Total	79	81	93

Table VI.10. The site classification results for the discriminant function analysis of *Leptocottus armatus* juveniles based on the elemental composition of the otolith core, middle, and edge transect. The $Mn•Ca^{-1}$, $Sr•Ca^{-1}$, $Ba•Ca^{-1}$, and $Pb•Ca^{-1}$ ratios were included in the model. The collection bay, sample size (*N*), and the percent of individuals correctly classified are included. Samples were split in half to generate an initial classification algorithm that was used to classify the remaining individuals. The results presented are for the percentage of the "new," or previously unclassified, individuals that were correctly classified. The sample size for Humboldt Bay South Bay was too small ($N = 7$) to split so that site was not included in the analysis.

Site (*N*)	**% Correct**		
	Core	**Middle**	**Edge**
Columbia River Channel (*8*)	75	78	100
Columbia River Old Young's Bridge (*10*)	90	100	100
Coos Bay South Slough (*11*)	75	91	100
Humboldt Bay South Jetty (*9*)	75	100	88
Total	79	93	98

maximum mean differences are ranked, from smallest to largest, according to scales of sampling variation. The smallest differences occurred between otolith regions and the largest between sites. Mean differences among bays and years were intermediate. The CVs for metal$•Ca^{-1}$ ratios included in this study averaged 17.7% (± 7.6% standard deviation), and ranged from 6.2% (for $Ba•Ca^{-1}$ ratios) to 33.7% (for $Sr•Ca^{-1}$ ratios) (Table VI.2). In general, CVs were smallest for $Mn•Ca^{-1}$ ratios and largest for $Sr•Ca^{-1}$ ratios. Overall, CVs were relatively consistent across spatial scales, e.g. 17.5% for bays, 16.5% for sites and 20.0% for otolith regions.

Table VI.11. The maximum percent differences observed in pair-wise comparisons of transformed metal•Ca^{-1} ratios in *Leptocottus armatus* otoliths. The spatial and temporal scales of variability examined in the study are included. The maximum differences between means and the average difference (± SD) for each element are presented. The maximum percent differences for each element are ranked, from smallest (1) to largest (4), for each of the four scales of variability examined.

	Maximum difference between means (metal•Ca^{-1})					
Scale	**^{25}Mg**	**^{55}Mn**	**^{66}Zn**	**^{87}Sr**	**^{138}Ba**	**^{208}Pb**
Bays	119.8	124.8	105.7	162.5	133.7	122.6
Sites	134.5	129.3	119.7	167.7	169.1	126.8
Otolith region	104.8	110.1	111.0	132.7	140.2	104.0
Interannual	123.5	104.0	107.2	109.6	111.0	101.3
Average	120.6 ± 12.3	117.1 ± 12.0	110.9 ± 6.3	143.1 ± 27.2	138.5 ± 23.9	113.7 ± 12.9
Ranks						
Bays	2	3	1	3	2	3
Sites	4	4	4	4	4	4
Otolith region	1	2	3	2	3	2
Interannual	3	1	2	1	1	1

Discussion

In summary, the objectives of this study were to determine 1) if there were significant differences in the otolith chemistry of the staghorn sculpin (*Leptocottus armatus*) collected from three estuaries and from different sites within those estuaries; 2) at what spatial scales such differences were detectable and whether otolith elemental

composition varied throughout ontogeny; 3) if there was interannual variation in otolith elemental composition and how the magnitude of that variation compared with spatial and intra-annual variation; and 5) which, if any, elements provided discriminatory information on the collection location of individuals both among and within bays. These objectives, all of which were met and are discussed in more detail below, contribute to an overall assessment of the utility of otolith microchemistry to track the movements of individual fish.

There were significant differences in otolith elemental composition at all spatial and temporal scales examined, including among bays, between sites within bays, among otolith regions, and between years. Overall, differences in mean otolith elemental composition were consistently the largest between sites and the smallest between otolith regions. The variation around mean measurements was moderate (average CV = 17.7 ± 7.6%). Differences in the metal•Ca^{-1} ratios among bays, sites, etc., ranged from 111 to 143% and averaged 124% ± 20% SD. Discriminatory ability was excellent (average = 95.5%) at the otolith edge, the otolith region which encompasses the period when the fish were most likely together for some time, i.e. at collection. Discriminatory ability was, however, still quite high for the otolith middle (average = 87%) and core (average = 79%) regions.

Bays

At the bay level, the largest spatial scale examined, there were significant differences in mean otolith metal•Ca^{-1} composition for Mg, Mn, Sr, Ba, and Pb. The

majority of these, Mg, Mn, Sr, and Ba, separated the Columbia River estuary fish from those collected in Coos Bay and Humboldt Bay. The Pb Ca^{-1} ratios distinguished Humboldt Bay from the Columbia River estuary and Coos Bay.

The differences in mean otolith elemental composition between bays were less than between sites but greater than between otolith regions or between years (2001 vs. 2002). This is perhaps a surprising finding; a reasonable expectation would be that greater differences, and possibly greater variance, would occur at larger spatial scales. This finding suggests that comparatively large variation in water chemistry exists at relatively small spatial scales, i.e. within bays or estuaries. Additional data on water chemistry are needed to test this prediction.

Sites within bays

The metal•Ca^{-1} ratios of Mg, Mn, Zn, Ba, and Pb varied significantly between sites within bays. However, only one ratio, Ba•Ca^{-1}, was significantly different between sites within both Coos and Humboldt Bay. Furthermore, > 85% of the fish (jackknifed estimate) were accurately classified to their collection site if only the Ba•Ca^{-1} ratios are used to discriminate between the two sites within each bay. The high average classification accuracy of fish to the five collection sites (98% at otolith edge) suggests that detectable variation in otolith microchemistry in *Leptocottus armatus* can occur at relatively small spatial scales (i.e. < 5 km). The maximum differences in mean otolith elemental composition and the most accurate classification of fish occurred at the scale of site. Here I have the most sites (N = 5) and smaller sample sizes and yet I found the

greatest differences in elements and some of the highest classification accuracy. The spatial variability in otolith elemental composition for *Leptocottus armatus* in this study was large enough to generate relatively accurate site classification throughout the life history.

Otolith region

Ontogenetic effects on elemental incorporation into otoliths have not been examined extensively (but see Dove et al. 1996; Fowler et al. 1995). Fowler (1995b) examined ontogenetic effects in reared larvae kept in constant temperature and salinity regimes. He observed significant ontogenetic effects in the metal•Ca^{-1} ratios of Sr, Ba, and Zn, although the effects on the Zn•Ca^{-1} ratios were just significant ($p = 0.049$). Dove et al. (1996) found higher Sr•Ca^{-1} ratios, but not Ba•Ca^{-1} ratios, at otolith edges compared with cores, in two temperate reef fishes. In this study, I found significant differences among otolith regions in the metal•Ca^{-1} ratios of Sr, Ba and Mn ($p < 0.01$) and Zn ($p = 0.02$). My results are similar to those of the laboratory studies: The differences in Sr•Ca^{-1} and Ba•Ca^{-1} ratios were due to increased levels at otolith edges while Zn•Ca^{-1} ratios were lowest in the middle of the otolith. These results, in conjunction with previous studies, support the contention that there may be intrinsic factors that, in part, regulate otolith elemental incorporation, at least for Sr and Ba (Fowler et al. 1995).

However, in this study, if the metal•Ca^{-1} ratios at each otolith region are separated by bay, the patterns of change are quite varied. In all cases, the bay with the lowest metal•Ca^{-1} ratios also exhibited the smallest differences among otolith regions, although

those differences were still statistically significant. Therefore, if variation in elemental composition across the otolith growth axis is driven by intrinsic, ontogenetic factors, the variation apparently can be mediated by environmental conditions. As noted by Fowler et al. (1995), there are likely interactions between ontogeny and the physical environment that affect the elemental composition of otoliths. Such interactions may be challenging to accurately identify, quantify, and interpret.

In all cases, the $Sr \bullet Ca^{-1}$ ratios of *Leptocottus armatus* were greatest at the otolith edge transect. The Columbia River collection sites, where salinities are often < 20, were located approximately 7 and 16 km from the ocean. The $Sr \bullet Ca^{-1}$ ratios of Columbia River fish were the lowest observed and displayed the least change along the otolith growth axis, i.e. from core to edge. Given that all fish were collected within estuaries, it is unlikely that these individuals had spent extensive periods of time outside the estuary prior to collection. Although additional data are needed on ambient water chemistry and ontogenetic variation in the otolith incorporation of strontium, this preliminary evidence supports the idea that *Leptocottus armatus* do not leave their natal estuary until later in life (Jones 1962). If this is true, then alongshore dispersal in this species would occur primarily during the late juvenile and/or adult stages.

The mean differences in otolith elemental composition among otolith regions were the smallest observed in this study. This finding suggests that variation in the otolith elemental composition of fish collected from different geographic areas may not be easily obscured by ontogenetic differences, particularly if fish of roughly equivalent ages are

used. Additional research on ontogenetic variation in otolith elemental incorporation is needed to determine the magnitude of such variation and identify the mechanisms which regulate that incorporation.

Interannual variation

As found in previous studies (Gillanders 2002; Thorrold et al. 1998), there were significant interannual differences in the otolith elemental composition of *Leptocottus armatus*. In this study, most of the elements examined were significantly different between years at one or more of the otolith regions ($Zn•Ca^{-1}$ and $Pb•Ca^{-1}$ ratios were not different). The trend was for larger metal$•Ca^{-1}$ ratios in 2001. The exceptions were the $Sr•Ca^{-1}$ and $Ba•Ca^{-1}$ ratios in 2001, which were lower or not different than 2002. There were also significant differences among otolith regions in both years. In general, they followed the same pattern described above for all 2002 fish (see **Otolith Region**), i.e. larger $Sr•Ca^{-1}$ and $Ba•Ca^{-1}$ and lower $Mn•Ca^{-1}$ ratios at otolith edges. Additionally, in both 2001 and 2002, the $Mg•Ca^{-1}$ ratios of Coos Bay fish were significantly lower at the otolith edge transect than at the core or middle transects.

The maximum differences between years in the mean otolith metal$•Ca^{-1}$ ratios were smaller than those among bays or between sites, but larger than among otolith regions. Therefore, spatial variation in otolith elemental composition may indeed be confounded by interannual variation. Hamer et al. (2003) noted that over a two-year period temporal variation did not confound spatial differences in black bream (*Acanthopagrus butcheri*), but over longer time periods, i.e. nine years, it did. They also

observed significant monthly variation in the $Mn \bullet Ca^{-1}$ ratios of black bream otoliths (Hamer et al. 2003). These differences, however, did not greatly confound their overall geographic classification within a year. In this study on *Leptocottus armatus*, relatively large interannual differences were observed in the ratios of $Mg \bullet Ca^{-1}$ and $Ba \bullet Ca^{-1}$. Additional sample collection at a greater temporal frequency would be required to determine more specifically the time scales, i.e. monthly, seasonally, over which such changes occur.

Classification

Classification to collection location was relatively good for both bays (jackknifed average for all three otolith regions = 87%) and sites within bay (= 82%). The elements most useful for discrimination among collection locations were Mn, Ba, Sr, and Pb. In fact, the $Ba \bullet Ca^{-1}$ and $Sr \bullet Ca^{-1}$ ratios alone accurately classified >75% of the fish (jackknifed average for all three otolith regions) to their collection location.

Classification success throughout ontogeny, i.e. at the otolith core, middle, and edge transects, was variable. The most accurate classifications occurred at the otolith edge (overall jackknifed average = 97%) and the least accurate at the otolith core (overall jackknifed average = 74%). The average percentage of individuals accurately classified to collection location declined > 20% between the otolith edge and core. The largest declines occurred at the Columbia River Channel and Humboldt Bay South Bay sites. For example, the accurate classification of Columbia River Channel fish to collection location dropped from 100% at the otolith edge to 56% at the core. Humboldt Bay South Bay

classification accuracy dropped from 83% at the otolith edge to 0% at the core. On the other hand, an average of 90% of the Columbia River Old Young's Bridge fish consistently grouped together throughout ontogeny. Do these data indicate that 90% of the Columbia River fish collected at Old Young's Bridge moved little since hatching while > 40% of the Humboldt Bay South Bay fish moved extensively? Or, alternatively, were there greater temporal changes in water chemistry at the Humboldt Bay site than at the Columbia River site? With additional information on water chemistry and the mechanisms of otolith elemental incorporation, there is great potential to provide a more detailed record of fish movements throughout ontogeny.

There are three primary pathways for the inclusion of trace elements into otoliths; 1) as a substitute for calcium in the aragonite crystal lattice, 2) via inclusion in interstitial spaces, or 3) in association with the organic, or proteinaceous, otolith matrix. Theoretically, the first of these, substitution for calcium by other divalent ions, is the most predictable process and, therefore most likely to consistently occur in some proportion to ambient water chemistry. This is why Thresher (1999) noted that the Group IIA elements (e.g. Ba, Sr, and Mg) and other elements that routinely form divalent ions (e.g. Pb) are likely to be relatively useful in stock discrimination studies. In this study on *Leptocottus armatus*, most of the elements that were useful for discrimination were Group IIA metals. Additionally, Mn, a transition metal, and Pb, a Group IVA element, were also useful. Elsdon and Gillanders (2003) observed no relationship between otolith and ambient water chemistry for Mn. However, several studies (Gillanders 2002;

Gillanders and Kingsford 2003; Hamer et al. 2003), including this one, have observed significant geographic differences in otolith Mn•Ca^{-1} ratios. More research is needed to identify the mechanisms by which Mn is incorporated into otoliths and determine whether it is a reliable metal for discrimination of geographically separate groups of fish.

In conclusion, I have documented significant spatial and temporal variation in the otolith elemental composition of staghorn sculpin (*Leptocottus armatus*). Differences in otolith the metal•Ca^{-1} ratios were most pronounced among bays and between sites. These data suggest that, for *Leptocottus armatus*, geographic variation in otolith elemental composition may typically exceed temporal variation, at least at the scales examined in this study. Although interannual and ontogenetic differences in metal•Ca^{-1} ratios were also significant and are important aspects that must be considered in future research, these data support the idea that otolith microchemistry can be useful for tracking the movement of individual fish within estuaries.

Chapter VII

Conclusions

In this dissertation, I addressed questions related to local and regional patterns of transport, dispersal, and exchange in coastal fishes. I provided new information on the cross-shelf and estuarine transport of coastal fishes, the extent of ocean-estuary coupling, and potential movement patterns of coastal fishes, specifically black rockfish (*Sebastes melanops*) and staghorn sculpin (*Leptocottus armatus*). Otolith microchemistry data provided evidence for limited larval and adult movements in black rockfish, and I augmented this work with DNA microsatellite analysis to determine if such limited movements led to population divergence. This comparative approach not only identified population structure in black rockfish at scales < 500 km, but it also provided specific information on potential isolating mechanisms, i.e. limited larval dispersal. Additionally, I presented a detailed examination of the scales of variation in the otolith microchemistry of staghorn sculpin. This work quantified the spatial and temporal variation in the otolith elemental composition of staghorn sculpin both within and among west coast estuaries and further evaluated the utility of otolith microchemistry for tracking movements of individual fish.

The delivery of material, including larval and juvenile fish, to the coast and its exchange between outer coastal and estuarine areas are key components of the population ecology of coastal and estuarine species. In coastal systems, the movements of planktonic and small pelagic organisms are strongly influenced by physical processes. Within the California Current system off Oregon, both cross-shelf and alongshore transport are important. In this dissertation, Chapters II and III describe the use of high-frequency light-trap collections to address questions of nearshore transport and estuarine ingress of larvae and juveniles. The goals of these studies were largely attained. I documented 38 taxa of larval and juvenile fishes within Coos Bay, Oregon. I found that > 70% of the total annual catch of those larval and juvenile fish at the sample location near the estuary mouth occurred between 1 Jan and 31 May, a predominantly downwelling period. However, < 27% of the total annual catch at the sample location < 1.0 km farther up estuary occurred during the same period; this indicates relatively large variation in habitat use within the estuary. I also found that some species, such as northern anchovy (*Engraulis mordax*) and surf smelt (*Hypomesus pretiosus*), exhibited extended periods of residence farther up estuary. I present information on the seasonal use of the Coos Bay estuary by juvenile northern anchovy, including what may be individuals from two distinct populations. Additionally, there were indications that shoreward transport and estuarine ingress occurred via selective stream tidal transport and/or internal tides and bores. The lack of much evidence for wind-driven transport suggests that the presence of

the larvae and juveniles within the Coos Bay estuary may, at times, be more controlled by a combination of reproductive timing and tidal transport than via wind-driven delivery.

The ocean-estuary component of my dissertation was one of the first studies to simultaneously document post-larval crab and juvenile fish abundance at an outer coastal and adjacent estuarine site. Here, I identified strong coherence in the peak abundance of juvenile northern anchovy (*Engraulis mordax*) and surf smelt (*Sardinops sagax*) and Dungeness crab (*Cancer magister*) megalopae at the two sites. Additionally, I identified numerous significant cross-correlations between fish abundance and the spring neap tidal cycle, most often around spring tides, which further indicate shoreward transport and estuarine ingress may have occurred via selective tidal-stream transport and/or internal tides and bores. This ocean-estuary work focused on transport only during the upwelling season. There was evidence for wind-driven transport than within the estuary. This may be due to a number of factors; 1) wind-driven transport may play a larger role along the outer coast than within the estuary, 2) there may be seasonal variation in the predominant cross-shelf transport mechanisms, or at least in their relative importance, and 3) seasonal, or possibly genetic, variation in larval and juvenile behaviors, such as photo- or rheotaxis, may occur and could affect (alter) their transport and dispersal.

I conclude, as did Doherty (1987), that light traps are selective but useful devices for determining the distribution and relative abundance of larval and juvenile fishes. They are also useful for addressing questions of transport, relative abundance, and habitat use in estuaries. And light traps can be used in temperate estuaries where, due to their

relatively high levels of turbidity, they have often been avoided (Hickford and Schiel 1999). However, further investigations on individual behaviors, including depth distribution and vertical migrations, are needed to determine more specifically how such behaviors interact with physical processes to regulate shoreward transport and estuarine ingress.

Information on larval dispersal distances is rare for marine species (Shanks et al. 2003). Yet dispersal distances of marine larvae affect gene flow and the geographic range and persistence of populations and species (Jablonski 1986; Sinclair 1988; Strathmann et al. 2002). A primary objective of the study presented in Chapter IV was to provide information on larval dispersal in black rockfish (*Sebastes melanops*), using a relatively new technique, otolith elemental chemistry. In this study, I found unique geochemical otolith signatures throughout ontogeny in juvenile *S. melanops* collected 120 – 460 km apart. These geochemical otolith signatures accurately classified individuals to their collection location between 67 and 87% of the time throughout ontogeny. A probable explanation of these data is that larvae from different geographic locations did not mix during ontogeny and possibly did not disperse long distances. Larval dispersal distances may be appreciably shorter, < 120 km, than previously assumed based on models of passive dispersal.

The otolith elemental chemistry of adult black rockfish (*Sebastes melanops*) (Chapter V) provided evidence for limited movement of most individuals through the adult stage. Such limited movement could logically lead to limited exchange among

populations and subsequent population divergence. Therefore, I explored the genetic population structure with another relatively new technique, DNA microsatellites (Chapter V). Here I found that data on *Sebastes melanops* collected with otolith microchemistry and DNA microsatellites yielded corroborative and complementary information. Specifically, using the otolith elemental chemistry, I was able to correctly classify an average of 70% of the individuals to collection location. Using microsatellite data, based on genotypic frequencies, I identified significant population division between the Washington and Oregon samples but no genetic differences within Oregon samples. Site classification success based on microsatellite data averaged 69%. Overall site classification success was similar with both methods and significantly greater than that expected by chance alone (i.e. 25%). This is the only study I am aware of that directly compared these two techniques on the same individuals. Taken together, these data indicate that there is population structure in *S. melanops* at scales < 500 km and that otolith microchemistry and DNA microsatellites may prove useful in providing corroborative information on population structure in marine fishes.

There are unknowns and uncertainties associated with the mechanisms that regulate otolith elemental composition. Therefore, Chapter VI aimed to quantify spatial and temporal variation in the otolith elemental chemistry of staghorn sculpin (*Leptocottus armatus*) in order to assess its potential to provide information on the movement of individuals in a more detailed fashion. In this study, I found significant differences in otolith elemental composition at all the spatial and temporal scales examined, including

among bays, between sites within bays, among otolith regions, and between years. Overall, differences in mean otolith elemental composition were consistently the largest between sites and the smallest among otolith regions. The relatively small differences in mean otolith elemental composition among otolith regions suggest that variation in the otolith elemental composition of fish collected from different geographic areas may not be easily obscured by ontogenetic differences, particularly if fish of roughly equivalent ages are used. The high average classification accuracy of fish to the five collection sites based on their otolith microchemistry (98% at otolith edge) suggests that detectable variation in otolith microchemistry in staghorn sculpin can occur at relatively small spatial scales (i.e. < 5 km). Although interannual and ontogenetic differences in metal to calcium ratios were significant and are important aspects that must be considered in future research, these data support the idea that otolith microchemistry will be useful for tracking the movement of individual fish within estuaries.

The classification accuracies throughout ontogeny indicate that, at five of the six collection sites, apparently little larval movement occurred in staghorn sculpin (*Leptocottus armatus*). These results are similar to those collected on juvenile black rockfish (*Sebastes melanops*). However, there are diverse and complex patterns of water circulation and greater variation in water characteristics, such as salinity, inherent in the estuarine collection sites compared with the outer coastal sites where black rockfish were collected. So, although the patterns in otolith microchemistry throughout ontogeny are similar and suggest, for both species, that the majority of larvae may not move great

distance, I felt that such conclusions for staghorn sculpin at this point were premature, particularly without corroborative genetic data. These results, however, are intriguing. They 1) support the notion that otolith microchemistry is a sensitive enough marker to detect movements within an estuary and along a coast and 2) suggest that these two species, with relatively distinct life histories, may have limited realized dispersal distances.

Information on larval dispersal distances and the extent of exchange among coastal populations is not only important for population biology and ecology but also necessary for the adequate management and conservation of marine species. Current conservation and management efforts are hindered by the lack of information on larval dispersal and the proportion of individuals within a population that disperse widely versus recruit into their parent population. How can we quantify the scale of openness in a biologically meaningful way that may also be useful for management and conservation purposes? The recovery of a depleted population depends, in part, on the proportion of larvae from those populations that disperse widely enough to provide new recruits to the depleted population. Therefore, the rate of recovery of such a population could be substantially slower in a species where typically 80%, compared with 20%, of the successful recruits are generated internally. Similarly, such principles apply in the design of marine reserves. Botsford et al. (2001), for example, conclude that successful reserve design requires knowledge of the mean dispersal distance as well as the proportion of successful recruits generated within the reserve. Much of the debate surrounding marine

reserve design, i.e. are single, larger reserves more successful than networks of smaller reserves, will remain largely theoretically until more specific information on larval dispersal distances, such as that presented in this dissertation, is generated.

To conclude, I return to Hjort (1914). At the end of his treatise that, in many ways, charted the course of marine fish population ecology for the next hundred years, he made some statements that are cited much less frequently than his insightful observations on early life history. When musing on the possible causes, or underlying mechanisms, behind the large fluctuations in the population sizes of marine fishes, he concluded, "a study of the fluctuations in the population of the sea, both fish and smaller organisms, and thus of the whole organic life existent in the ocean, is therefore the soundest possible basis for marine research, whether with theoretical or practical ends in view." He further concluded, however, that "a final solution of the problem of fluctuations in the fishery by any permanently valid formula must be regarded as an impossibility, and all assertions as to the discovery of such a solution may be safely relegated to the sphere of pure imagination." In other words, he saw a continual need for new information to refine theories and generate new hypotheses but that we may never come up with a consistently valid answer. However, the development and refinement of new technologies, such as otolith microchemical and DNA microsatellite analyses, in conjunction with rapid expansion in remote sensing capabilities, novel insights into the mechanisms that regulate marine populations can be made that will further both theoretical and practical endeavors. Some of the studies presented here, for example, indicate that larval dispersal distances in

Sebastes melanops may be much shorter, i.e. < 120 km, than those predicted based on larval duration alone and may contribute to genetic divergence in this species along the Oregon/Washington coast.

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Chapter VII

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